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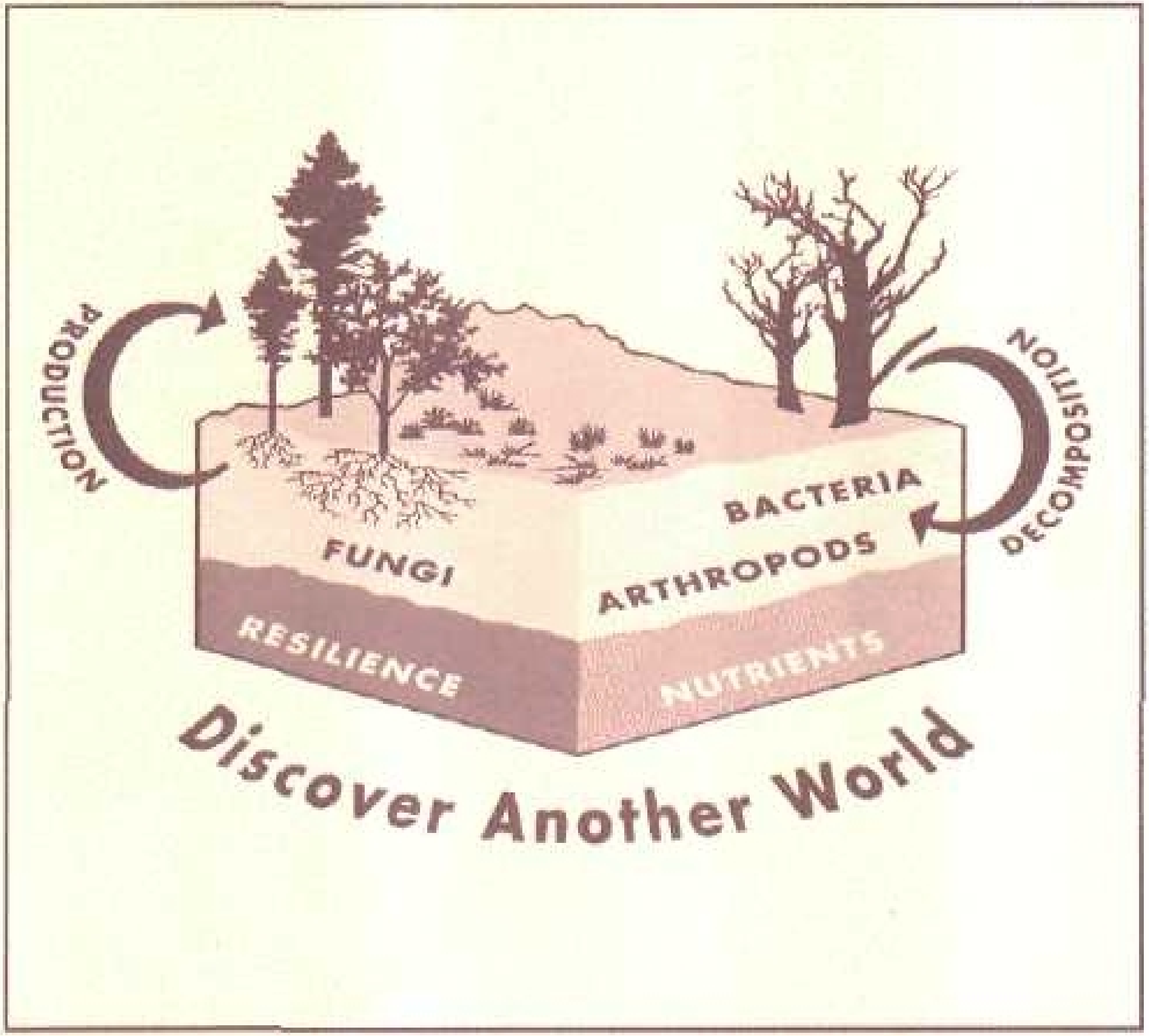

Technical Editors

Robert T. Meurisse (Retired) is formerly Regional Soil Scientist, USDA Forest Service, Pacific Northwest Region, Portland, Oregon.

William G. Ypsilantis is District Soil Scientist, USDI, Bureau of Land Management, Coeur d'Alene, Idaho.

Cathy Seybold, is Soil Scientist, USDA Natural Resources Conservation Service, Soil Quality Institute, Oregon State University, Corvallis, Oregon.

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Proceedings: Pacific Northwest Forest & Rangeland Soil Organism Symposium

Robert T. Meurisse, William G. Ypsilantis, and Cathy Seybold, Technical Editors

Pacific Northwest Forest and Rangeland Soil Organism Symposium:
Organism Functions and Processes, Management Effects on Organisms and
Processes, and Role of Soil Organisms in Restoration

LaSells Stewart Center, Oregon State University,
Corvallis, Oregon
March 17-19, 1998

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ABSTRACT

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Soil organisms have become a focus of attention for addressing issues of soil quality and health, and ecosystem sustainability. Land managers are challenged to ensure that their actions are beneficial to belowground organisms and processes in the long-term. Research about soil organisms, their populations, roles, and management effects is fragmented and often esoteric. The diversity of soil organisms is tremendous. The principal organisms include bacteria, actinomycetes, fungi, arthropods, nematodes, worms, insects, and mammals. In order to provide a "state-of-the-science" about soil organisms related to management, a symposium was convened to address soil organism functions and processes, management effects on soil organisms and processes, and describe some roles of soil organisms in restoration and applications for land management. The focus of the symposium was on Pacific Northwest forest and rangeland ecosystems.

Keywords: Soil organisms, soil quality, nutrient cycling, nitrogen transformations, foodwebs, ecosystem integrity, soil resilience, ecosystem resilience, bacteria, fungi, arthropods, root diseases, soil crusts, disturbance, interactions

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OPENING REMARKS

OPENING REMARKS

William G. Ypsilantis[1]

I'm pleased to join the rest of the steering committee and speakers in welcoming each and every one of you to the Pacific Northwest Forest and Rangeland Soil Organism Symposium. It's encouraging to see so many of you in attendance at this important symposium in spite of the tight travel restrictions we all are enduring. I understand we have over 200 registrants for the symposium which is fantastic. We have attendees from several agencies, universities, and the private sector, and from as far away as Dundee, Scotland.

The purpose of this symposium is to present state-of-the-science information on the important roles and functions of soil organisms and some key management implications in Pacific Northwest forest and rangeland ecosystems. When Bob Meurisse, US Forest Service's Region 6 soil scientist, and I first got together over a year ago to discuss soil organisms, we felt it was important to focus the efforts of a symposium towards forest and rangeland managers and a broad array of resource specialists. The steering committee wanted to make sure that this symposium helped make a difference in how we do business in managing forests and rangeland and was not just another symposium to be soon forgotten.

A diverse partnership of organizations joined together to sponsor this symposium including the Bureau of Land Management, US Forest Service, Natural Resource Conservation Service's Soil Quality Institute, Oregon State University and Oregon Society of Soil Scientists. Our steering committee put together a wonderful program and guest list of speakers. The enthusiastic participation by our outstanding lineup of speakers and poster presenters was especially gratifying. World renowned researchers from the Pacific Northwest, Canada, and such distant points as Yale University and Sofia, Bulgaria will present papers and posters. Elaine Ingham and Andy Moldenke graciously agreed to organize the field tour to provide opportunities for attendees to view field indicators for forest soil organisms. After many months of hard work and coordination by the steering committee and the Forestry Conference Office at Oregon State University we have finally arrived at this momentous kick-off to our event.

Our goal for this symposium is to share knowledge with you about a topic that has only recently begun to be recognized and understood as vital to the sustainability and health of ecosystems. When I was in school we didn't spend that much time studying soil organisms nor have we dealt with them that much in forest and rangeland management up until fairly recently. They have come to the forefront of peoples awareness and now seems a perfect time for this symposium. Decision makers want to know the long range implications of their management actions. It is up to the scientific community to provide the knowledge needed to understand the functions and processes of the soil biological components of the forest and rangeland ecosystems. Another role of the scientific community and resource specialists is to convey this information to the decision makers in a clearly understandable manner that relates to the bottom line of ecosystem health and sustainability. Hopefully, the outcome of this symposium will be to do exactly that, to convey some of this knowledge in an easily understandable and digestible manner. Another hoped for outcome is that it brings together some of the stakeholders in a way that will lead to partnerships and sustainable resource management on our forest and rangeland ecosystems.

This is a very ambitious program we have put together. The realm of soil organisms is a vast topic that we can't hope to cover in depth in a 3 day symposium. If time permits a few questions will be answered by the speakers immediately after their presentations. Otherwise, at the end of each half day session there will be 15 minutes set aside for questions for the speakers. We hope that this symposium will spark additional communications between research and applied management about soil organisms so we have provided biographical sketches of our speakers in your handouts with phone numbers and e-mail addresses. Please feel free to keep up the dialogue started here.

Proceedings will be published for this symposium to provide the valuable information shared here to those who were not able to attend. All registered attendees will receive a copy of the proceedings.

Don't forget the poster session and mixer tonight at O'Callahan's restaurant at the Ramada Inn. This is a

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[1] William G. Ypsilantis is a soil scientist with the Upper Columbia - Salmon Clearwater Districts, USDI Bureau of Land Management, 1808 N. Third St., Coeur d'Alene, Idaho 83814.

wonderful opportunity to meet and share ideas with some of your peers and others who share a common interest with you in an informal setting.

I apologize that we could not accommodate all the attendees who wanted to participate in the field tour. We felt that we could most effectively communicate with small groups in such a setting. Those of you who are registered for the field tour on Thursday afternoon, we will be boarding the busses in front of the LaSells Stewart Center and departing at 1:00 o'clock sharp. Be sure that you are prepared for foul weather as the tour will be conducted rain or shine.

In summary, I encourage each of you to participate in the symposium as much as possible and to have a productive and enjoyable three days here. So come with us to "Discover Another World;^{11} the remarkable world of soil organisms. Thank you.

ASSESSMENT OF BELOW-GROUND ORGANISM FUNCTIONS AND PROCESSES

A NON-VALUE BASED FRAMEWORK FOR ASSESSING ECOSYSTEM INTEGRITY

Kristiina A. Vogt[1], Daniel J. Vogt[2], Paul Boon[3], Anna Fanzeres[4], Philip Wargo[5], Peter A. Palmiotto[6], Bruce Larson[7], Jennifer L. O'Hara[8], Toral Patel-Weynand[9], Eva Cuadrado[10], and Joyce Berry[11]

ABSTRACT

Indicators of ecosystem state change are currently selected based on the human value for some resource (e.g., biodiversity, water quality, etc.) or the human desired end-point of a system (e.g., existence of late successional forests, lack of insect or pathogen outbreaks, etc.). Examples are used from ecosystem studies and forest certification protocols to highlight the problems of selecting indicators based on our derived values. Selection of value-based indicators may misidentify the important constraints controlling the functioning of a system and may result in poor predictions of system sustainability. Several examples are presented on how to develop a non-value based framework of analysis to select parameters capable of predicting how a system functions, or to identify the dominant constraints for each site. The value of using large data sets that can be analyzed to select non-human value-based constraining variables at different scales is discussed. This process of selecting the dominant constraints also highlights why the same suite of indicators cannot be used automatically for all sites.

Keywords: indicators, value-based indicators, biodiversity, late successional forests, forest certification protocols, ecosystem constraints, sustainability

INTRODUCTION

There is a great deal of interest in identifying and defining criteria that can be used to determine or assess whether an ecosystem is sustainable under different types of management activities, or to select indicators that will sensitively reflect potential changes in ecosystem condition (i.e., ameliorating or degrading) (Bormann and others 1993; Mangel and others 1996; EPA 1996; Vogt and others 1997; Wijewardana and others 1997). Emphasis on indicators to assess ecosystem sustainability and/or change has resulted in the identification of a broad suite of indicators as part of the assessment process, selection of indicators 'a priori', and the use of the same indicators at all sites. This suite of "generic" indicators are not specific to any site but have been identified to be important in controlling system function in some way. Several questions need to be addressed prior to the acceptance of such an approach to assess sustainability. For example: have the appropriate indicators that identify system sustainability been included in the analysis? Is the emphasis on understanding an acknowledged problem going to result in the identification of a wrong set of indicators (value-based) which are not sensitive to detecting that the system resistance or resilience is changing? Is it appropriate to assume that the same suite of generic indicators will automatically transfer to all sites? What scale of analysis is most appropriate? Will we have to always scale information from the small scale (with its high data needs) to the large scale (smaller data needs) to make it relevant for policy?

To answer these questions we need to examine how indicators are chosen, and how and when they reflect a human value that we have for a resource and when they do not reflect the driving variables maintaining system resistance and resilience (Vogt and others 1997). Using a value-based approach to drive the selection of indicators may not be a problem when the

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[1] Kristiina A. Vogt a professor of ecosystem ecology at the School of Forestry and Environmental Studies (FES), Yale University, New Haven, CT.

[2] Daniel J. Vogt a professor in ecosystem ecology and forest soils at Yale FES.

[3] Paul Boon a research technician in GIS at Yale FES.

[4] Anna Fanzeres a tropical ecologist, forester and Research Assistant at Yale FES.

[5] Philip Wargo a plant pathologist and Project Leader at the USDA FS Northeastern Center for Forest Health Research, 51 Mill Pond Road, Hamden, CT.

[6] Peter A. Palmiotto a tropical and temperate forest ecologist and Research Assistant at Yale FES.

[7] Bruce Larson a professor of stand development and Director of Yale School Forests at Yale FES.

[8] Jennifer L. O'hara a tropical and temperate forest ecosystem ecologist and Research Assistant at Yale FES.

[9] Toral Patel-Weynand a tropical and temperate forest ecosystem ecologist and Research Assistant at Yale FES.

[10] Eva Cuadrado an agricultural ecologist and Research Assistant at Yale FES.

[11] Joyce Berry a social ecologist and Lecturer at Colorado State University, Ft. Collins.

identified value-based indicators is related at the holistic level to the condition of the system. For example cryptogamic crusts are not only highly valued visual aspects of desert ecosystems but also play an important functional role in sustaining the system by deterring the loss of soil by wind erosion (West 1982). In this case, the identification of a value-based indicator is highly relevant and an extremely useful way to identify an important constraining or functional indicator of site condition.

When human value-based indicators do not reflect system integrity, the ability of detecting potential system degradation becomes difficult. Frequently, the value identified indicators may not change in a measurable manner during the time-scale of the assessment period or changes in the indicator do not reflect system degradation or loss of system resilience (Vogt and others 1997). One such indicator is Net Primary Production (NPP) which can be perceived as a value-based indicator since it documents the amount of potential wood product output of a site and how well a system is growing ecologically; typically higher NPP is translated as being positive since more wood can be harvested from a site and a system must be functioning well since sufficient photosynthate is present to maintain all components of the system (Vogt and others 1997). However, when measuring the impact of atmospheric N additions into ecosystems, early monitoring of NPP would reflect the initial fertilizer effect of these inputs but not the potential future decreased NPP and possible "impending degradation" of the ecosystem. A focus on measuring NPP would not initially detect the fact that continuous atmospheric inputs of N will eventually result in leaching losses of base cations from the soil which results in nutrient deficiencies limiting plant growth (e.g., decreases in NPP) (Ingestad and Agren 1992; Lawrence and others 1999).

Problems that can occur when selecting human value-based indicators over non-value-based indicators are highlighted in studies using insect and pathogen outbreak status as an indicator of forest or ecosystem condition. The absence of serious insect pests or pathogen problems would indicate a "healthy" system whereas presence or abundance would indicate degradation in the system. However, in some systems, by the time pests are obvious, significant changes may have already occurred (e.g., secondary chemical production for defense, carbon allocation changes, loss of symbionts on root systems, soil chemistry changes, etc.). However, the pests may only be acting as secondary agents and merely responding to some other ecosystem changes (Wargo 1979, 1981; Lawrence and others 1999; Shortle and others 1999). Even organisms considered as "primary stress agents" (i.e., those capable of affecting healthy trees) may be responding to changed ecosystem conditions. In the past, research focused on controlling the pest rather than understanding its relationship to forest or ecosystem condition.

Current analyses of pest problems within ecosystems have taken a more holistic approach (Wargo and others 1993; Shortle and others 1999). The insect or pathogen is no longer automatically looked upon as the problem. The treatment of the value-indicator results in the reduction or eradication of the pest. Rather the pests can be evaluated as an indicator of other problems or changes within the system that allows the pests to reach outbreak conditions. This approach leads to the development of other indicators of change that occur prior to the subsequent problem of pest outbreaks. However, some pests can become established in response to ecosystem change and subsequently they can become the constraining variable in that system. Armillaria root disease in western conifer ecosystems is an excellent example of this relationship (Shaw 1980; Wargo 1981). However, it is still important in these systems to identify and define other potential constraints which could function as controlling variables that maintain system function (e.g., soil chemistry) and perhaps even override the effect of the pathogens (Vogt and others, in review).

In other situations, management may produce value driven end-points that may result in a desire to maintain a system in a particular condition that cannot be sustained by the driving variables. This may result in system instability that may proceed undetected because the wrong indicators were chosen. Maintenance of a human value indicator may actually result in the degradation of a site or may require large expenditures of energy to keep the system in the desired or valued state because this management goal may conflict with the natural dynamics of the system. A good example of this is the late successional forests in the Pacific Northwest in the United States. In this case, the value indicator is the maintenance of late successional or old growth forests for the associated old-growth dependent species (e.g., spotted owl, marbled murrelet, etc.) (Hansen and others 1991; Spies and Franklin 1991; FEMAT 1993). However, most systems are so dynamic, or our knowledge may be insufficient, so that it is extremely difficult to maintain certain stages of forest succession. In this case, the valued condition is late successional forests to be set aside as reserves and maintained as part of the forest landscape - the spatial mapping of these forests with potential corridors identified and establishment of reserves with no tree harvesting as critical elements of this approach. However, the future presence of each forest fragment will vary between fragments depending on their location within the matrix landscape, the quality of its edge environment and legacies persisting in the system (which is controlled by past land-use and the disturbances particular to that region) (Franklin and

Forman 1987; Franklin and Spies 1991; Vogt and others 1997; Vogt and others, unpublished data). Natural disturbance cycles and the manner in which our landscapes have been fragmented have resulted in development of late successional forest fragments which have a higher rate of tree turnover than the about one percent turnover seen in a less fragmented landscape (Franklin and Forman 1987; Vogt and others 1997).

VALUE-BASED INDICATORS OF TWO FOREST CERTIFICATION PROTOCOLS

The recent push to develop certification protocols for forest management (Upton and Bass 1996) also demonstrates the problem of how to select and use indicators of changing forest conditions that reflect sustainable social and natural systems under different management regimes (Vogt and others 1997). These certification protocols are being developed because there has been a loss of 'trust' by the public in how our natural resources are being managed and harvested.

Since many of the certification protocols were designed by groups with particular philosophies, they strongly reflect the values of the organization designing the protocols. For example, the goals of the Silva Forest Foundation protocols are to have ecologically responsible forest use (e.g., ecosystem based approach to plan and carry out human uses giving priority to protection, maintenance and restoration of ecosystems) and ecologically responsible timber management (e.g., timber management plans and activities developed and carried out to protect, maintain and restore fully functioning forest ecosystem at all temporal and spatial scales) (Hammond 1997). The goal of Smartwood - Rainforest Alliance protocol is to sustain the capacity of forests to maintain their health, productivity, diversity and overall integrity for long temporal scale while being managed for human activity and use (Smart Wood Certification Program 1997).

The existing forest certification protocols generally identify two categories of certifier organizational generated values to monitor: 1) maintain biodiversity and water quality and 2) alleviate poverty of local people. These values are reflected in the amount and type of data required to be collected for the two certification protocols (table 1). The other fact that is important to note is the scoring system used for these two certification protocols results in some information receiving a greater weight and therefore having a greater chance of influencing the success or failure of being certified. The Silva Forest Foundation protocol has a scoring system that varies from -3 to 3. As part of this system, scores are given for the listed indicators which are eventually tallied and used to determine whether a threshold of points had been achieved and whether the forest should be certified. The Smart Wood Rainforest Alliance protocol uses a scoring system that goes from 1 (extremely weak) to 5 (outstanding performance) with a minimum score of 3 required for certification. Again, the total number of points obtained from assessing the different indicators are used to assess whether sufficient points were achieved for certification. The scoring is very subjective since clear thresholds that indicate when one should move from one scoring level to another is difficult to identify. The bias towards biodiversity can be seen in several categories in which species inventories or species composition appears in the protocol; this bias results in weighting the information needs toward the values embedded in the protocol. The type of information required for these protocols can be separated into several different groups and is summarized in table 1.

After examining table 1, one should immediately notice the tremendous amount of data that are required as part of each of the two protocols presented above and how the data needs are relatively similar for both protocols. However, these protocols are not designed to identify if different driving variables are controlling the functioning of a system (i.e., the non-value based indicators of ecosystem integrity). In fact, there exists a perception that if an assessment framework is to be credible, a clear list of indicators must be used that do not vary between different assessments.

Certain types of information are not required to be collected as part of the data needs of the certification protocols. For example, no knowledge of the following ecosystem components is required: microbial components, decomposers, symbionts, soils (physical or chemical characteristics), pests and pathogens, and nutrient or trace element (e.g., Al, Zn, Pb, etc.) cycling or pools. These components are not included because they require more complicated approaches or specialized knowledge since they cannot be analyzed using visual criteria. The absence of these components is noteworthy since there is a great deal of documentation on the impact of human activities on these variables and they have been identified as the driving variables causing changes in ecosystem resilience and resistance (Vitousek 1994; Vogt and others, 1997; Shortle and others 1999; Lawrence and others 1999).

ANALYSIS OF PROTOCOL EFFICACY

An analysis of the two protocols in table 1 shows the strong bias towards measuring and documenting

Table 1 —The value- based indicators required to be collected for the Silva Forest Foundation and Smart Wood - Rainforest Alliance certification protocols (Hammond 1997; Smart Wood Certification Program 1997).

Values	Silva Forest Foundation	Smart Wood - Rainforest Alliance
Law enforcement Adequate rules Land security Tracking products Credibility for consumers	1.2/4.3. Mission and objective statements are clear and ecosystem-based. There is a commitment to constant improvement. 1.3 Timeframe of plan is at least 1 50 years. Projections of successional processes and provisions for the maintenance of successional composition and structure are described. Schedule of economic development, infrastructure maintenance, and ecological restoration is defined and includes predictions of management impacts. 2.1.3/2.2.2/2.3.5/2.4.3/2.5.3/5.1.3 / 5.2.2 Permitted uses are designed to maintain full ecosystem functioning. Agriculture, ranching, mining, buildings, roads, vehicles, and logging generally are not permitted (except for watercourse crossings in 5.1.3). 2.3.6 If old growth is rare, all old growth stands and fragments are protected. 2.5.1 At least 5% of applicant lands are in whole protected watersheds. 3.1 Allocation of forest uses across the landscape is ecologically responsible and balanced. 3.3.1 Large protected reserves are at least 5 times the size of the largest natural disturbance to be expected in the landscape. The overall size of the landscape in question will influence the actual size of large protected reserves. 3.3.2 At least 5% of applicant lands are in large protected reserves. 3.3.3 Permitted uses of reserves are designed to maintain full forest functioning. 3.3.4 Logging and mining are not permitted in large protected reserves. 4.4. Strategies and prescriptions can be expected to achieve objectives. 5.2 Ecologically sensitive (ES) sites are protected. 7.2 Pesticides, synthetic fertilizers, and other chemicals are not used except in special cases described in standards document. 7.2.1 No pesticides, herbicides, or synthetic chemical fertilizers are used. 7.5 Wastes are properly handled and disposed of. 7.5.3 Applicants participate in recycling and reuse programs where they exist. 9.2.3 No exotic or genetically engineered species or stock are planted. 9.3.2 No mechanical site preparation is done. 9.3.3 No non-tree species are targeted for elimination. 9.3.4 No pesticides, herbicides, or synthetic chemical fertilizers are used. 10.1 Salvage logging is in agreement with all other SFF standards except as described below. 10.2 No live trees are cut in salvage operations. 11.3/1 2.3 No logging is done on areas under dispute. 13.2 Health and safety standards meet all applicable laws and regulations. 14.2 Financial considerations do not dictate management decisions.	1.0 General Information: name, address, person in charge, total volume produced per year, processing facilities, owner, ownership, identification of local communities affected by the project, etc. 1.8 Percentage of timber supply from: - forest land that is directly managed by the applicant; - forest land that is managed by a known third party, or; - open market log timber purchases (from independent loggers). 2.1 Land title is clear and legally secure, boundaries are identified on the ground and timber harvest is legally permitted. 2.4 A maximum of 10% of the lands (in area and number) under management supervision leave the program each year, with specific records kept explaining the reasons for leaving the program. 2.5 No enrollment of "single harvest only "individual forest ownership is taking place. 5.1 Forest management operations exceed or comply with current Federal, State and Municipal laws and regulations including Best Management Practices (BMP) and all necessary permits have been obtained. 5.4 Roads, stream crossing and log landings are designed to meet or exceed State Best Management practices. 5.1 5.iv) roads into closed compartments blocked to prevent unauthorized entry. 6.10 Based on the identification of fragile, endangered, unique or uncommon natural communities, appropriate areas, considered within a landscape ecosystem context, are designated as "Reserves or Special Management Zones "on maps and in the field. 6.13 Operation has a policy for soil and watershed management, addressing riparian buffer zones and watershed protection. At minimum, the policy complies with State BMPs to maintain or improve water quality and aquatic health, and to minimize on-site and downstream damages caused by harvesting operations. 6.14 Operation has a policy for steep slope harvesting. Policy is written and implemented. 6.15 If chemicals are used, operation has a written policy addressing the ecological rationale(s) for their use, including the types used and methods of application. Operation implements the policy. 7.5 Taxes on forest land and timber are paid in a timely manner in accordance with state and local tax laws. 7.6 Known archeological sites, and sites of cultural, historical, community or aesthetic significance are included in special management zones or protected during harvest operations. 9.1 Documentation of management activities on all forests blocks should be available to facilitate monitoring and certification audits. 9.2 Certified forest products should be clearly identified through marks, labels, tags, or

Values	Silva Forest Foundation	Smart Wood - Rainforest Alliance
	18.2 Indicators of impacts due to timber management are appropriate, cost-effective, and adequate.	separately documented loads, in order to facilitate chain of custody processing at mills. - Specific Smartwood Chain of Custody Guidelines.
Empowering the poor Rights of indigenous peoples/local communities Labor rights Other social benefits	1.6 Social and economic needs of local communities are analyzed. Provisions for these needs are clearly stated. 3.1.1 All local ecologically responsible forest user groups are given access to the landscape in proportion to their needs, zoning ensures fair, balanced land bases for ecologically responsible users. 3.1.3 Zoning of uses serves the specific social and economic needs of local communities. 4.7 Social and economic needs of local communities are analyzed, provisions for these needs are clearly described. 11.1 Indigenous people control activities on their territories. 11.2 Needs for protection and support of indigenous culture are met. 12.1 Traditional and customary rights are protected through participation by local communities in decision-making and planning. 12.3 Compensation and/or mitigation is made for avoidable and predictable damage to public values and resources due to logging. 12.4 Management strives to contribute a maximum of value and stability to local communities through ecosystem maintenance, ecosystem restoration, investment, employment, value-added manufacturing, etc. 13.1 Remuneration packages and contracting agreements are fair and equitable to all parties. 13.3 Rights of workers to organize and bargain collectively are protected. 13.4 Worker sharing in the benefits of business success is encouraged. 18.1 Management reviews ecological, social, and economic impacts of activities immediately after each entry and thereafter on at least an annual basis.	1.21 Local communities that are involved with/affected by forest management activities: (name organizations, adjoining owners and individuals). 6.17 Employees are trained in proper handling, storage and disposal of chemicals, apply chemicals according to label direction, and protective equipment is available and used. 7.1 Where appropriate forests are used as a training and/or educational resource for local people in conjunction with schools, community colleges, and/or other providers of training and education and/or forest managers contribute in some way to public education about forestry practices, sustainable forestry and the values of forest ecosystems. 7.2 Summaries of forest management policies are available to local communities upon request. 7.3 Local communities and businesses are considered for employment, recreation and benefits related to forest management activities. 7.4 Forest management considers community goals for forest and natural resource use and protection as articulated in current and approved community plans and is consistent with community zoning laws. 7.7 Wages, facilities and other benefits (health, retirement, worker's compensation, housing, food) are fair and consistent with (not lower than) prevailing local standards. More successful operations should provide better benefits. 7.8 Worker safety and training is an explicit element of all aspects of forest operations.
Documentation/data collection Planning Maps	1.1.1 Ecosystem types, including distribution, tree age, composition, and area, are described. 1.1.2 Natural disturbance types, patterns, frequencies, and sizes are described. 1.5 Description and maps of protected areas and human use areas are adequate to guide on-the-ground activities. 1.8 Plans for monitoring impacts of management are clearly described, including indicators to be monitored and timing of monitoring. 2.2.1 Identification of ES (Ecologically sensitive) sites is accurate and comprehensive. 2.3.2 As much as possible or at least 5% of lands are in OG (old growth) nodes and OG recruitment. 2.3.4 Nodes are designed to represent a maximum of ecosystem types indigenous to the landscape, rare, threatened, and endangered types are preferred. 2.4.2 Corridors are at least 150 m wide, plus a 50-m buffer on either side where only partial cutting	1.11 Types of forests that are being managed. 1.12 Are there any plantations? 1.13 Total acres being managed (commercial production vs non-productive lands). 1.14 Are there any management plans? If so, how many and covering how many acres? 1.15 Total volume of timber coming from each type of forest. 1.16 Acreage of forest being harvested each year. 1.17 Year in which harvesting operation began. 1.18 Do harvesting operations include construction of primary roads? 1.19 Modes of timber extraction (mechanical or manual, specify equipment used). 2.2 Land is dedicated by owners to long-term forest management. 2.3 A clearly defined pool of lands has been established. 3.1 Sufficient information exists on which to base forest management plan. 3.2 Long-term monitoring is implemented to enable

Values	Silva Forest Foundation	Smart Wood - Rainforest Alliance
	to SFF standards is practiced, corridor frequency is at least 1 for every 3 km of valley length. 2.5 On lands of over 20,000 ha, whole protected watersheds are designated. 2.5.2 Whole protected watersheds are as big as possible or at least 2000 ha. 2.5.4 Whole protected watersheds are designed for optimal representation of the full range of ecosystem types found within the larger landscape. 3.2 Roads and landings are designed to maintain the full forest functioning. 3.2.1 Roads are generally located on stable and moderately stable terrain, roads are fit into terrain, soil, and moisture constraints imposed by ecosystem characteristics. 3.2.2 Main road and spur road density is defined. 3.3 On lands of over 100,000 ha, large protected reserves are designated. 3.3.5 Large protected reserves are designed for optimal representation of the full range of ecosystem types found within the larger landscape. 4.1 Description of character and condition of applicant lands is adequate to guide management activities. 4.1.1 Ecosystem types, including distribution and area, are described. 4.1.2 The frequency of non-tree plant species are described by layer or height class. 4.1.3 Tree species, heights, diameters, ages, growth rates, and general health are described. 4.1.4 Snag species, heights, and diameters are described; large fallen tree species, lengths, diameters, and decay classes are described. 4.5 Descriptions and maps of location and human uses of the protected network of ecosystems are adequate to guide on-the-ground activities. 4.8 Plans for monitoring impacts of management are. clearly described, including indicators to be monitored and timing of monitoring. 5.1 Protected riparian ecosystems (PRE's) are designed to maintain full ecosystem functioning. 5.1.1 Protective measures in PRE's are justified from a site-specific ecosystem-based perspective. 5.2.1 Identification of ES (Ecologically Sensitive) sites is accurate and comprehensive. 6.1 At least 10% of dominant and co-dominant trees are marked/mapped and reserved as full-cycle trees. 6.2 Full-cycle trees represent all dominant and co-dominant species present in the stand previous to logging. 6.3 At least 25% of the pre-logging number of snags are retained, including at least 50% of large-diameter-class snags. 6.4 At least 50% of the pre-logging volume of large fallen trees are retained. 6.7 Trees are felled, limbed, and bucked on-site. no whole-tree harvesting is done. 7.1.2 Only partial cutting to SFF standards is practiced, windfirm trees are favored. 7.1.4 All fallen trees and 80% of pre-logging	adjustment of management plans and strategies. 3.5 Forest management plan is implemented in the field as written. Necessary modifications and/or revisions are appended to the plan. 3.6 Maps are produced at an adequate detail, scale, and provide operational guidance for management activities and facilitate on-site monitoring. 4.3 Management strategies prevent over harvesting of individual tree species. 4.4 Management strategies emphasize long term stand quality. 3.4 A forest management plan is written and available that includes: i) multi-year planning, ii) clear landowner and management objectives, iii) analysis of cruise and inventory data relating to target species including regeneration, iv) description of specific silvicultural prescriptions to achieve desired future condition, v) description of access issues and constraints, vi) protection measures identified for special management areas, vii) forest insect and disease conditions that may affect long term forest health condition, viii) forest management practices for soil conservation, water quality protection, sensitive sites, unique natural communities, aesthetics, chemical use and handling, ix) monitoring and update schedule. 5.2 The road, log landing and skidding are designated prior to harvest and are minimized, while providing transportation safety and hauling needs. 5.3 Maps have been prepared before harvesting or road construction, which specify areas which are suitable only for dry-weather and/or frozen conditions and indicate locations of truck roads, landings, main skid trails, no-cut zones, and other conservation areas. 5.5 A pre-harvest inventory and sale area reconnaissance is implemented. 5.6 Trees are marked or clearly designated prior to harvest. 5.7 An operating/harvesting plan is written, available, and used in the field that includes: i) silvicultural objectives, ii) volume and basal area targets, iii) residual species composition, and iv) transportation and access issues. 5.8 Pre-harvest silvicultural activities are undertaken, as appropriate to the operation's needs, scale and intensity. 5.11 Skid trail placement is acceptable for site conditions and minimized. 5.13 Log landing and hauling activities are appropriate for the scale of the operation. 5.15 Appropriate timber sale area closure actions are taken in areas that are no longer in use.

Values	Silva Forest Foundation	Smart Wood - Rainforest Alliance
	number of snags are retained. 7.3 Roads and landings are designed to maintain full forest functioning. 7.3.1 Road and landing layout agrees with the landscape plan. 7.3.3 Right-of-way generally is less than 12 m, with no unnecessary disturbance on cut slopes, fill slopes, and road surface . 7.3.8 roads and landings are built to last as permanent structures. 7.3.9 Old roads are rebuilt wherever this will reduce overall degradation of lands. 7.3.10 Roads are not used during periods of instability (e.g. during freeze-up or break-up). 7.3.11 Impacts from construction are minimized, and less than 10% of lands with in a logging unit are affected by all roads taken together, including skid roads and landings. 7.3.12 Maintenance of roads and landings when not in use is adequate to prevent an increase in impacts through deterioration. 7.4.1 Ground-based systems are used only on slopes less than 40%, with skid roads on microslopes less than 20%. slopes between 40% and 60% are logged only with cable or aerial systems. 7.4.2 All spur roads, skid roads, and landings are pre-located in the field. 7.4.3 Area of disturbance by spur roads, skid roads, and landings is less than 10% for ground-based systems and less than 7% for cable and aerial systems within a logging unit. 7.4.4 Spur roads, skid roads, and landings are designed as permanent structures. 8.2 Cutting over any period removes no more than 80% of the growth for the same period. 9.1.1 Management for natural regeneration is integrated with the planning and implementation of logging activities. 9.1.2 Damage to advance regeneration during logging is minimized. 18.3 Reserved areas, composition, and structures are clearly marked, mapped, or otherwise designated to guide on-the-ground activities now and in the future.	
Production Economic returns Finances	8.3.2 tree selection will result in improvement of the stand's timber value. 10.3 Salvage logging is necessary from an economic viewpoint. 14.1 The applicant has the financial means to carry out the management plan. 15.1 Product wastage is minimized. 1 5.2 Systematic efforts are made to diversify product types and to maximize the value of extracted wood.	1.6 Total volume (actual and estimated) of timber produced per year. Includes different type(s) of product(s) being produced and the volumes of each type. 3.7 Non-timber forest products have been considered and their management is incorporated into planning process where appropriate. Where applicable this may include: ginseng, mushrooms, maple syrup production, or provision of recreational opportunities. 4.1 An allowable cut has been derived based on well-documented estimates of growth and yield to provide a non-declining sustained yield of forest products and this target is being followed in harvest planning. 8.1 Stumpage rates being paid to landowners are fair and representative given logging conditions, timber quality, volume and local experience with log markets.

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		8.2 Revenue received is sufficient to financially support long-term forest management, e.g. planning, inventory, resource protection and post-harvest management activities such as silvicultural treatments, road maintenance, growth and yield monitoring, and other actions to ensure long-term forest health. 8.3 Financial benefits of forest management are reinvested into long-term management. 8.4 Financial situation, investment objectives, and debt load do not place undue pressure on the operation to sacrifice management for short term high output harvesting production. 8.5 Under-utilized timber species are being evaluated for harvest and commercial opportunities. 8.6 Forest operation encourages, where appropriate, the utilization of non-timber forest products and recreation to enhance forest potential. 8.7 Merchantable log loss and waste in the forest is minimized. 8.8 Logs and lumber are handled so as to minimize potential loss in value from degrade, exposure, and parasites. 8.9 Forestry operation seeks the highest and best uses for individual tree and timber species and products.
Biodiversity - (plants, animals, composition, structure)	1.1.3 Relationship between ecosystem types and disturbances are analyzed. 1.1.4 Present condition is compared with natural ranges of variability as estimated by the best available information. 1.4 Identification and accommodation of ecological limits are accurate and ecosystem-based. 1.7 Minimum landscape-level requirements for stand-level applicants are met. 1.7.1 Description and analysis of successional processes on applicant lands are adequate to guide ecosystem-based planning. 1.7.2 Plans to mimic and maintain successional processes are clearly described. 2.3 Old growth nodes and old growth recruitment will provide specialized habitat throughout the landscape. 2.3.1 nodes are as big as possible or large enough to provide at least 50% forest-interior habitat (areas over 250 m from nearest edge). 2.3.3 Nodes are designed to provide habitat for indigenous rare, threatened, and endangered species. 2.4 Cross-valley corridors can be expected to provide opportunity for movements of all forest organisms known to require mature or undisturbed forest. 2.4.1 Corridor design provides useable linkages among components of the protected landscape network and other ecologically important landscape ecosystems. 2.5.5 Whole protected watersheds are designed to provide habitat for rare, threatened, or endangered species. 3.1.2 Zoning of uses is designed to maintain full forest functioning across the entire landscape.	1.20 What ecologically sensitive , critical or unique natural areas are known to exist in the vicinity of harvesting? 4.2 Boundaries of harvest areas are respected and controlled between cutting cycles so as to prevent disturbance to regeneration. 5.10 Felling techniques minimize damage to residual forest. 6.2 Management activities maintain continuity of forest cover at the watershed level and minimize forest fragmentation. 6.3 Management addresses the diversity, composition and structure of the forest at the stand, watershed, and landscape levels. 6.4 Gap sizes and canopy openings are appropriate to the local ecology and sufficient to regenerate the stand while minimizing fragmentation of the structure and diversity of the forest at the watershed level. 6.6 Management practices addresses the retention of cavity, den and/or snag trees for wildlife habitat. 6.7 Management practices actively addresses the management and/or enhancement of existing wildlife habitat elements. 6.8 Management activities reduce risks from invasion or expansion of exotic species in the forest. 6.9 Conservation of threatened, rare, endangered and unusual plant and animal species, natural communities and critical habitats, are explicitly incorporated into management and harvesting plans. 6.12 Design and layout of reserves or special management zones is considered at the watershed and landscape level. Connectivity of

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	agriculture, mining, buildings, and ranching are not permitted in the PLN (Protected Landscape Network). 3.3.6 Large protected reserves are designed to provide habitat for rare, threatened, or endangered species. 4.1.7 Rare, threatened, and endangered species are inventoried. 5.3 Rare, threatened, and endangered species and ecosystems are protected from logging impacts. 6.5 Species, decay class, and size diversity of retained snags and large fallen trees approximates pre-logging diversity, with emphasis given to larger size classes. 6.6 Spatial distribution of retained composition and structures approximates patterns caused by natural disturbance. 7.4.5 Damage to retained trees is less than 5% of residual stems. 8.1 Logging is designed as much as possible to mimic and maintain natural disturbance regimes and the ecosystems they form. 8.1.1 Disturbances being mimicked and maintained are natural to the site. 8.1.2 Cutting levels do not cause significant interruption or alteration of natural nutrient storage and cycling processes. 8.1.3 Cutting patterns mimic common natural disturbance patterns as much as possible. 8.1.5 Composition and structures are permanently reserved as required by protected network of ecosystems. 8.3 Selection of cut trees maintains the natural biodiversity of the stand, improves tree quality, and develops a viable economic resource. 8.3.1 Selection favors trees resistance to windthrow, disease, insects, etc. 8.3.3 Tree selection imitates successional processes at the individual, species, and community levels. 9.2.2 Planted trees represent the full range of species for the successional phase being mimicked, planting stock is taken from within the local biogeoclimatic subzone. unfertilized bare-root planting stock is preferred. 9.3 Brush control and site preparation are designed to maintain full forest functioning. 9.3.1 Brush control and site preparation mimic natural successional processes and patterns. 10.4 Salvage logging removes less than 50% of the fallen trees and less than 50% of the snags remaining after the disturbance. Trees removed are be representative of natural species, diameter, and height class distribution on the site.	forested areas should be considered in planning of reserves or special management zones.
Water and soil	2.1.1 Protective measures in PRE's are justified from a site-specific ecosystem-based perspective. 2.1.2 Average riparian buffer width is at least 25 m on all sides of watercourse or water body, with none less than 15 m. no-logging portion is at least 10 m wide, cutting in remainder agrees with standards in 6.1. 4.1.5 Terrain slope, stability, and aspect are	5.9 Strategies for protecting highly erodible areas or designated buffer zones and wetlands are being followed during harvest. 5.12 Skidder operators work with sufficient care to avoid residual stand damage and minimize impacts to soil and water resources. 5.15 i) temporary stream crossing structures removed and stream banks restored, ii) landings reshaped to secure adequate surface

Values	Silva Forest Foundation	Smart Wood - Rainforest Alliance
	described. 4.1.6 Soil types, drainage, stability, and depths are described. 4.6 Descriptions of protective measures for soil, water, and permanently reserved composition and structure are clear, and estimation of impacts due to timber management are accurate (within 5% of actual impacts). 5.1.2 Average riparian buffer width is at least 25 m on all sides of watercourse or water body, with none less than 15 m. no-logging portion is at least 10 m wide, cutting in remainder agrees with standards in 6.1. 7.1 Where permitted, logging in riparian ecosystems is designed primarily to maintain full functioning of those ecosystems with particularly large margins of precaution. 7.1.1 Cutting patterns and levels are justified from a site-specific ecosystem-based perspective. 7.1.3 Exposure of mineral soil and/or soil compaction is less than 5%. 7.1.5 Felling is designed to minimize degradation, felling is away from watercourse or water body and away from no-logging reserves. 7.1.6 No roads or vehicles are permitted in protected riparian ecosystems, except for watercourse crossings. 7.1.7 No products are piled in protected riparian ecosystems, felling equipment is refueled in specified zones outside of protected riparian ecosystems. 7.3.2 Roads are located on stable areas with minimal cut and fill, roads are fit into terrain, soil, and moisture constraints imposed by ecosystem characteristics. 7.3.4 Road drainage structures, including road profile, road cross-section, ditches, culverts, bridges, etc. maintain natural drainage patterns and minimize concentration of flow. 7.3.5 Watercourse crossings are minimized. 7.3.6 Watercourse crossings accommodate 100-year floods and span the entire riparian *zone* (but not necessarily the riparian ecosystem). 7.3.7 Watercourse crossings maintain fish passage and watercourse bed structure. 7.4 Skidding or yarding systems are designed to maintain soil and water structure and functioning. 7.4.6 Bonus points may be awarded for specific measures taken to protect soil and water during skidding or yarding.	drainage and reseeded, preferably with non-exotic species, iii) functional cross drains constructed on roads where appropriate, v) active erosion control measures (mulching, silt fence) are implemented as needed in accordance with State BMPs. 6.5 Management practices addresses structural heterogeneity, potential for soil improvement and nutrients enrichment on the forest floor by maintaining or restoring the presence of coarse woody debris (CWD). 6.11 River and stream corridors, steep slopes, fragile soils, wetlands, vernal pools, lakes and pond shorelines, and other hydrologically sensitive areas are automatically designated as special management zones.
Miscellaneous management practices Silviculture methods Chemicals/wastes/ pollutants Restoration Plantations	7.2.2 If a chemical is used with ecological justification, choice of chemical and method of application are designed primarily to minimize damage to ecosystems and non-target impacts. 7.5.1 Toxic and inorganic wastes are disposed of in approved disposal sites, generally located outside the forest. 7.5.2 Pollution is minimized in all phases of operation. 8.1.4 Silvicultural treatments (e.g. prescribed burns) imitate natural disturbance regimes. 9.1 Natural regeneration is preferred over planting.	Generic Guidelines for Assessing Plantations 3.3 Forest management objectives and prescriptions are documented and based on site history, owner's objectives, forest condition, ecology, management needs, and other relevant factors. Silvicultural prescriptions are substantiated using current research, silvicultural guides and applicable growth and yield models. 4.5 Management addresses the restoration of degraded or low quality forest stands. 4.6 Planting incorporates ecological factors or is utilized as a silvicultural tool to restore high-graded

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	9.2 Where tree planting is done, it is designed to maintain natural biodiversity. 9.2.1 Planting is justified from a site-specific ecosystem-based perspective. 14.3 Investment in equipment and infrastructure will minimize pollution and degradation. 16.1 Restoration is designed to mimic, maintain, and, where necessary, reintroduce disturbance regimes natural to the site and landscape. 16.2 Where practiced, artificial restoration is justified as a necessary interim stage to allow eventual restoration of natural composition, structures, and functioning. 17.1 Restoration activities do not create negative impacts in excess of expected long-term benefits. 17.2 Restoration activities account for the reestablishment and maintenance of natural biodiversity at all scales of time and space.	stands to natural species mix and forest cover. 4.7 Planting where it occurs, utilizes mixed species of native stock, rather that exotics. 5.14 Post-harvest silvicultural activities are implemented where planned with reliability and success, 6.1 Silvicultural prescription have a primary objective of perpetuating a sustainable forest ecosystem. Silviculture is practiced with the goal of conserving and restoring ecological diversity and ecosystem function. 6.16 A constant effort is made to: minimize the use of chemicals, use targeted application methods, use the least toxic chemical possible, and phase in non-chemical alternatives. Waste (e.g. sawmill residues, chipping, debarking, waste oil, and landing debris) is being properly disposed.

biodiversity-a value based indicator. Central to the implementation of the certification analysis is the measurement, maintenance and restoration of biodiversity which reappears several times in the different categories of required data presented in table 1. However, the effectiveness of focusing on biodiversity measurements to assess system sustainability is debatable. It has been assumed that biological diversity is directly correlated to the maintenance of system carbon and nutrient cycles (Karieva 1994). The ability to characterize a site condition by focusing on species numbers and assuming that there is a direct cause and effect link between species diversity and function would simplify our capability to assess the effect of site disturbance or a particular management regime. Unfortunately such a direct relationship has not been shown for most plant communities (Johnson and others 1996). This lack of clear links between biodiversity and ecosystem function is unfortunate since it would greatly simplify our ability to detect or even predict changes in ecosystems.

It has also been suggested that the biodiversity of ecosystem components other than plants should be pursued as indicators of change in system function. For example, similar to the biodiversity relationships suggested for plants growing in grasslands (Tilman and Downing 1994), there has been interest in using symbiont diversity as an indicator of how the system was responding to anthropogenic activities. In the field, the diversity of mycorrhizal species can be high and has been shown to vary from 7 to over 20 different fungal species found colonizing the root system of one tree species at any given time period under undisturbed conditions (Vogt and others 1981; Gardes and Bruns 1996). However, preliminary information suggests that the diversity of ectomycorrhizal fungal species found on plants' roots may not be directly related to how successfully plants occupy a site. In one greenhouse study where the diversity of symbionts on roots were controlled, researchers were unable to show that increasing the diversity of fungi on roots conferred an advantage to the seedlings (Benecke and Gobi 1974; Parladé and Alvarez 1993). A focus on diversity of species found on root systems does not address the fact that the functional diversity may be much more useful to monitor, especially since the efficiency at which different fungal species acquire abiotic resources has been documented to be highly variable (Harley and Smith 1983). If one knew how spatially heterogeneous the abiotic resource availabilities were in the ecosystem and the individual efficiencies of the different fungi, one might begin to predict how many functional groups would be needed to optimize resource acquisition. For plants growing in grassland ecosystems, increasing the number of plant species beyond 10 did not confer increased stability to that system suggesting a threshold for this system (Tilman and Downing 1994).

Another example with Bishop pine (*Pinus muricata*) also highlights the importance of assessing factors other than diversity to monitor ecosystems. In this case, the ability of Bishop pine to have up to 20 different species of mycorrhizal fungi on its roots (Gardes and Bruns 1996) was not relevant in assessing its effectiveness in competing for abiotic resources and outcompeting other plant species at the same site (Northrup and others 1995). The success of Bishop pine and its ability to acquire abiotic resources was dependent not on the diversity of fungal species present but on the ability or efficiency at which the symbionts utilized organic N forms {Northrup and others 1995). In this example, it was the ability of Bishop pine to produce litter higher in polyphenolics with slower decomposition rates that result in most of the available N being present in the organic N form. In this example, several indicators could have been used to assess the sustainability of Bishop pine on the site - tree NPP, N availability in the soil, water availability, mycorrhizal diversity, litter decomposer biomass or community composition or decomposition rates. Out of all these potential indicators, the most sensitive to assess Bishop pine health would be changes in polyphenol levels in decaying litter and the presence of symbionts capable of utilizing organic forms of N. In this case, the determination of NPP, mycorrhizal diversity or the development of detailed N budgets would probably not have been sensitive indicators to monitor; even if changes in these parameters would be measurable, they are not the driving variables controlling how the system responds.

ALTERNATIVE FRAMEWORK FOR DETERMINING NON-VALUE BASED INDICATORS

To shift these protocols away from the human value based approach, we developed a framework that produces a "road map" identifying what information is relevant to each site and also shows that the information used to evaluate a site might change between different locations (Vogt and others, unpublished data). Our framework utilizes a process of identifying legacies and the key driving variables controlling the resistance and resilience of an ecosystem; those indicators that are typically not identified when using a value-based approach. These non-value based indicators constrain the ability of a system to function and influences the response of the system to perturbations. Our framework will address the problem of the large data needs of the Certification protocols by identifying those site specific variables relevant to monitor.

One of the problems identified with the certification protocols (table 1) is the need for large amounts of documented data. The presence or absence of these data and their content determines whether or not a site will be certified as sustainable. This need for large amounts of data makes it almost impossible to assess many sites because some data may not be available at some given site. This requires the acquisition of missing data to fulfill the certification requirements without even knowing if any of the missing data are relevant for the site being assessed. This highlights the need for a method that can determine what information is associated with or influences the functioning of a system. It is also important to accept the fact that the information needs will vary between different sites and we should not be attempting to use the exact same information to assess different sites (Vogt and others 1997). The framework presented in Vogt and others (in review) is important because it develops a road map that can be used to assess what the information needs are for different sites. This framework takes one from assessing a site based on a pre-requisite set of tools that are used at all sites to a researcher assessing a specific site by identifying what the driving variables are that control or constrain how the system functions.

Large data sets which already exist can be quite useful (Vogt and others 1996) for identifying what are the constraints controlling the functioning of a site. Identification of these constraints is especially important because they frequently are not characterized by the value-based indicators but function in controlling or driving how that system functions (Vogt and others, unpublished data). These constraints are also important to identify since they are the driving variables that would be important to monitor to determine if the condition of the site is changing.

Determining the constraints of an ecosystem using a large data set would then help identify the non-value based indicators that control system function. It is important that analyses do not occur only at higher spatial scales (see table 2) but that analyses are conducted at scales at which the system is sensitive to a particular management activity (table 3). For example, climatic variables may be identified as important driving variables controlling the productivity that is achievable on a site at higher spatial scales (table 2). However, at smaller scales, productivity may be poorly predicted by climatic variables (see table 3). The scale sensitive to assessing the system must be the one utilized for analysis - whether this occurs at the smaller or larger scale. Therefore, when climatic variables exert a strong influence on the functioning of that system and climate change has been recorded, a manager's focus should expand to assessing the impact of climate change on ecosystem processes. In this example, the influence of climate would have to be considered as a constraint on the site, even though it cannot be managed, since it changes how the system responds.

The information synthesized in table 2 from Vogt and others (1996) highlights how variable the important driving parameters are in controlling the aboveground productivity of sites in general (Vogt and others 1996). These data encompassed information from the boreal to the tropical forests and showed that climatic variables explained about one third of the changes in Aboveground Net Primary Production (ANPP). At this scale, information on organic matter accumulation in the soil or on the surface of the soil explained about one-fifth of the variability recorded in ANPP (table 2). These variables do not appear to be useful to predict how ANPP might change in response to management activities at these larger spatial scales. Interestingly, past analyses of these large data sets revealed that climatic variables were effective at explaining the amount of surface organic matter (e.g., forest floor) but not soil organic matter (SOM) accumulations (Vogt and others 1996).

Table 2—Variables predicting Aboveground Net Primary Production when data were combined from all sites given in Vogt and others (1996).

PREDICTIVE VARIABLES	r^2(p = 0.001)
Forest Floor Mass Content	0.22
Soil Organic Matter Content	0.24
Minimum Annual Temperature, C	0.31
Mean Annual Temperature, C	0.37
Forest Floor N MRT[a]	0.67

[a] MRT = mean residence time (years)

The information in table 2 shows that the mean residence time (MRT) of N in the surface organic horizons may be quite useful as an indicator to monitor systems. If forest floor mass is useful for predicting NPP, litter decomposition rates may be useful as indicators of the productivity changes on the site. Since it was the mean residence time of N in the forest floor that explained a greater proportion of the changes in ANPP, it may be worthwhile monitoring the decomposer organisms located in the surface organic horizons as indicators. Whether it would be useful to monitor the decomposer organisms directly associated with the litter turnover or whether changes in forest floor N MRT would be sufficient and a more sensitive parameters to monitor is not clear. This suggests that we need to be able to detect changes in the forest floor N MRT at a level that is sensitive to the changes occurring in the ecosystem. This analysis, is of course, at a very large spatial scale and the ability to go to any given site to predict how the system is responding to a disturbance may be difficult. They do give at a large spatial scale, the large scale constraints that may exist on a site and are therefore useful indicators of variables that should be monitored.

The information needs will vary depending on the scale at which the system is being analyzed. It is usually generalized that less information is needed at larger spatial scales and that the information needs increase dramatically as one scales down (Vogt and others 1997). The generalizable relationships shown with ANPP and all sites combined (table 2) do not transfer readily to all systems located at smaller spatial scales (table 3). These relationships have been quantified using a large data set (Vogt and others 1996) and expressed at different scales of analysis. Further scaling down of these predictive relationships show that the correlations between SOM and ANPP vary depending on the forest climatic type (Vogt and others 1996). When all forest climatic types were pooled together, about a fourth of the ANPP variability could be explained by SOM levels. However, in the warm temperate, subtropical and tropical climatic forest types, there existed no predictive ability between these variables. This contrasted with the cold temperate climatic type where 34% of the variability in ANPP could be explained by the SOM levels and the boreal climatic type where 26% of the variability could be explained. Pooling of data from all climatic types suggested a certain predictive capability and what might be general constraints on the growth achievable on all forests. However, zoning down to lower scales immediately showed that certain forest types do not have the surface organic matter or soil organic matter accumulations functioning as constraints on ANPP.

Interestingly, the ability to predict total NPP using the forest floor mass accumulations (r^2 = 0.43, p= 0.01) or SOM levels (r^2 = 0.53, p = 0.01) was higher than for ANPP in the boreal forest climatic type (Vogt and others 1996). In the boreal forests, these results suggested that decomposition variables are very useful indicators of system response. In fact, research from specific sites suggested that most of the system energetics flux through the decomposers. This contrasted with the cold temperate climatic types where the forest floor accumulations had a poorer predictive ability while the ability of SOM accumulation to predict total NPP was the same as for ANPP. This suggests that monitoring the decomposers might not be as useful in many of the cold temperate forest climatic types. In the cold temperate forest ecosystems, data shown in table 3 suggest that plants might be a better indicator of changing conditions in the site.

If total NPP was predicted using forest floor accumulations and the data are separated by soil order instead of climatic types, the ability to identify strong predictive relationships under certain conditions is highlighted (fig. 1; Vogt and others 1996). For example, forests growing on an Inceptisol soil order had strong relationships between forest floor mass accumulation and total NPP with 62% of the variation in total NPP explained. No significant relationships were found for any of the other soil orders. The

Table 3—Variables predicting Belowground Net Primary Production (BNPP) and Belowground Biomass (BB) are shown by Forest Climatic Type (e.g., Boreal, Cold Temperate Needleleaf, Warm Temperte Broadleaf Deciduous, Subtropical Broadleaf Evergreen, Tropical Broadleaf Evergreen) (data from Vogt and others 1996).

Forest climatic type • Independent variables	Dependent variable r^2 (p = 0.01)	
	BNPP	BB
Boreal		
• max. annual air temperature	0.83	—
• min. annual air temperature	0.83	—
• aboveground litterfall N	—	0.99
• aboveground litterfall P	—	0.95
• FFN MRT[a]	—	0.63
Cold Temperate Needleleaf		
• annual precipitation	0.13	—
• aboveground litterfall N	0.15	—
• aboveground litterfall K	—	0.74
• aboveground litterfall P	—	0.64
Warm Temperate Broadleaf Deciduous		
• soil texture	0.75	—
• FFN[b]	0.66	—
Warm Temperate Needleleaf		
• mean annual temperature	0.61	—
• soil texture	—	0.73
Subtropical Broadleaf Evergreen		
• soil texture	—	0.84
Tropical Broadleaf Evergreen		
• maximum annual temperature	-	0.81
• aboveground litterfall N/P ratio	0.99	—
• aboveground litterfall P	—	0.53

[a] FFN MRT = forest floor nitrogen mean residence time
[b] FFN = forest floor nitrogen

relationship found for Inceptisols is probably related to the fact that these are young soils and are characterized by low nutrient availability. The other soils orders may also have low nutrient availabilities but are dominated by vegetation and symbionts that have evolved with the nutrient levels inherent to that site.

Further identification of indicators that would suggest what type of variables should be monitored can be identified by examining the information given in table 3 (data from Vogt and others 1996). This information highlights nicely how the same indicators should not be automatically transferred to all sites to assess the condition of a site or how it responds to disturbance. The data show how indicators vary depending on the climatic forest type and by whether biomass or productivity data are being assessed (table 3).

Information given in table 3 also showed how variable the type of information used to predict the productivity and biomass of fine roots across these different forest climatic types can be. When aboveground litterfall nutrients are more effective in predicting biomass or productivity, this is probably reflecting the plant/symbiont level adaptations to the site. When temperature or the mean residence times of surface organic matter appear as useful predictors of achievable biomass or productivity, decomposer variables may be quite useful as indicators to monitor.

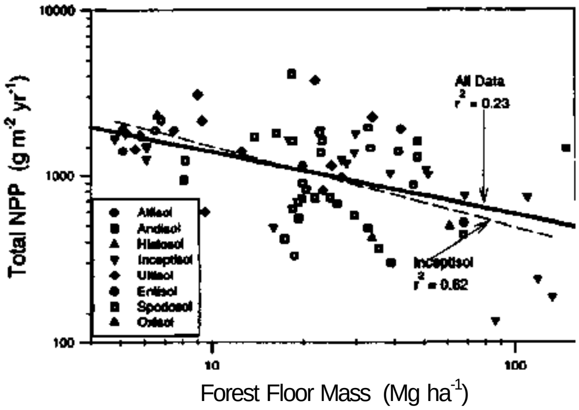

Figure 1—Net Primary Production predicted using forest floor mass where the data were grouped by soil order (data synthesized in Vogt and others 1996 was used).

The scale of measurement analysis can be critical in determining when a sensitive level of analysis has been identified and whether the right indicator was selected. If the incorrect scale is chosen, analysis of impact may show no impact of an activity when in fact the system may already be changing. A good example of the varying sensitivity of detecting system response can be seen by looking at how organic matter in the soil is determined - as a total mass or by fractionating it into its components. For example, determination of total organic matter in the soil may not show a response to management since such a high proportion of the carbon may be in a recalcitrant pool (Oades 1988; Johnson 1992). Thus, an analysis of its component parts may be extremely useful and may reflect that the system is changing in the short time scale in response to some management activity. SOM is generally composed of different stages of decomposed organic matter each of which have different turnover rates (Baldock and others 1992).

This raises the question of identifying the scale at which the system is sensitive to an activity and then measuring the system at the appropriate scale. This will probably vary depending on the activity being measured. The information needs will also vary by scale and again more factors can be shown to be important in controlling a pool size. As an example, at smaller scales, many factors have been identified as important in affecting the stability of soil organic matter as shown in table 4 (Stevenson 1965; Lugo and others 1986; Oades 1988; Johnson 1992, 1995; Vogt and others 1995). Each one of these factors may function as a constraint or driving variable in different sites and thus become crucial to measure and monitor for changes in the system. In most cases, one will probably not measure these factors unless one of them has been shown to be sensitive to management activity (e.g., acid deposition and decreases in soil pH and Ca levels; Lawrence and others 1999).

Table 4—Some general factors controlling soil organic matter accumulation that are external or internal to the soil (Stevenson 1965; Lugo and others 1986; Oades 1988; Johnson 1992, 1995; Vogt and others 1995).

External to Soil	Internal to Soil
Temperature	Clay composition & dominance
Precipitation	PH
Vegetation type	Base saturation percent
• deciduous, evergreen	
• litterfall chemical quality	
Disturbance	N, Ca availability
• type	
• time since disturbance	
Type of Management	Decomposer types and dominance
	Al, Fe - form and abundance
	Soil texture

In other cases, a focus on the composition or pool size of SOM may better integrate many of the factors listed in table 4; the analysis framework should be used to determine at what level of analysis is the system most sensitive to and reflecting the changing system. For example, when human activities have changed the pool sizes and fluxes of nutrients, changes in SOM may be a very useful parameter to measure. Also some factors such as N availability may have a significant effect on the total pool of organic matter found in the soil (Vogt and others 1995). Vegetation type also controls the N availability and the type of carbon compounds produced (e.g., simple and complex) both of which directly affect the organic matter accumulation in the soil. For example, SOM accumulation has been shown to be higher in deciduous dominated forests and forests composed of a mixture of deciduous and evergreen species than in evergreen dominated forests where N availabilities are lower (Vogt and others 1995). In this case, the effect being measured is excess N inputs but the sensitive variable to monitor in the ecosystem could be leaching losses of N below the rooting zone or changes in the SOM content of soil.

CONCLUSION

An examination of indicators used in the existing frameworks for assessing ecosystem health or sustainability shows that they are mostly human value-based. These value-based indicators selected for use in the protocols for forest certification generally reflect the interests of the organizations developing them and are unfortunately considered to be uniformly applicable across all sites examined. Most of these protocols focus on biodiversity which has not been shown to be directly linked to ecosystem sustainability except in a few cases. These assessment protocols also have high data needs which reduces their utility in many systems since the data may not be available or would cost too much to collect. The perception that much data should be monitored is augmented by our uncertainty of how a system functions and our inability to begin to identify relevant indicators. To develop an efficient framework for certifying forest management one needs to create as few protocols and/or indicators to check, measure, or monitor in a forest site as possible and yet still be able to insure that ecologically, environmentally, silviculturally, etc. sound forest management has been, or is being, conducted. One step to accomplish this in part would be to determine what indicators are directly or closely linked to the functions of a system, such as those that drive or constrain the system. It is not surprising that many of theses indicators might be associated with soil ecology. Monitoring these types of indicators would allow one to know if the system is changing and, if so, whether the changes are a consequence of natural events and/or forest management practices.

Acknowledging the role of value-based indicators in the selection of indicators to assess system health is critical because they may incorrectly identify a suite of indicators which are not sensitive to site conditions. The value based indicators need to be monitored in any assessment but if they do not reflect the system holistically, priority should be given to monitoring those non-value based indicators. These non-value based indicators would be identifying those factors that constrain the functioning of a site. Using a framework that allows for non-value based indicators to be identified is crucial for producing effective assessment protocols.

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SOIL QUALITY AND HEALTH-SOME APPLICATIONS TO ECOSYSTEM HEALTH AND SUSTAINABILITY

Robert T. Meurisse[1]

ABSTRACT

Sustainability of forest and rangeland ecosystems is intricately linked with healthy and productive soils. Soils vary widely in their quality. Their health is a condition of the soil relative to their inherent quality and ability to perform vital soil and ecosystem functions. Soils in Pacific Northwest forest and rangeland ecosystems are particularly heterogeneous. For example, selected soils from six Ecoregions, have organic carbon contents that range from about 40,000 to more than 800,000 kg/ha. Total nitrogen content ranges from less than 2,000 to more than 50,000 kg/ha.

There is a close relationship between soil quality and health and ecosystem quality and health. Ecosystem stresses can be increased by management activities that compact soils and alter soil moisture and nutrient status and processes. Forest health in Inland Western forests is intricately linked with carbon and nutrient cycling. A high percentage of soil organisms make their home in the soil and play a critical role in the functions of ecosystems. Alteration of soil physical and nutrient conditions can alter the incidence of soil borne diseases which, in turn, affect the health of ecosystems.

Specific quantitative soil standards, or thresholds, are needed to determine detrimental conditions. The National Forests have established a variety of measures of detrimental conditions. A variety of physical measures, such as bulk density changes, displacement and erosion, and detrimental burn conditions are emphasized.

Soils vary widely in their resiliency, or ability to rebound from impacts. A model of soil resiliency adopted from Szabolcs (1994), includes physical, chemical and biological buffering and pedological and anthropological soil fluxes. Several soils from six Pacific Northwest Ecoregions are rated for their resiliency. Criteria for chemical, biological and physical buffering is included.

Keywords: soil quailty, soil health, soil functions, soil resiliency, ecosystem health, ecoregion

INTRODUCTION

Concerns about sustaining the productivity and health of forest ecosystems have been the subject of much research, debate, and federal actions (Perry and others 1989; Gessel and others 1990; Everett and others 1994; Harvey 1994; Denniston 1995; Jurgensen and others 1997). Forest and livestock grazing management practices and their impacts on the environment are scrutinized daily by the media. A committee of the National Research Council was convened to examine the scientific basis for inventorying, classifying and monitoring rangelands. It included a strategy for evaluating rangeland health. Recent flooding and landslide events in the west have resulted in debates about watershed health. The decline of salmonids in northwestern streams is attributed to declines in watershed health, among other factors. Although often overlooked, soil conditions and soil degradation often underlie the concerns about ecosystem health and attempts to restore ecosystem health must consider and understand soil conditions and processes (Meurisse and Geist 1994). Soil quality and health, and methods for assessing them, have been the subject of several symposia and publications (Griffith and others 1990; Doran and others 1994; Greenland and Zabolcs 1994; Doran and Jones 1996). Soil health and quality are implicitely embedded in statute for the National Forests and Grasslands of the United States. But what do we mean by ecosystem health, watershed health, soil health, and soil quality? When there is not even complete agreement about human health (Clements and Hales 1997), can we reach consensus about soil health or ecosystem health?

My objectives are to define soil quality and health and link them to vital soil functions. Secondly, I will describe and illustrate some relationships between soil health and ecosystem health, including a discussion of soil quality standards as thresholds for soil health. Thirdly, I will discuss soil resiliency concepts, some criteria and ratings of soils in Pacific Northwest

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[1] Robert T. Meurisse is Regional Soil Scientist, Retired, USDA Forest Service, Pacific Northwest Region, Portland, OR 97208

ecosystems and the importance of resiliency to restoration of ecosystem health and sustainability.

REASONS FOR CONCERN ABOUT SOIL QUALITY AND SOIL HEALTH

Soil and Civilizations

"For humankind, soil is the essence of life and health." This opening sentence of the Preface to the Soil Science Society of America Publication, Defining Soil Quality for a Sustainable Environment, captures the significance of the soil resource for sustainability of human life and economic well being (Doran and others 1994). The importance of definition of soil quality and establishment of quantitative indicators or thresholds can not be overemphasized (Doran and Parkin 1994). Definition is important for communication. Establishment of quantitative measures is critical for monitoring conditions. The importance of sound soil and water management in the development and advancement of civilization, particularly in the Middle East, is described by Hillel (1994).

Soil Degradation

Worldwide soil degradation is estimated to be nearly two billion ha. (Szabolcs 1994). Principal causes are from water and wind erosion, with lesser amounts from chemical and physical causes. Asia and Africa are estimated to have more than 700 and 400 million hectares of degradation, respectively. South America is third with about 200 million hectares of degradation. Although Mexico and Central America and North America are among the least degraded of all Regions, many millions of hectares are degraded. In North America, there is little measurable amount estimated for physical and chemical degradation. Studies have shown that many areas have reduced productivity and quality largely because of erosion and physical degradation from soil compaction (O'Laughlin and Pearce 1984; Froehlich and McNabb 1984; Sullivan 1988; Berg 1988; Geist and others 1991). Most of the degradation in forest systems is due to erosion and physical degradation, namely soil compaction (Sullivan 1988; Froehlich and McNabb 1984) and erosion (Megahan 1981; O'Laughlin and Pearce 1984; Berg 1988). On rangelands, erosion and sedimentation is the principal source of degradation (Smith 1989).

SOIL QUALITY AND HEALTH-WORKING DEFINITIONS

Terms such as soil quality, soil health, forest health, and ecosystem health, are anthropomorphic concepts with relative values, just as human health is. The terms soil quality and health often are used interchangeably. However, subtle differences exist between them. A 1995 National Cooperative Soil Survey Soil Quality Committee defined soil quality as: "the capacity of a specific soil to function, within natural or altered land use boundaries, to sustain or improve plant and animal productivity, water, air quality, and human health and habitation." This definition is similar to one defined by Doran and Parkin (1994). Pedogenesis imparts specific qualities to soils with resultant differences in their inherent capacity to function. The American College Dictionary defines health as "freedom from disease or ailment; the general condition of the body or mind with reference to soundness or vigor. So, I define soil health as "the condition of the soil with reference to its inherent quality and ability to perform vital ecosystem functions." The distinction is the capacity to function relative to a soils' inherent qualities.

Relationship of Soil Quality and Health to Vital Soil Functions

Definitions of soil quality and health are linked to the ability to perform vital soil functions. There is general agreement among soil scientists about the major functions of soils, though they may be stated in different ways. I characterize them as follows: (1) Sustain biological productivity, activity, and diversity; (2) store and cycle nutrients and other materials; (3) partition water, energy and solute flow; (4) filter, buffer, immobilize, and detoxify organic and inorganic materials; and (5) support structures and protect archeological treasures. Therefore, we can say a soil is unhealthy if soil properties are altered to the extent that vital soil functions are impaired to some measurable degree. Further, where specific soil quality standards, or thresholds, are established, and those standards are exceeded so that the ability to perform vital functions is impaired, we can consider the soil as unhealthy.

Soil properties that affect the capacity to function vary depending on the specific function. For example, properties important to productivity or biological activity usually will be somewhat different from those functioning to detoxify, buffer or immobilize materials. But some properties are common to multiple functions. Properties such as organic carbon, total nitrogen, porosity, soil depth, particle size distribution, acidity, and ion exchange capacity are examples of properties that are critical to multiple soil functions, though their relative values for a given function may be significantly different. Additionally, soil moisture and temperature regimes are important soil variables contributing to the capacity of a soil to function. Soil quality generally can be judged by soil properties that regulate the ability to store and cycle nutrients and carbon, store and release water, and provide favorable gas and heat exchange for specific functions.

Soils vary widely in their quality and capacity to perform vital functions. This is particularly true in the Pacific Northwest where there is extreme heterogeneity in the factors of soil formation and soil forming processes. In particular, rates and magnitudes of carbon and nitrogen cycling and accumulation vary widely (Meurisse and others 1991). For example, soil organic carbon ranges from about 40,000 kg/ha in some Interior Northwest soils to nearly a million kg/ha in some coastal Andisols (table 1). Similarly, total nitrogen ranges from less than 2,000 to more than 50,000 kg/ha. Variation within a soil series may be related to presence or absence of N-fixing species such as snowbrush (*Ceanothus velutinus*). This is illustrated for the Lapine series (table 1). The coastal Andisols contain some of the highest amounts of organic carbon in the world (Homann and others 1995). Those soils also are among the most productive in the world (Meurisse 1988a). Shallow and moderately deep Mollisols contain amounts of organic carbon and nitrogen comparable to deep and very deep Andisols in Ecoregion M242C and M332G (table1). Grasses and forbs are the dominant lifeform on these soils.

SOME SOIL HEALTH AND ECOSYSTEM HEALTH CONNECTIONS

There is a close relationship between soil quality and health and the quality and health of forest, rangeland, and watershed ecosystems. Forest health usually is considered in terms of insects and diseases and their effects on tree mortality. These often are only symptoms to more underlying stresses regulated by soil/climate systems. Such stresses often are the result of some management action. Management activities that change soil moisture and nutrient status through soil compaction, displacement and severe burning often are major contributors to stresses that cause mortality (Everett and others 1994). For example, the effects of soil compaction and related loss of soil structure on tree establishment and growth is well documented (Froehlich and McNabb 1984; Clayton and others 1987; Powers and others 1990). Compaction increases soil strength, decreases root penetration, decreases moisture and nutrient availability and decreases gas exchange. These all contribute to plant stress and loss of vigor. Stress induced in part of an ecosystem permeates the entire system (Waring 1985).

Moderate and severe soil compaction significantly reduced nonmycorrhizal root tip abundance on both Douglas-fir and western white pine after one year of outplanting in northern Idaho (Amaranthus and others 1996). Similarly, ectomycorrhizal root tip abundance and diversity was reduced on Douglas-fir seedlings in severely compacted soils. These unhealthy soil conditions directly effect forest health and sustainability by directly affecting vital functions of productivity, diversity, and biological activity.

Management activities affect long-term productivity and sustainability of forest ecosystems by altering soil conditions and processes. Where soil health is maintained or improved, productivity potential will be maintained or improved. When soil functions are imbalanced and soil health degraded, plant vigor and productivity is reduced (Waring 1985). Several symposia have addressed relationships between management activities, soil conditions and processes and long-term productivity of Western Montane and Northwest forest ecosystems (Perry and others 1987; Gasboro and Slaughter 1988; Gessel and others 1990; Harvey and Neunschwander 1991). Jurgensen and others (1997) provide a comprehensive and critical review of timber harvesting impact on soil organic matter, nitrogen, productivity and health of Inland Northwest Forests. They conclude that maintenance of adequate soil organic matter levels is critical for sustaining forest health and productivity under the variable soil moisture and temperature conditions of the region. Soil organic matter plays a major role in forest soils and their productivity, activity and diversity and is a major factor in the global carbon cycle (McFee and Kelly 1995). Detrimental displacement, erosion, severe burns, or acidification results in loss of organic matter and nutrients and affects the ability of soils to replace losses because of decreased plant productivity.

Soils vary widely in carbon sequestration processes and magnitudes. Similar variations occur with nutrients, especially nitrogen (table 1). The flow of energy through the soil system is intricately linked with carbon mineralization, or decomposition. Even though many PNW soils have high reservoirs of total N, most PNW forest sites are nitrogen deficient (Chappell and others 1992; Moore and others 1994). However the deficiency often is related to availability rather than total supply. Forest health in Inland Western forests is intricately linked with carbon and nutrient cycling. Constrained cycling, due to fire suppression and increased activities of endemic insects and diseases, are critical factors in these stressed ecosystems (Harvey 1994).

Soil organisms are increasingly the subject of study for their effects on forest soils and forest health. Soils have a high degree of biological diversity (Richards 1987; Allen 1991; Molina and Amaranthus, 1991). A high percentage of all organisms make their home in the soil. There is an evolving body of literature defining ecological linkages between soil processes, plant growth, and community dynamics in the rhizosphere

Table 1 —Classification, depth, organic carbon (OC) and total nitrogen (TN) contents of selected soils in Pacific Northwest ecosystems. Data from National Coop. Soil Survey laboratory characterization. Except, Tolo, Klicker and Helter data from Geist and Strickler 1987).

SECTION[a]	SERIES	SOIL GREAT GRP	FAM PARTICLE SIZE	DEPTH	OC (10^3 kg/ha)	TN (10^2 kg/ha)	MOIST REG	TEMP REG
M242A	KLISTAN	HAPLUDANDS	MEDIAL-SKELETAL	D&VD	318	191	UDIC	MESIC
	SLICKROCK	FULVUDANDS	MEDIAL/LOAMY	VDEEP	806	536	UDIC	MESIC
	BOISTFORT	FULVUDANDS	MEDIAL/CLAYEY	VDEEP	582	233	UDIC	MESIC
	MINGPOINT	HAPLUDANDS	MEDIAL/CLAYEY	VDEEP	521	385	UDIC	ISOMESIC
	SALANDER	FULVUDANDS	MEDIAL	VDEEP	812	323	UDIC	ISOMESIC
	KILCHIS	HAPLUMBREPTS	LOAMY-SKELETAL	SHALLOW	133	122	UDIC	MESIC
	HEMBRE	HAPLUMBREPTS	FINE-LOAMY	DEEP	327	210	UDIC	MESIC
M242B	CINEBAR	HAPLOXARANDS	MEDIAL	VDEEP	269	282	XERIC	MESIC
	COLTER	VITRICRYANDS	ASHY-PUMICEOUS	DEEP	73	72	UDIC	CRYIC
	LASTANCE	HAPLOCRYODS	LOAMY-SKELETAL	D&VD	70	17	UDIC	CRYIC
	ASCHOFF	HAPLUMBREPTS	LOAMY-SKELETAL	VDEEP	90	44	UDIC	MESIC
M242C	LAPINE (PUTR)	VITRICRYANDS	ASHY-PUMICEOUS	VDEEP	42	18	XERIC	CRYIC
	LAPINE (CEVE)	VITRICRYANDS	ASHY-PUMICEOUS	VDEEP	55	24	XERIC	CRYIC
	SHANAHAN	VITRICRYANDS	ASHY/LOAMY	VDEEP	61	23	XERIC	CRYIC
	NARD	HAPLOXERALFS	FINE-LOAMY	DEEP	97	n/a	XERIC	FRIGID
	DESCHUTES	HAPLOXEROLLS	COARSE-LOAMY	MDEEP	37	50	XERIC	MESIC
M261A	JOSEPHINE	HAPLOXERULTS	FINE-LOAMY	DEEP	96	73	XERIC	MESIC
M332G	TOLO	VITRIXERANDS	ASHY/LOAMY	VDEEP	62	38	XERIC	FRIGID
	KLICKER	ARGIXEROLLS	LOAMY-SKELETAL	MDEEP	67	37	XERIC	MESIC
	HELTER	VITRICRYANDS	ASHY/LOAMY	D&VD	124	80	XERIC	CRYIC
	FIVEBIT	HAPLOXEROLLS	LOAMY-SKELETAL	SHALLOW	68	33	XERIC	FRIGID
	LIMBERJIM	UDIVITRANDS	ASHY/LOAMY-SKLTAL	DEEP	57	50	UDIC	FRIGID
M333A	NEVINE	VITRIXERANDS	ASHY/LOAMY-SKLTAL	DEEP	82	47	XERIC	FRIGID
	RATHDRUM	VITRIXERANDS	ASHY	VDEEP	41	18	XERIC	FRIGID

Ref. McNab, W. Henry, and P.E. Avers. 1994.

(Molina and Amaranthus 1991). Mychorrizae affect soil structure by producing humic compounds. Interrupting flow of organic materials to mychorrizae can cause a deterioration in soil structure and aggregate stability, and reduce forest regeneration and root growth (Amaranthus and others 1990). Healthy populations of mychorrizal fungi and other soil microbes are essential for the growth and survival of tree seedlings, particularly on droughty and nutrient-poor sites.

Soil microorganisms play a critical role in the functions of ecosystems. They are particularly important for nutrient and carbon cycling and energy flow, nitrogen fixation, and nutrient and moisture supply through mychorrizal symbiosis (Richards 1987; Amaranthus and others, 1990; Allen 1991: Harvey and others 1994). Habitat provided by variable soil conditions influences the species and populations of soil biota. Significant changes in the habitat from management practices can greatly alter micro flora and fauna species and their abundance (Wells and others 1979; Amaranthus and others 1990; Page-Dumroese and others 1991). Such changes can significantly change the vital soil function of carbon and nutrient storage and cycling with subsequent effects on plant performance (Molina and Amaranthus 1991; Harvey and others 1994: Jurgensen and others 1997).

Soil borne diseases may be increased when soil health is impaired by compaction and changes in soil nutrient and moisture conditions. Wilks and others (1983) reported increases in spread of black stain in ponderosa pine under impaired aeration and high redox potentials. Such conditions can occur from soil compaction. Unpublished surveys and personal observations have revealed black stain in Douglas-fir and in ponderosa pine in compacted soils. Changes in nutrient status, especially nitrogen, may affect incidence of other diseases such as laminated root rot (*Phellinus weirii* (Murr.) Gilb.) Nelson (1975) found lower incidence with high dosages of nitrogen fertilizer. He attributed the results to antagonists of *P. weirii.* Similarly, Mika and others (1992) suggest that stresses from moisture and nutrient deficiencies can result in increased tree mortality from diseases. In particular, tree root chemistry, altered by thinning and N-fertilization, stimulated incidence of Armillaria ostoyae (Entry and others 1991). However, fertilization with potassium resulted in decreased incidence of Armillaria (Moore and others 1994). Thus, nutrient balance is important for maintaining healthy soils and healthy ecosystems.

Watershed Health

Watershed health has a direct linkage with soil health. Hydrologic function and water quality is impaired when soils are compacted and eroded. The literature is replete with studies that document effects from silivicultural practices, land use and fire on soil and water resources (Megahan, 1981; O'Loughlin and Pearce, 1984; Berg, 1988). Practices that significantly decrease infiltration and increase volume and timing of runoff, affect the manner in which water and energy are distributed within a watershed. Such effects can lead to increases in peak flows and accelerated erosion, including gullies and landslides (Swanson and Dyrness 1975; Jones and Grant 1996). When soil compaction exceeds about 12 percent of a watershed, significant changes in peak flows have been reported in Western Oregon (Harr 1976). Accelerated erosion from poorly designed or improperly applied practices decreases water quality and productivity (Megahan 1981; O'Laughlin and Pearce 1984; Berg 1988). Properly functioning watersheds are dependent on properly functioning, healthy soil systems.

The connections between forest and rangeland ecosystems and watersheds are dynamic and complex. They are highly variable in their qualities and in their conditions or health. Fundamentally, all are underlain and regulated largely by the quality and health of the soil ecosystem and its complex, dynamic web of properties, processes and functions.

SOIL QUALITY STANDARDS

It is national Forest Service policy to have soil quality standards to ensure sustainability and long-term productivity of forest ecosystems. Several Regions have developed and implemented standards, or measures, of soil quality since the 1970's. The general concepts and standards are described by (Griffith and others 1990). Specific standards vary by region. The Pacific Northwest Region developed the first comprehensive set of quantitative soil quality standards and a procedure for measuring soil physical conditions. These procedures are described by Meurisse (1988b) and Geist and others (1991). Sullivan (1988) presented some of the most complete data that illustrates the use of the sampling methods and the effects of some management practices on soil conditions. Understanding the role of soils is crucial to understanding stress processes within ecosystems and establishment of measurable soil quality standards is a means of expressing desired soil conditions (Meurisse and Geist 1994).

The most common measures of soil quality used on the National Forests are various physical properties. There are others such as erosion, organic matter, and degree of burning. A general description of the common measures follows.

Physical measures: Bulk density, porosity, soil displacement, infiltration, rutting and puddling.

Erosion measures: These are more indirect and include soil loss tolerance, some specified percentage of topsoil loss, effective soil cover, and some percent of forest floor removal.

Organic matter measures: X percent loss in surface layers, amount of organic matter less than some specified quantity, amount of large woody debris, and large woody debris sufficiency.

Detrimental burning: This is a measure of loss of O horizons and signs of oxidation, change in soil color at the surface together with the next cm depth blackened.

Specific quantitative standards, or thresholds, determine detrimental conditions. The detrimental conditions are presumed to be "unhealthy" soil conditions because they are impaired in their ability to perform one or more of the vital functions. In most cases, functions of concern are productivity and diversity, water quality and changes in water and energy flows, and effects on nutrient and carbon cycles.

SOIL RESILIENCE

The concept of resilience is fundamental to assessing soil quality or soil health. Resilience is particularly important for considering restoration priorities and treatments. Resilience is defined variously as the ability to rebound or recover from some condition or stress. Szabolcs (1994) defines resilience as follows:

$$SR = BC_{ph} + BC_{ch} + BC_{b} + {}_{t1}^{t2}\, dPSF/dt + {}_{t1}^{t2}\, dASF/dt$$

Where: SR = Soil resilience
BC_{ph} = Physical buffering
BC_{ch} = Chemical buffering
Bc_{b} = Biological buffering
PSF = Pedological soil fluxes
ASF = Anthropological soil fluxes

Such an approach to resilience can contribute not only to its interpretation, but to its modelling and estimation through further studies. Because the concept of resilience is crucial to characterization of soil health, interpretations of soil resilience need to be made. Some of the important dynamic factors that contribute to resilience are organic carbon, soil nutrients, especially nitrogen, and soil structure. Other intrinsic properties include moisture and temperature regimes, depth, particle size distribution and permeability. The relative importance of the factors vary depending on whether one is rating for chemical, biological or physical buffering. Thus a soil may have a different rating for physical buffering than for chemical or biological buffering. Soil organisms play crucial roles because of their function in pedoturbation and carbon and nitrogen cycling.

Soil resilience ratings for selected soils from several broad ecoregions are displayed in table 2. Rating classes of very high to low are shown. For chemical and biological buffering, organic carbon and total nitrogen contents are major factors, together with moisture and temperature regimes and soil depth (table 3). Organic carbon, family particle size and moisture and temperature regimes are important criteria for physical buffering (table 4). Because the criteria for chemical, biological and physical buffering include several pedological properties, I considered the buffering ratings to be equivalent to resiliency ratings. These factors that are important for resilience also contribute directly to soil quality.

Table 2—Soil resiliency ratings as a function of chemical/biological and physical buffering, for selected soils in six Pacific Northwest Ecoregions.

SECTION	SERIES	CHEM/BIOLOGICAL	PHYSICAL
M242A	KLISTAN	HIGH	MODERATE
	SLICKROCK	VERY HIGH	VERY HIGH
	BOISTFORT	VERY HIGH	HIGH
	KILCHIS	MOD LOW	LOW
M261A	JOSEPHINE	MODERATE	MODERATE
M242B	LASTANCE	LOW	MOD LOW
	ASCHOFF	MOD LOW	MOD LOW
M242C	LAPINE (PUTR)	LOW	MODERATE
	LAPINE (CEVE)	LOW	MODERATE
	DESCHUTES	MOD LOW	LOW
M332G	TOLO	MOD LOW	HIGH
	KLICKER	MOD LOW	MOD LOW
	HELTER	MODERATE	MODERATE
M333A	NEVINE	MODERATE	MODERATE
	RATHDRUM	MOD LOW	MODERATE

Restoration of stressed sites, and ecosystem processes, is an integral component of sustaining forest ecosystem health (Everett 1994). An understanding of soil resiliency is critical for implementing cost-effective restoration programs. Generally, the most resilient soils are those from the Oregon and Washington Coast Ranges. The most resilient are Andisols (Slickrock, Boistfort), with organic carbon content in excess of 500,000 kg/ha and 30,000 kg/ha total nitrogen (table1). Soils with less than 70,000 kg/ha organic carbon and 5,000kg/ha total nitrogen are rated moderately low oil resiliency is critical for implementing cost-effective restoration programs. Generally, the

Table 3—Resiliency criteria for chemical and biological buffering in selected Pacific Northwest soils.

Rating	OC (thous kg/ha)	TN (thous kg/ha)	Depth Class	Moisture Regime	Temperature Regime
Very High	500 plus	30 plus	D & VD	Udic	Iso-mesic, Mesic
High	200-500	20-30	D & VD	Udic	Iso-mesic, Mesic, Frigid
Moderate	70-200	5-20	MD & D	Xeric/Udic	Mesic, Frigid Cryic
Mod. Low	30-70	3-5	MD & SH	Xeric/Udic	Mesic, Frigid Cryic
Low	< 30	<3	SH & MD	Aridic/Xeric	Cryic/Frigid Mesic

SH = Shallow; MD= Moderatley Deep; D = Deep; VD = Very Deep
0C = Organic Carbon; TN - Total Nitrogen

Table 4—Resiliency criteria for physical buffering in selected Pacific Northwest soils.

Rating	OC (thous kg/ha)	Family Particle Size	Depth Class	Moisture Regime	Temperature Regime
Very High	500 plus	Medial, Loamy Medial/Loamy	D & VD	Udic	Iso-mesic, Mesic
High	200-500	Medial/Clayey Ashy/Loamy	D & VD	Udic	Iso-mesic, Mesic, Frigid
Moderate	70-200	Ashy-Pumiceous Fine-Loamy Ashy/L-Skeletal Medial-Skeletal	MD & D	Xeric/Udic	Mesic, Frigid Cryic
Mod. Low	30-70	Loamy-Skeletal	MD&SH	Xeric/Udic	Mesic, Frigid Cryic
Low	< 30	Skeletal Coarse-Loamy	SH & MD	Xeric/Aridic	Mesic, Cryic

SH = Shallow; MD= Moderatley Deep; D = Deep; VD = Very Deep
OC = Organic Carbon

most resilient soils are those from the Oregon and Washington Coast Ranges. The most resilient are Andisols (Slickrock, Boistfort), with organic carbon content in excess of 500,000 kg/ha and 30,000 kg/ha total nitrogen (table 1). Soils with less than 70,000 kg/ha organic carbon and 5,000 kg/ha total nitrogen are rated moderately low and low for chemical and biological buffering. Some of these same soils, Tolo, Lapine, Helter, Nevine, are rated moderate to high for physical buffering, or resiliency. Priorities for restoration treatments should be based on knowledge of the soil condition and soil resiliency. Those that are most resilient, may recover without costly treatments.

SUMMARY

A key to managing the soil resources to sustain their health, is to have knowledge of the soils and their behavior in response to management practices. This includes having knowledge of pedogenic processes and carrying capacity of the soil. Development of quantitative soil quality standards, assessment of soil health conditions and application of sound management practices is essential for sustainable development and survival of civilizations.

Sustainable, healthy forest and rangeland ecosystems and watersheds are intricately linked with healthy soil conditions. An understanding of the basic soil ecosystem properties and processes, including soil resiliency, is essential to sustaining soil quality and soil health. Life and civilization depends upon sustaining the quality of soils and their ability to perform their vital functions.

QUESTIONS FROM THE SYMPOSIUM FLOOR

Q: Microfauna can survive higher temperatures under dry conditions, then is fall burning preferable to spring burning?

A: Not necessarily. It depends upon the conditions of the soil and organic matter when ignited and it depends on whether or not the burn is within prescription. There simply are too many variables to make a categorical statement that one season is better than another.

Q: What are some field keys to look at in assessing organic matter health for forests?

A: There are several simple keys. (1) Observe the amount and degree of surface soil disturbance relative to the natural condition of similar soils. Make estimates of classes of disturbance based on depth and extent of disturbance. (2) Consider the distribution of surface organic matter (OM). Is the OM uniformly distributed, or is it limited to a few concentrations? (3) Consider whether the amount of OM appears to be within the range of natural variability.

Q: At what point do we become concerned about OM levels of a particular stand?

A: I think that if more than 15% of the mineral soil organic matter is lost, there would be some loss in site productivity. However, this seldom occurs under current management regimes. I think that if surface organic matter, including coarse woody debris, is far outside the range in natural variability for the site, then we should be concerned. Many of our forests have considerably more surface OM than what was present prior to the aggressive fire suppression activity of the past 50 to 75 yrs. But where surface OM is reduced to less than about 10 to 20 T/Ac, some short term reductions in productivity can be expected. We need to know and understand the nature of the soils and vegetation at a given site or stand. But, too often we make broad generalizations that may not be applicable.

Q: Can you discuss "case hardening" of down woody debris (DWD) by fire? Do they decompose faster or slower?

A: Unfortunately, I am aware of no substantive data to answer this question. My observations suggest there is slower decomposition, especially on relatively dry sites common in the Interior Northwest. But I am not sure if the same relationship exists on the very moist West Cascade and Coast Range forests.

Q: Please estimate the fraction of PNW forests (total public and private) that are managed according to systems that have been demonstrated not to cumulatively degrade them.

A: (I assume the question means not to degrade the soils, which may be different from degrading the forest per se). I have no data to make a credible estimate for all forests. I can only make an estimate for the National Forests, and it is only a rough estimate. I believe that more than 90% of westside national forests are managed without measurable soil degradation. On the eastside, where ground impacting equipment is dominant, multiple entries are common, most of the monitoring that is done indicates there is commonly about 20 to more than 30 percent in detrimental condition prior to rehabilitation. Also, there are increasingly frequent wildfires of moderate to high intensity burns that have cumulative adverse impacts. There is a lot of rehabilitation on national forests, so the cumulative effect of actively managed forests, probably is less than 20% degraded.

Q: Do you think the role of soils and biological activity would receive more attention if there was a Clean Soil Act-like Clean Water Act & Clean Air Act?

A: It probably would increase attention to the soil resource, including soil biology. There has been some discussion of promoting a Soil Quality Act, but it hasn't progressed very far.

Q: Background: An eastside pine community, low to mod. site; burned during Aug. 1994 - moderate to high intensity; no burned area emergency rehab. Grass seeding the next summer; several high intensity summer thundershowers mobilized 0.5 - 6 inches of soil. The area was salvage logged during summer of 95 & 96. Replanting took place in Spring of 96 & 97. The current proposal is to decrease shrub competition by 100% herbicide application. What are the implications of the herbicide proposal to soil ecosystem? What are the cumulative effects to the soil ecosystem?

A: My initial answer is "I don't know." But, based on what is emerging from levels of growing stock studies at Pringle Falls Experimental Forest, removal of shrub understory, regardless of whether it is done mechanically or with herbicides, may have some long-term adverse affects on stand productivity. Also, some of the shrubs likely are N-fixing species that would normally add replacement nitrogen to the site that may have been lost in the fire. Herbicide effects on soil organisms probably would be short term and of low significance. Further, loss of 0.5 to 6 inches of soil over areas larger than 100 $ft.^2$ probably would have significant detrimental effects. So, I would expect some measurable, cumulative adverse effects under this scenario.

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SOIL-DWELLING ARTHROPODS: THEIR DIVERSITY AND FUNCTIONAL ROLES

Andrew R. Moldenke[1]

ABSTRACT

Soil-dwelling arthropods are extremely diverse and abundant. Northwest forest soils may support an average of 250,000/m^2. Knowledge of functional roles within the soil ecosystem is limited. Some of the prominent functional groups are fungivores, micro-predators, macro-predators, and shredders.

Soil food webs involve complex functions and the basic structure requires a minimum of four components. These components are (1) the living plant root, (2) soil bacteria and fungi, (3) fauna that graze on microbial biomes, and (4) predator fauna. Some critical environmental determinants for ensuring persistence of functional links are described. Three categories of determinants are epigeic habitats, soil surface phenomena, and hypogeic habitats.

Keywords: arthropods, keystone species, fungivores, predators, shredders, nutrient cycling, food web, epigeic habitats, hypogeic habitats

INTRODUCTION

The majority of the world's arthropods live within the soil (Southwood 1978). The vast majority of all animal life are species of arthropods (Wilson 1992). This amounts to a fabulously rich soil fauna in all terrestrial ecosystems (Petersen and Luxton 1982). In the forests of the western United States there may be as many as several hundred species of arthropods (insects, mites, spiders, centipedes, millipedes, skunk-spiders, and their relatives) in every square meter of soil (Moldenke personal observation). The identity and relative abundance of these myriad creatures vary in response to every climatic microhabitat. Thus, the species richness encompassed within several square miles is at least several thousand (Parsons and others 1991). The great majority of these species are widespread geographically, inhabiting territory encompassing thousands to tens of thousands of square miles. If we assume that these species could not coexist unless several aspects of their biological functions were unique, then the roles these creatures play must be remarkably diverse (Moldenke and others 1994).

Not only are soil arthropods diverse, but they are numerically significant as well. A single square meter of Northwest forest soil may support an average of 250,000 arthropods (Moldenke 1990). The most numerous are the turtle-mites (perhaps 100-150,000/square meter) and springtails (50-100,000/square meter)(Petersen and Luxton 1982). All of these small creatures sum to a significant biomass. The length of adult turtle-mites span the range from only 100-1200 microns, averaging about 300 microns; however the living biomass of the turtle-mites alone in a Northwest conifer forest soil is equivalent to 156 entomologists per square mile (Moldenke 1989). Nearly all of the species of vertebrates inhabiting the Pacific Northwest derive a significant portion (or all) of their nutrition from arthropods (yes, even spotted owls do too; Meslow personal communication). Even though abundance, diversity and biomass of arthropods are high, it is quite likely that food limitation is a significant limiting factor for many vertebrates. Not all invertebrate species are alike in nutritive value, and few are easy to capture. During any given season, the majority of the diets of most vertebrates are probably confined to a very restricted list of arthropod taxa. As entomologists, wildlife ecologists and land managers, we know very little specific information about the diet of "insectivorous vertebrates." Many of the "sensitive " and "endangered" taxa are largely insectivorous; to manage them effectively we need to know what they consume.

Due to both the exceptional abundance and high diversity of arthropods, it is probably safe to assume that there is no ecological process in which numerous arthropods do not play a significant role. All too frequently, theoretical "process-centered" ecological discussions degrade into whether species A "regulates/drives" species B, or B "regulates" A. In the real world, both species A and species B are co-dependent and neither is likely to function normally without the other. This is especially important for "ecosystem managers" to comprehend, since the

Andrew Moldenke is Research Associate in Entomology, Department of Entomology, Oregon State University, Corvallis, OR 97331

nature of nearly all real-life processes are better represented as complex food-webs rather than as simple food-chains.

We could theoretically simplify the forest entomologist's realm by stating that: a) Douglas-fir needles fix carbon by photosynthesis; b) these needles are fed upon by sucking insects (aphids) or chewing insects (caterpillars); c) these caterpillars and aphids are fed upon by small insect predators (lady beetles and ichneumon wasps); d) these predators, in turn, are fed upon by thrushes; e) which are in turn fed upon by small hawks, etc., etc. [the classical food-chain model]. But, even when a single herbivore species is pre-eminently abundant (i.e., the Douglas-fir tussock-moth), feeding relations are extremely complex. Studies by Fichter (1984) have shown that: 1) under most non-outbreak conditions, arthropod predation is sufficient to keep significant persistent populations of the pest in check; 2) that control is exerted by a diversity of predators; and 3) that it is the *diversity,* itself, which is most significant, not the individual species of predators. For instance: first instar caterpillars are consumed primarily by orb-web spinning spiders which intercept the wind-dispersed larvae; by day, larger caterpillars are captured as they feed by sit-and-wait crab spiders and, as they locomote, by visual-pursuit jumping spiders; by night, the active hunting *Anyphaena* spiders and the concealed pouncing gnaphosid spiders exact a toll. Even larger caterpillars disperse to lower branches to feed and are intercepted by the sheet-web spiders. Any one form of predation is insufficient to control populations; loss of any hunting strategy would allow the tussock-moth to escape in either space or time and for populations to increase dramatically. It takes a diversity of hunting strategies to achieve "control".

Entomologists have a limited knowledge of the functional roles of soil-dwelling arthropods. We lump them into diverse groups, such as: fungivores, micro-predators, macro-predators, shredders, etc. This categorization, overly simplified by the abysmal lack of knowledge about their behavior and functional linkages within the soil ecosystem, leads to the logical questioning "Well, if so many species all do this same thing (i.e., fungivory), aren't they 'redundant'? Couldn't the ecosystem function just as well without large numbers of these species?"

I can't answer this question because: 1) this redundancy is largely artifactual, caused by scientists' lack of knowledge; and 2) the "redundancy" of, say, fungal-feeding arthropods is closely tied to the "redundancy" of soil-dwelling fungi. Tiedge (1994) estimates there may be as many as 40,000 species of bacteria and fungi in a single teaspoon of forest soil. The more silviculturists study the symbiotic mycorrhizal fungi, the more they are convinced that diversity is necessary for forest health (Trappe 1977; Molina and others 1982; Amaranthus and Perry 1989). Numerous investigations have shown the positive feedback between diverse fungivores and the diversity of the fungus community (Newell 1984; Visser 1985; Mitchell and Parkinson 1976). It is greatly upsetting for a scientist to say that we don't understand the significance of diversity, but that we "believe" it is important. But in 1998, that is primarily the case. We know that an attribute of all natural ecosystems is high species diversity, and that the attribute of all "efficient" arthropogenic systems is species-reduction. As scientists, we hedge and say that in some way high species richness confers long-term stability on the ecosystem. But, we don't as yet understand the complex values of biodiversity.

In the event that loss of a single species from a complex ecosystem engenders an unexpectedly large system-wide effect, ecologists hold that such is not the usual case and they coin the expression "keystone species" to emphasize the uniqueness of species with such system-wide importance. There is no way to determine how many keystone species inhabit a given environment. There may be many; there may be few. Only the loss of one (or more) will tell. As Aldo Leopold (1987) says, "The intelligent tinkerer keeps all the parts."

THE CAST OF CHARACTERS

Fungivores

Turtle-mites (Oribatida or Cryptostigmata; fig. 1) are major elements of soil fauna worldwide, but nowhere more so than in the temperate conifer forests (Petersen and Luxton 1982). Most species possess an extremely impenetrable exoskeleton as adults, and like turtles have forsaken speed and agility as an escape strategy. There may be as many as 4 to 6 dozen species in a square meter of forest soil (Moldenke 1989). Historically, most have been described as generalist fungivores. Rearing experiments by Mitchell and Parkinson (1976) revealed that individual cohabiting species prefer different species of fungi, and more recent studies on gut enzymes reveal that some species gain nutrition primarily from the plant matter in their diets, some from the fungus matter, and some from a mixture of both (Seipel and de Ruiter-Dijkman 1993). The composition of the liquid diet of the more primitive species is not known, nor is the degree to which some species feed upon other arthropods (Moldenke and others 1998).

The commonest turtle-mites around the world are in the genus *Oppiella.* Studies by Stefaniak and Senizak (1978) upon their feeding biology are relevant to the

Figure 1 —A fungivorous turtle-mite, *Belba.* Mites have 4 pairs of legs. This species carries its former shed skins (4) on top of its back.

discussion of species redundancy. Stefaniak and Senizak found that *Oppiella* feed upon a number of fungi in the environment, but that they consistently refused to eat four species and would choose to starve to death in their presence rather than consume them. They would feed upon several other species, not eagerly, but the fungi could sustain their growth. Several others would be fed upon eagerly, the mites could mature, but no viable eggs could be laid (and length of time required for maturation was prolonged an additional 25-50%). Only three individual species, of all the ones tested, were able to sustain both growth and reproduction. In the soil, rather than a Petri-plate, turtle-mites probably never encounter enough of a single species of fungus to feed upon for their life span (from 1 to 12 months), so they are continually forced to prune whatever is available. Judging from Stefaniack and Senizak's experiments, most of what turtle-mites find is barely capable of maintaining them. Soil is filled with fungi, but through the evolutionary miracle of biodiversity, each fungivore finds the various fungus species differentially appetizing.

Springtails (Collembola; fig. 2) are the most universal of all the soil arthropods, living even in Antarctica and the snowfields of Mt. Everest (Hopkin 1997). Their name derives from the appendage at the rear of the body, which is held doubled-back under the abdomen during normal activity. Since springtails have an exoskeleton, they are able to achieve a heightened blood pressure by contracting the major longitudinal body musculature (similar to filling a balloon with air). When threatened by a predator, they release a forceps-like tail-retainer under their abdomen. Blood instantly rushes into the base of the tail, which is now free to expand, and the tail pushes off the ground, catapulting the springtail into the air. A springtail can jump 20 to 100 times its body length.

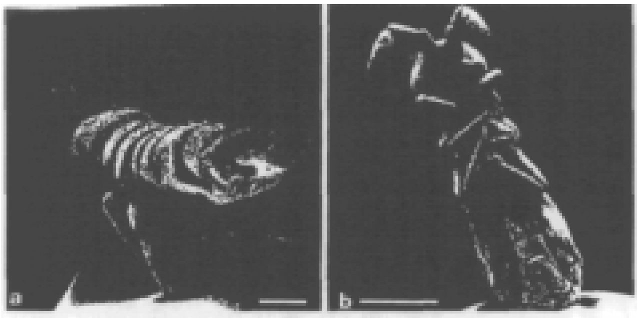

Figure 2-A fungivorous springtail, *Isotoma.* Springtails have 3 pairs of legs and antennae. At the rear of the body is a forked appendage normally retained under the abdomen (2b). Blood pressure, kept extremely high during normal foraging, can flood into the base of the tail and extend the Y-shaped appendage. When this occurs the tail is slapped onto the surface of the ground and the springtail is catapulted through the air and away from potential enemies.

Kilbertius and Vannier (1981) documented the most impressive significance of these tiny creatures (1-5 mm) in the oak forests of Europe. *Tomocerus* springtails (which also live in the oak forests of the Pacific Northwest) are keystone species that regulate the rate of leaf decomposition. Oak leaves (living or dead) are filled with a highly reactive chemical (i.e., phenol) which prevents most caterpillars from damaging the living oak leaves. This chemical also prevents arthropod shredders from crushing the dead plant cells into units that expose the nutrients for microbial decay. *Tomocerus* can overcome this chemical deterrent by filling its digestive system with inorganic clay particles, before ingesting the oak leaves. The cation exchange capacity of the clay prevents the phenols from polymerizing and impeding digestion. After passing through the digestive system of the *Tomocerus,* the phenol remains detoxified in the feces. The detoxified feces are then available for exploitation by all the rest of the diverse soil fauna, which would otherwise be unable to recycle the nutrients in the forest litter. This detoxified and efficient nutrient recycling by *Tomocerus* permits oak trees on clay soils to be tall and robust, but oaks on sandy soil are forced to be shrubby and stunted.

Predators

Pseudoscorpions (Chelonethida; fig, 3) are abundant predators in all soil habitats (Weygoldt 1969). They have the general body form of a scorpion, to which they are not related, but without the tail and its terminal sting. The pseudoscorpion's sting is in the thumb of their large pincers. Though generally only 1/10-1/4 of an inch in length, their venom is sufficient to kill all but the largest insect prey. There are several dozen species of pseudoscorpions in the Pacific Northwest, some of which habitually move long distances by hitching rides on winged insects. Though diminutive, these efficient predators display complex behavior associated with mating and rearing their young.

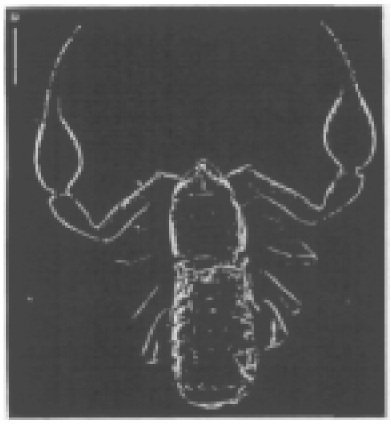

Figure 3-A pseudoscorpion has 5 pair of legs, with the first pair modified into lobster-shaped capture devices. Pseudoscorpions usually grow to 0.1-0.4 inches in length.

Predacious mites (Gamasida; fig. 4) are the most abundant arthropod predators. There are probably several thousand gamasid mites in each square meter of Northwest forest soil, less in the basin rangelands. Gamasid mites (as well as psuedoscorpions) seem to be particularly sensitive to human-caused disturbances. Augmentation of gamasid and other predatory mites to control agricultural pests has been a boom industry in the past twenty years. Though most effective against herbivorous mite species, individual predacious mites are often capable of killing large caterpillars as well. Most groups of predaceous mites are agile, fast moving and bright red to reddish-tan in color.

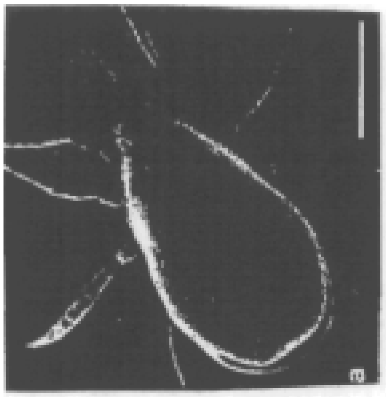

Figure 4-Predaceous gamasid mites are capable of rapid motion. They kill their prey with poison secreted in small scissor-shaped appendages at the front of the body.

Ants (Formicidae; fig. 5), though primarily predators, perform a wide variety of ecosystem functions. Their composite effect on aeration and water infiltration of compacted soils is unparalleled. During the period of maximum brood rearing, their predatory vacuuming of the environment may extend for 100m from the central burrow. Many species supplement their diet with flower nectar and aphid honeydew, which they obtain by tapping their "aphid-cows" with their antennae. In the Great Basin, the most conspicuous ants *(Pogonomyrmex)* harvest the seeds of plants; the dense abundance of ants and the rank preference order for seeds of different species shapes the vegetative community of annual plants.

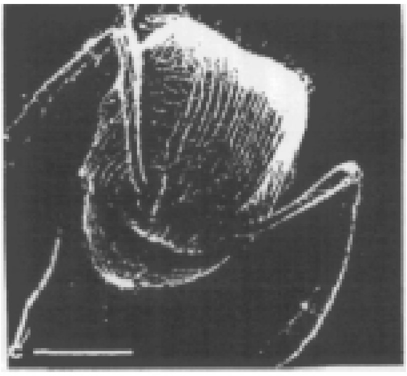

Figure 5-The face of an ant. Most ants are efficient predators.

Shredders

The shredders of the soil ecosystem initiate the process of nutrient recycling. Shredders come in a variety of sizes (macroshredders—millipedes; mesoshredders - sciarid gnats; and microshredders—penknife turtle-mites; fig. 6). Most shredders consume fallen leaves, but the native sowbug *(Ligidium gracile)* consumes the final stages of class V log decay (Moldenke personal observation). By crushing intact plant cells, a millipede has been documented to increase the surface area availability for microbial enzyme attack 10,000 fold (Camatini 1979). The cyanide-producing millipede *(Harpaphe haydeniana)* is the most critical shredder on the west side of the Cascade Mountains (Moldenke 1984); it is 1 % to 2 inches long and black with a lateral pair of red to yellow stripes. The odor of roasted almonds that it produces when captured by hand is hydrogen cyanide gas, perhaps the most efficient metabolic poison known; as a consequence, it is nearly immune from predation (except for one species of beetle, *Promecognathus laevissimus;* fig. 7). The presence or absence of shredders in the soil can alter the total overall rate of nutrient mineralization by ten-fold, and the growth of tree seedlings by four-fold (Anderson and others 1985).

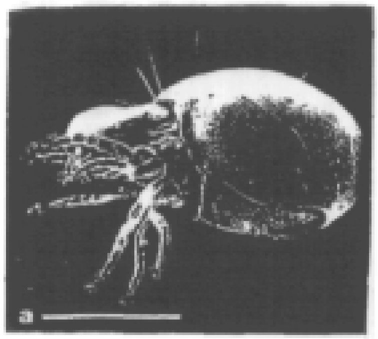

Figure 6-The micro-shredder penknife-mite, *Phthiracarus.* When threatened by a predator the mite can retract its head and all 4 pair of legs into its posterior "shell," covering all the tender structures with the flat plate seen over the head.

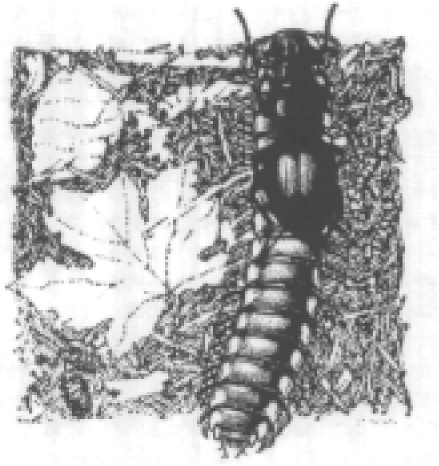

Figure 7-The macroshredder millipede, *Harpaphe* haydeniana and its specialist-feeding predator, the groundbeetle *Promecognathus laevissimus.*

SOIL FOOD WEBS

The Functioning of the Soil Food Web

The basic structure of all natural soil food webs requires a minimum of four components; (1) the living plant root, which is incapable of enzyme production, but obtains nutrients for the plant passively through water absorption; (2) the soil bacteria and fungi, which are in most circumstances fuel (carbohydrate)-limited, but are capable of a bewildering diversity of degradative enzymatic decomposition processes; (3) the fauna which graze upon the microbial biomass, thereby releasing, as part of their waste products, water-soluble (and hence "useful") forms of plant nutrients; and (4) the predator fauna which keep the population of microbial grazers below levels which might limit the microbes in their pivotal role as the "biological sponge" which prevents loss of nutrients from an ecosystem.

This cycle of growth and decomposition is driven by photosynthesis. Plants send from 25 to 50% of the carbon fixed by photosynthesis directly to the roots to be excreted in order to facilitate microbial growth. This fuel is shared with both specific symbiotic fungi (mycorrhizae) and the general microbial population of the rhizosphere (the volume of soil within 1-2 mm of a living root tip). Bacteria are important as local foci of intense metabolic activity on a scale of several millionths of a pinch of soil. Fungi are capable of slower metabolic activity, but because their basic body form, similar to a railroad system, allows the simultaneous exploitation of widely spaced, yet different, required nutrients, activity can be maintained continually. Both bacteria and fungi are relatively incapable of movement; they require insects and other arthropods to bring them to sites of new resources or to physically mix the resources currently available. Arthropods which graze upon the fungi are seldom able to consume them entirely, resulting in stimulation of rapid regrowth (like a cow in a pasture). The result of all of this microbial growth is the immobilization of nutrients into living biomass. The long-term health of any ecosystem is intimately dependent upon minimizing the rate of nutrient loss; the greater the biomass of soil microbes, the slower the rate of nutrient loss. The decrease in soil organic matter (both living and dead) is a major factor leading to chemical pollution in waterways in the United States.

The grazing by soil fauna leads to momentary availability of soluble nutrients for two reasons. (1) The ratio of carbon to nitrogen in the tissues of bacteria and fungi is less than that of animals. As a consequence, an organism feeding on a bacterium or fungus must excrete any nitrogen in excess of its own requirements (or become poisoned by it). (2) As an animal locomotes in search of food, it burns (respires) carbohydrates for energy. As CO_2 leaves the body, other nutrients (nitrogen, etc.) must leave it as well in order to maintain the ratio within living cells. Any nutrient release by the fauna is immediately recaptured by microbes in their vicinity, unless the release is close enough to a root to be swept into the plant by the inward rush of water caused by transpiration from the leaves. Since most faunal activity is within the rhizosphere, faunal activity does result in nutrient uptake (but only when the stomata are open).

Soil is physically and chemically diverse at the scale of microbes and arthropods. The movement of arthropods aerates the soil and transports microbial inocula. Microbial diversity, though fundamental, is difficult to measure. Arthropod diversity is far easier to monitor and is likely to reflect microbial diversity. Soil degradation is associated with a decrease in soil fauna diversity. Some forms of degradation are more easily measured structurally or physically, for instance the depth of litter or the resistance to a penetrometer. But complex chemical changes may best be monitored through arthropod biodiversity. Any change in invertebrate diversity should be interpreted not just in isolation, but as an integral part of the basic functioning of the soil foodweb, which supports all plant life.

Management Considerations

A generalized foodweb of the diversity of soil- and litter-associated invertebrates is represented in figure 8. There are indistinct boundaries on the definition of soil-associated arthropods; the herbivorous fauna on the grass, forb and sometimes shrubby vegetation is a major component of the food resource of epigeic macropredators. Though many invertebrate predators (i.e., *Calosoma sycophanta)* routinely ascend tall trees to hunt, they represent exceptions and are not considered in this discussion. Far more important, are all the species of truly arboreal herbivores, which descend to the ground to pupate. Such "amphibious" species not only provide food resources to soil-dwelling predators, but they represent important additional linkages between potential canopy health and prescribed burning protocols.

The actual dynamics of the soil foodweb in any Pacific Northwest community is far more complex than the one outlined in figure 8. The foodweb structures among differing community types (forest, desert, grassland) are likely to differ significantly, both in terms of the relative sizes of the boxes and the rates of energy flow between them. No foodweb analysis of invertebrates has ever been attempted in the Pacific Northwest on other than a very generalized basis, figure 8 represents: (1) a structure into which most communities can be accommodated; and (2) a structure which is adapted for invertebrate bio-indicator use.

The biomass of organisms high in the trophic pyramid is relatively insensitive to shifts in species composition of the lowest trophic levels and is theoretically sensitive only to the total primary production of the ecosystem. However, the species comprising the higher levels of the trophic pyramid are very sensitive to changes in management policies. To understand whether management practices will affect community structure, it is necessary to differentiate the producer biomass into the separate components within column I and to quantify how efficiently this biomass is transformed into column II. The majority of the biomass and species richness of any community is contained within column II. Any (and perhaps, every) major change in management policy will alter the percentages of biomass between boxes within column I, and consequently within column II as well. Such changes are not necessarily "bad", but it is important to recognize such a change (and quantify it) when it occurs. The organisms within column II are the engines that drive these 20 separate functions within an ecosystem. In general, increases either in the biomass of resources or their spatial heterogeneity will favor increased species richness.

The farther to the right one proceeds in figure 8, the larger the individual organisms become and the easier they are to collect and monitor. However, the further to the right one proceeds, the lower is the species richness and the more generalized is the behavior (and therefore the less useful it is at indicating basic changes in energy functioning within the ecosystem).

There are far more than 10,000 species of arthropods (though many of them do not even have scientific names yet) within the Pacific Northwest. Though the specific identity of the members of any one box in figure 8 will vary between community types and between sites, at the family-level of taxonomic resolution there is considerable consistency. I present the taxa in table 1, as a checklist for comparing different sites. This list is certainly not all-inclusive, but it attempts to encompass the great majority of arthropod taxa found associated with the soils of the Pacific Northwest. It is not yet possible to try to enumerate all the species of arthropods at any one site, but it is certainly logistically practical to monitor several of the component groups when most of the species are collected in a particular trapping system. For instance, epigeic macropredators, macroherbivores and macrodetritivores can be collected in pitfall traps and compared between treatments. The trapped specimens can be weighed to get an estimate of biomass, and morphospecies analysis of the component groups can indicate significant changes in species richness.
These taxa are listed in the table, not as an attempt to facilitate another one-species-at-a-time "bologna" approach to conservation/monitoring, but rather as an educational device. Most ecosystem managers are unaware of the functional roles played by invertebrates, and even if they are aware of the roles, they have never learned who does what. If we are serious about managing our natural resources for the long-term, then we have to ensure the persistence of all the functional links in the community.

CRITICAL ENVIRONMENTAL DETERMINANTS

I have grouped the critical environmental determinants into three categories to fit with figure 8: epigeic habitats, soil surface, and hypogeic habitats.

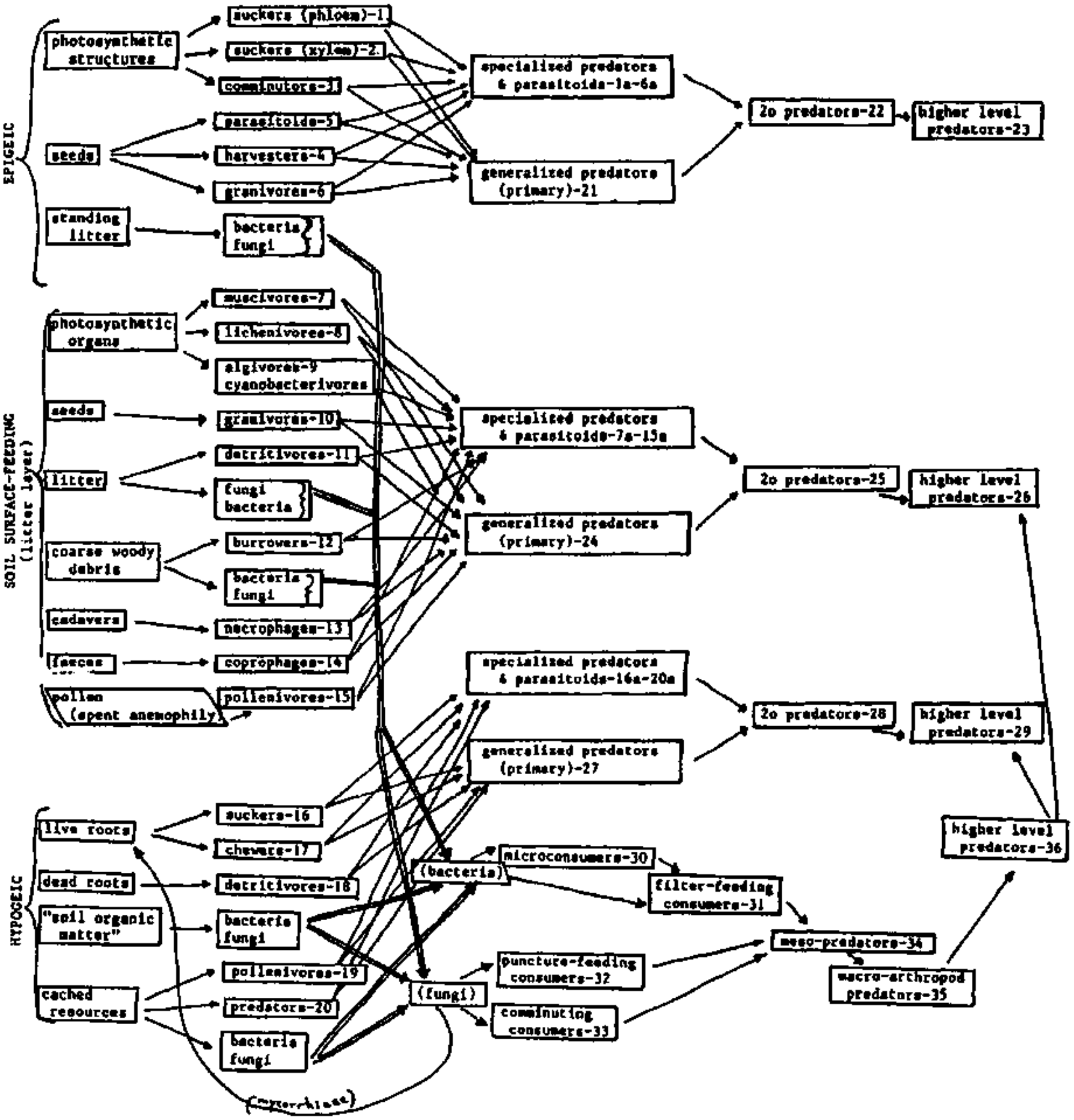

Figure 8-Structure of the invertebrates in a typical soil foodweb. The numbers in the boxes refer to the taxa in table 1. The arrows represent the pattern of energy flow (food intake) within the community.

Table 1 —The usual components of the soil foodweb in nearly all ecosystems. Taxonomic names ending with -idae are family level groupings.

EPIGEIC

1- phloem suckers
Aphidae +

1a- Coccinellidae
Nabidae

2- xylem suckers
Cicadelloidea
Fulgoroidea

2a- Strepsiptera (pt)

3- cominutors
Acridoidea
Tettigonioidea
Grylloidea
Noctuoidea +
Mollusca
Sminthuroidea

3a- Trombidiidae
Ichneumonidae
Sphecoidea
Anconema (Mollusca)
Aeliothripidae +

4- seed harvestors
Pogonomyrmex
Pheidole

5- seed "parasitoids"
Eurytomidae
Curculionidae
Bruchidae

5a- Euryopis
Myrmeliontidae

6- granivores
Lygaeidae
Harpalinae+

SURFACE DWELLING

7- muscivores
Endeostigmata (pt)
Byrridae
Tingidae (pt)
Boreidae

8- lichenivores
Polyxenes
Machilida
Oribatida (pt)

9- algivores/cyanobacterivores
Endeostigmata (pt)
Liposcelidae
Nematoda (pt)

10. granivores
Lygaeidae
Tenebrionidae
Silvanidae
Ptinidae
Dermestidae

11.- detritivores
Isoptera (pt)
Tenebrionidae
Ptyctimina
Diplopoda
Raphidiphorinae?
Isopoda
Camptosomata (pt)

11a-Promecognathus
Zarhipis
Trombidiidae
Lampyridae?

12- CWD burrowers
a) Isoptera
b) Scolytidae
c) Cerambycidae
Buprestidae
Kylophagidae
Anobiidae
Bostrichidae
d) Camponotus

12a-Stephaniidae
Orussidae
Cleridae
Cucujidae
Ostomidae
Histeridae (pt)

13- necrophages
(Including 2o predators on
bacteria/nematodes/etc)
Histeridae
Silphidae
Hydrophilidae (pt)
Staphylinidae (pt)
Dermestidae
Tineidae
Muscoidea
Trogidae
Phoridae

14- coprophages
Scarabaeidae (pt)
Muscoidea
Scatophagidae
Silphidae (pt)
Leiodidae
Hydrophilidae (pt)

15- pollenivores
Collembola
Oribatida (pt)
Anthicidae?

HYPOGEIC

16- root suckers
Cicadidae
Cydnidae
Eriococcidae (pt)
Ortheziidae+
Tylenchida+

17- root chewers
Grylloyalpidae
Stenopelmatidae
Curculionidae
Scarabaeidae (pt)
Elateridae
Chrysomelidae
Hepialidae
Pyralidae
Symphyla (pt)

17a-Tiphiidae
Scoliidae

18- root detritivores
Curculionidae
Tipulidae
Elateridae
Tenebrionidae
Oligochaeta

19- pollen cachers
Apoidea

19a-Meloidae
Strepsiptera
Bombyliidae

20- cadaver cachers
Sphecoidea
Pompilidae

21- primary predators
    Aranae (pt)
    Formicidae
    Vespidae
    Geocoris
    Nabidae
    Reduviidae
    Carabidae (pt)
    Cantharidae

22- secondary predators
    Araneae (most)
    formicid colonies
    vertebrates

23- higher level predators
    vertebrates

24- primary predators
    Formicidae
    Carabidae
    Staphylinidae
    Sphecidae
    Chilopoda
    Araneae
    Phalangida
    Acarina (pt)
    Panorpidae

25- secondary predators
    Araneae (large spp)
      Gnaphosidae
      Antrodiaetidae
      Agelenidae
      Lycosidae
    Lithobiomorpha
    Scorpionida
    Solifugida
    vertebrates
      Flicker
    formicid colonies

26- higher level predators
    vertebrates
    shrews
    lizards
    birds

27- primary predators
    Formicidae
    Geophilimorpha
    vertebrates

28- secondary predators
    Formicidae
    Geophilimorpha
    Diplura-Japygidae

29- primary predators
    Formicidae
    Geophilimorpha
    Diplura-Japygidae

30- secondary predators
    Formicidae
    Geophilimorpha
    vertebrates

31- higher level predators
    vertebrates
      Talpidae

32- microconsumers
    Protozoa
      Amoebae
      Ciliates

33- filter-feeding consumers
    Rhabditoidea
    Rotifera

34- puncture-feeders
    Tylenchida +
    Protozoa (pt)

35- comminuting consumers
    Oribatida
    Endeostigmatida (pt)
    Collembola

36- meso-predators
    Tardigrada
    Mononchida
    Gamasida
    Endeostigmata (pt)

37- larger meso-predators
    Gamasida
    Endeostigmata (pt)
    Micryphantidae
    Scydmaenidae
    Pselaphidae
    Pseudoscorpionida
    Geocoris
    Rhaphidoptera
    Staphylinidae
      Aleocharinae +
    Throscidae
    Palpigrada
    Notiophilus/Leistus

38- larger comminutors
    Mycetophilidae
    Sciaridae
    Cecidomyiidae
    Phoridae
    Drosophilidae
    Protura
    Campodeidae?
    Thysanura?
    Thysanoptera
    Staphylinidae (pt)
    Ptiliidae
    Scaphidiidae
    Cisidae
    Derodontidae
    Nitidulidae
    Endomychididae

39- macroarthropod predators
    Formicidae
    Chilopoda
    Vespidae
    Pompilidae
    Sphecidae
    Reduviidae
    Thysanoptera (pt)
    Nabidae
    Carabidae
    Cicindelidae
    Staphylinidae
    Cantharidae
    Mydaeidae
    Phalangida Araneae

Epigeic Habitats

Grazing—In general, any photosynthetic structures that end up in the stomach of a vertebrate grazer are subtracted from the resource base for invertebrates. A reduction in grazing by mammals will also increase habitat structure and refugia.

Drought—Precipitation is generally highly unpredictable. Total annual precipitation coupled with periodicity determines gross primary productivity in large part.

Habitat Refugia—Every species requires refugia of some sort; the more numerous and diverse the potential refugia, the more individuals and species will prosper. Litter depth and coarse woody debris are often cited as examples of refugia.

Soil Surface Phenomena

Surface compaction/cementation—Any change leading to a decreased ability of the fauna to pass through the boundary layer or a decreased infiltration of precipitation is generally detrimental. In many arid environments a cyanobacterial crust (see Belknap, this volume) forms on the surface of the soil. The relationship that this crust has on the total community is unclear; one would expect it to facilitate faunal diversity due both to its nutrient biomass and ability to absorb water.

Litter depth—In forest environments the litter layer is apparently positively correlated with increased density and diversity (Madson 1998). Litter serves as both a food source and in a three-dimensional habitat capacity. In scrublands a definitive litter layer is generally absent, but individual detrital pieces are the center of soil invertebrate activity, especially after they are anchored in place by fungal hyphae and are no longer subject to wind displacement. Early in the morning vertical migration of the microfauna creates an evanescent hot spot of activity within the litter (Wallwork 1970).

Erosion—In forest environments erosion is promoted principally by fire. However, on steep slopes within semi-arid forests, the passage of mammals (cows, deer, man) can also seriously disrupt the fragile litter layer. Under circumstances in which nutrients are limiting, the continual flux of recyclable litter and nutrient-rich topsoil downslope is likely to pose a serious stress to upland vegetation. In the scrublands, erosion (both wind and surface rainwater) is accelerated by any disturbance of the surface layer; the most usual form of disturbance is by mammalian passage.

Condensation/seasonality— For much of the year many of these surface soil microenvironments are severely limited by water; the only reliable source of water is dew formation. Any physical or chemical attributes of the soil surface that promote condensation should be encouraged.

Habitat refugia—In any region, other than the more mesic forests, a premium must exist on physical means that promote vertical circadian migration patterns. In forested systems, consolidated clay soils are frequent, which limits vertical movement to those few taxa that have the actual ability to burrow, or to those fauna that can utilize the burrows created by other species. Very few soil invertebrates are physiologically capable of true burrowing; most of them, such as anecic earthworms and geophilomorph centipedes are absent from drier soils. Cicadas, millipedes, gryllotalpids and stenopelmatids may exercise "ecosystem engineer" keystone roles in these environments. In unconsolidated desert soils, true burrowing is not required and many/most taxa may be able to bury themselves sufficiently to prevent dessication.

Fire, the ultimate consumer of resources—For dominant "climax" organisms, most effects of fire must be detrimental. Historically there were probably a number of beneficial effects upon the subdominant and early successional taxa, as there clearly are in the grassland/savanna biomes worldwide. The multitudinous roles of fire in Pacific Northwest forest and desert communities have never been examined with respect to their effects on upon non-pestiferous invertebrates. Any features of a fire protocol that increases heterogeneity and promotes islands of unburned soil surface will minimize the detrimental effects of fire.

Hypogeic Functions

Water-holding capacity—In most of these environments anything that favors infiltration and deep water-holding capacity is paramount. Most of these variables are long-term soil genesis properties that are liable to remain the same under different management scenarios. Though coarse woody debris acts as a sponge anywhere in the soil profile, it probably has its greatest hydrating potential below the surface layers. Stumps, with their vascular bundles oriented to facilitate upwards water flow, may not be as useful in retaining water below-ground as an equivalent amount of coarse woody debris oriented parallel to the surface.

True deep-burrowing—Vertebrate burrows within the mineral soil are probably an important resource (both occupied and unoccupied burrows) in all ecosystems as they are in the well-publicized Florida sand pinelands (Myers 1985). There must be numerous inquiline and accidental "guests", that require such borrows for persistence in the community. The percentage of the fauna dependent upon vertebrate burrows probably increases with aridity. Classic studies by Ehrlich and others, have shown the population density of the *Euphydryas* butterfly to be largely controlled by the populations of gophers, whose burrowing activity alters host-plant phenology, permitting caterpillars to reach a threshold body weight before aestivating. Community-wide effects of mammal burrowing are also documented in many temperate communities in which bumblebees are the major pollinators; bumblebees require abandoned burrowing-mammal nest chambers in which to establish their colonies in the spring.

Deep soil compaction (through overgrazing or mechanized vehicle use)—This is probably the ultimate threat in any environment, since as far as I know it is biologically irreversible. It creates an abiotic environment and potentially permanently immobilizes resources within it.

CONCLUSION

Many of a land manager's concerns are biologic - the growth of trees, the yield of cattle. However, the inorganic aspects of soil have always been seen as critical determinants. But soil ecologists now realize that the biologic aspects of soils are perhaps even more important. This realization has been driven largely by the perceived changes in soil properties of agricultural soils. Maintenance of the diversity and integrity of a complex soil foodweb appears to be critical, in many ways that are currently without adequate scientific explanation.

The biodiversity within our Northwest soils is miraculous. I personally have witnessed degradation of forest and rangeland soils in numerous parts of North and South America, all instances associated with a synchronous depletion of soil arthropod diversity as well. Before we can fully understand the multitudinous functions carried out by these diverse creatures, we need to know more about our native fauna. Basic descriptive natural history precedes analytic interpretation. *One purpose of this symposium is to stimulate land managers region-wide to become involved in this basic learning process.*

The interpretation of basic descriptive data is enhanced by the utilization of similar procedures and similar sample designs region-wide. The development of user-friendly data archiving and interpretive literature is also critical. Funding for the study of arthropods and their roles in soil processes will never be more than a few percent of the funds devoted to owls, salmon, and other charismatic megafauna. Due to these funding limitations we need to work jointly in academia and management to develop a continuing fiscal support base that can: (1) generate local reference material in a systematic way regionwide, (2) acquire and organize the necessary literature and consultant references, (3) train district personnel on a rotating basis, and (4) enlist the public to participate in a comprehensive monitoring program. Without ultimate hands-on ownership by the public, long-term stewardship is not attainable. Such stewardship is our challenge. The diversity of both the speakers and the audience at this symposium holds potential for a solution to eventual stewardship.

I am developing a network of tools for the study of soil arthropods: standardized methodologies for capture; user-friendly identification techniques; a system for archiving physical specimens and electronic data; and a network of participants region-wide. It's easy; it's cheap; it's fun; but most importantly its critically needed. For more information contact the author. Please join our network.

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BIOLOGICAL DIVERSITY AND ECOSYSTEM FUNCTIONS OF FOREST SOIL FUNGI: MANAGEMENT IMPLICATIONS

Randy Molina[1], Thomas O'Dell[2], Susie Dunham[3], and David Pilz[4]

ABSTRACT

This chapter provides a brief overview of the ecosystem function and biodiversity of forest fungi, which are critical to the health and sustainability of forest ecosystems. Species diversity of fungi is second only to arthropods but it is their functional diversity that makes fungi so important in forest ecosystems. In addition to participating in the entire nutrient cycling process, they also are fundamental parts of the forest food web, and many forest organisms depend on them in mutualistic and other symbiotic associations. Recent efforts to conserve rare fungi and manage the commercial harvest of edible forest mushrooms for sustainable production provide examples of integrating fungi into ecosystem management schemes.

Keywords: mycology, mycorrhizae, biodiversity, survey and manage, conservation biology, population biology, edible mushrooms, special forest products, nontimber forest products

INTRODUCTION

Ecologically sound management of natural resources requires a broad understanding of how ecosystems function. Likewise, conserving biodiversity requires knowledge not only of the population biology of individual organisms but also of the interactions and interdependencies of organisms. Such understanding provides a means to include the myriad of less visible organisms along with the megafauna and megaflora in our management schemes.

This integrated approach is essential for managing the great diversity of species and functions of soil microorganisms in forest ecosystems. Total species richness is greatest in the soil, but most importantly, the functions of soil microbes power the complex biochemistry of nutrient cycling that yields soil fertility and, ultimately, plant and animal productivity.

This paper briefly discusses the biological diversity of forest soil fungi and emphasizes their functional roles in forest ecosystems. Two current examples of managing forest fungi to conserve rare species (survey and manage species listed in the northwest forest plan, USDA and USDI 1994) and to sustain their productivity (commercially harvested edible mushrooms) provide a basis for integrating fungi into ecosystem management plans.

INTRINSIC VALUES OF FOREST FUNGI

Many fungi produce beautiful and elegant reproductive structures known as mushrooms. These fruiting bodies or sporocarps are collected regularly by thousands of amateur and professional mycologists who marvel at their complex forms, learn their identifying characters, study their ecology, or simply savor the edible species for their unique and delectable tastes. Regional mushroom clubs and societies are scattered across North America and other continents. They organize collecting trips and meetings to discuss their findings and share their mycological experiences. Just as we recognize the enthusiasm of bird watcher, native plant, and other nature loving societies, so too must we recognize society's long-time interest in, and fondness for, gathering fungi as a valued recreational activity.

Perhaps the most obvious social value of fungi comes from their use in medicine. Many molds are famous for their production of antibiotics such as penicillin. Ancient pharmacopoeia list numerous medicinal uses of fungi. Yet, we have barely explored the medicinal

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[1] Randy Molina is a research botanist and team leader, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis OR 97331.

[2] Thomas O'Dell is the regional mycologist, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis OR 97331.

[3] Susie Dunham is a graduate student in the Department of Forest Science, Oregon State University, Corvallis OR 97331.

[4] David Pilz is a botanist, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis OR 97331.

potential of fungi. Any conservation discussion that emphasizes efforts to preserve plant species for as yet unknown medicinal value must include the fungi.

Several species of wild, edible, forest mushrooms are harvested commercially in Alaska, Oregon, Washington, Idaho, and California, and a multimillion dollar wild mushroom industry has developed (Molina and others 1993, Schlosser and Blatner 1995). This new industry has created conflicts between traditional recreational users of forest mushrooms and commercial mushroom harvesters which has prompted resource managers to develop new permit systems to protect and regulate this resource. The monetary value of this new special forest product and the regional conflict over its proper use has brought attention to this previously unheralded group of forest organisms. Such social and economic values underscore the need to understand the biodiversity of fungi in relation to both forest and human communities. The management of special forest product fungi is discussed in greater detail later.

ECOSYSTEM FUNCTIONS OF FUNGI

All fungi are heterotrophs and they obtain energy, directly or indirectly, from organisms that can photosynthesize. Fungi that decompose dead organisms are called saprotrophs, those that get energy directly from a living host are called biotrophs. Saprotrophs include the various cultivated mushrooms, yeasts and many other species. Biotrophs include those fungi that form symbioses with living plants (such as mycorrhizal or lichenized fungi) and many pathogens. Some pathogenic fungi span the gradient from biotroph to saprotroph, colonizing a living host and persisting to decompose its remains.

Miller (1995) organizes the primary functions of fungi in ecosystems into three general categories, each with several subcategories:

- Physiological and metabolic
  - Decomposition of organic matter; volatilization of C, H, and 0; fragmentation
  - Elemental release and mineralization of N, P, K, S, and other ions
  - Elemental storage: immobilization of elements
  - Accumulation of toxic materials
  - Synthesis of humic materials
- Ecological
  - Facilitation of energy exchange between aboveground and belowground systems
  - Promotion and alteration of niche development
  - Regulation of successional trajectory and velocity
- Mediative and integrative
  - Facilitation of transport of essential elements and water from soil to plant roots
  - Facilitation of plant-to-plant movement of essential elements and carbohydrates
  - Regulation of water and ion movement through plants
  - Regulation of photosynthetic rate of primary producers
  - Regulation of C-allocation belowground
  - Increased survivability of seedlings
  - Protection from root pathogens
  - Modification of soil permeability and promotion of aggregation
  - Modification of soil ion exchange and water holding capacities
  - Detoxification of soil (degradation, volatilization, or sequestration)
  - Participation in saprotrophic food chains
  - Instigation of parasitic and mutualistic symbioses
  - Production of environmental biochemicals (antibiotics, enzymes, and immunosup presants)

The first category encompasses the physiological and metabolic attributes of fungi. Fungi are most well known for their decomposition of organic matter. In forest ecosystems they play a significant role in the depolymerization of cellulose, hemicellulose, and lignin, the primary constituents of wood (Cooke and Whipps 1993, Miller 1995). A primary outcome from the complex biochemical degradation processes is the release of elements and mineralization particularly of N, P, K, S and other ions. Of course, these become nutrients available for uptake by plants. Another critical function in this category is the storage of nutrients within the vast body of fungi in the soil. Fungi are well known as nutrient accumulators, and some of their mycelial structures, such as rhizomorphs, tenaciously maintain elements in organic form, thus preventing their loss from the ecosystem.

Fungi also participate in many ecological processes that reverberate through the ecosystem (Trappe and Luoma 1992). Related to the elemental storage capacity noted above is the direct movement of energy in the form of photosynthetic carbon (sugars) between aboveground and belowground ecosystem components. For example, mycorrhizal fungi obtain their primary carbon from photosynthate directed towards the fine roots; as much a 50 percent of the carbon fixed in photosynthesis can move to mycorrhizal fungi (Smith and Read 1997). This significant source of carbon fuels many of the rhizosphere organisms and their processes in the soil (Molina and Amaranthus 1991). As noted by Moldenke (this volume), for example, this nutrient rich fungal mycelium is a food source for the majority of soil microarthropods.

At larger spatial scales, fungi also contribute to development of critical niches for myriad forest organisms (Miller 1995). For example, although many soil fungal pathogens directly kill or weaken forest plants, the dead snags or the softened tissue of infected trees allow for cavity construction by birds and other wildlife (Parks and Shaw 1997, Schowalter and others 1997). At a forest gap or stand scale, root pathogens such as *Phellinus weirii* (Murr.) Gilbertson or *Armillaria* species create openings in the forest that allow for successional development of understory, thus enhancing biodiversity and providing resources such as browse for large mammals (see Thies, this volume). Although it is important that we not exacerbate diseases with our management practices, it is important to realize that pathogens are a natural component of forest ecosystems and contribute to landscape and biological diversity. Schowalter and others (1997) provide a framework for integrating the ecological roles of pathogens and mycorrhizae in managed forests.

Miller (1995) defines the third functional category as mediative and integrative and emphasizes numerous ways other organisms are affected by fungal presence and processes. These range from facilitating the movement of water and nutrients from soil to roots to providing protection against some root pathogens and increasing seedling survival. From a holistic ecosystem perspective, fungi can mediate restoration of severely disturbed sites and thus act as key resiliency factors (Amaranthus, this volume, Molina and Amaranthus 1991, Perry and others 1989a). Nowhere is this integrative function exemplified better than with the mycorrhizal symbioses.

MYCORRHIZAL FUNGI OF FOREST PLANTS

Mycorrhiza literally translates as "fungus-root" and defines the common association of specialized soil fungi with the fine roots of nearly all forest plants. Mycorrhizal associations represent one of the more widespread forms of mutualistic symbioses in terrestrial ecosystems. Indeed, these plant-fungus associations have coevolved over the eons such that each partner depends on the other for survival.

The mycorrhizal fungus basically serves as an extension of the plant root system, exploring soil far beyond the reach of the roots and transporting water and nutrients to the roots. The uptake of phosphorus and nitrogen are especially critical functions of mycorrhizal fungi, which can release bound forms of these nutrients otherwise unavailable to the roots. In return, the plant is the primary energy source for the fungus, providing simple sugars and vitamins produced in photosynthesis and transporting them to the roots and then the fungus.

Mycorrhizal fungi have limited saprophytic ability; that is, they possess fewer enzymes needed to efficiently break down complex organic matter in the soil than do true saprotrophs . Hence, their survival in natural ecosystems depends on the supply of sugar (photosynthate) from their associated host plants. Likewise, many plants strongly depend on their mycorrhizal fungi for nutrient and water uptake. This coevolution in dependency reinforces the need to view organisms through their relations within the forest.

There are several classes of mycorrhizae, but only ectomycorrhiza will be discussed (see Smith and Read 1997 for a complete review on mycorrhizae). Ectomycorrhiza is the most common type on forest trees in the Western United States and Canada. Ectomycorrhizal hosts in our region include all species in the Pinaceae *(Abies, Larix, Picea, Pinus, Pseudotsuga,* and *Tsuga),* Fagaceae *(Castinopsis, Lithocarpus, Quercus),* Salicaceae *(Populus, Salix),* and Betulaceae *(Alnus, Betula, Cory/us).* Additionally, genera such as *Arbutus, Arctostaphylos, Cercocarpus,* and *Eucalyptus* form ectomycorrhizae. The dominant nature of these species in western forest ecosystems, especially Pinaceae, contributes to the pervasiveness of ectomycorrhizae in western forests.

Ectomycorrhizae develop on the short, feeder roots. The fungus forms a sheath or mantle of fungal tissue around the feeder root. The mantle serves as a storage tissue for nutrients received from mycelium in the soil and physically protects the fine roots from some pathogens and desiccation. The fungus also penetrates between the root's cortical cells to form a network of fungus tissue called the Hartig net. Nutrient exchange occurs within this extensive, intimate contact zone: sugars and vitamins move from plant to fungus, and water and nutrients move from fungus to plant. Many ectomycorrhizal fungi produce plant hormones that cause extensive branching of colonized feeder roots. This branching greatly increases the root surface area and provides an extensive contact zone between the fungus and root.

The fungus grows from the colonized roots into the surrounding soil. Mycelial colonization of the soil differs among ectomycorrhizal fungi; some may grow only a few centimeters into the soil and others can grow several meters from the ectomycorrhiza. Some fungi produce dense, hyphal mats that strongly bind the soil and organic matter. If the mycelium is white or brightly colored, these extensive mats may be readily visible when a bit of the upper organic layer is removed. Other fungi produce colorless or dark mycelia that are more difficult to see with the unaided eye, but their growth into the soil is likewise extensive.

Thousands of ectomycorrhizal fungus species occur in our region; Douglas-fir *(Pseudotsuga menziesii* (Mirb.)

Franco) alone associates with nearly 2,000 species (Trappe 1977). Most ectomycorrhizal fungi are basidiomycetes and ascomycetes, and many produce mushroom fruiting bodies that abound in western forests during the moist times of the year. Many ectomycorrhizal mushroom-forming fungi are especially prized for their edibility. Well-known edible species occur in the genera *Cantharellus* (chanterelles), *Boletus* (boletes), *Lactarius* (milky caps), *Tricholoma* (matsutake), *Hydnum* (tooth fungi), and *Ramaria* (coral fungi) (see Molina and others 1993 for a complete listing of ectomycorrhizal fungus genera). Another large and diverse group of less well-known ectomycorrhizal fungi are the truffles, which produce fruiting bodies beneath the duff or soil surface. Only a couple of truffle species are harvested commercially, but as will be discussed later, truffle fungi are a central part of the forest food web.

The habitat requirements of ectomycorrhizal fungi and their interactions with particular plant species are poorly understood. Some fungi are more abundant in certain age classes of forests (O'Dell and others 1992b). As plant-species composition changes during forest succession, the fungus communities similarly undergo change. This fungal succession is in response to changes in tree composition, tree age, and soil qualities such as accumulation of organic matter. The ecological requirements of mycorrhizal fungi, particularly their relation to forest community succession and disturbance events, represent large knowledge gaps needing research attention.

Research on the biodiversity of ectomycorrhizal fungi in the Pacific Northwest has focused on the relations and interdependencies among mycorrhizal plants and fungi rather than on total number of fungal species. It is within this context of relations that the functional characteristics of ectomycorrhizal fungi emerge. Many ectomycorrhizal fungi, for example, have broad host ranges; others are host specific, typically restricted to a single genus of host (Molina and others 1992). In the Pacific Northwest, Douglas-fir forms ectomycorrhizae with numerous host-specific fungi; *Pinus* species similarly associate with a wide array of *Pinus*-specific fungi. At the same time, both Douglas-fir and *Pinus* species are compatible with many broad-host-ranging fungi. Thus, a forest composed of different ectomycorrhizal host species will exhibit a spectrum of ectomycorrhizal relations with diverse fungi. Molina and others (1992) hypothesize that host-specific fungi may provide different benefits to their specific hosts than do more generalist, broad-host-ranging fungi. Perry and others (1989b) found that host-specific fungi can reduce competition among different tree species compared to broad-host-ranging fungi.

The ability of different host species to form ectomycorrhizae with mutually compatible fungi also influences forest succession and community development (Molina and others 1992). Read and others (1985) demonstrated that forest trees can be connected by common mycorrhizal fungi and that photosynthate, minerals, and water pass among plants via the fungal linkage. Understory plants, especially seedlings, may benefit from this linkage if photosynthate passes from the overstory tree to a shaded understory plant (Simard and others 1997). Or, a plant entering in the later stages of forest succession can grow into a community of ectomycorrhizal fungi that has been nourished and maintained by early successional plant species. Perry and others (1987) hypothesize that these functional connections in time between successional stages as mediated by compatible mycorrhizal fungi contribute significantly to forest resiliency and recovery following disturbance. Thus, as an ecological management tool, resource managers may chose to maintain a compatible stocking level of commercially nonvaluable pioneering and understory plants following tree harvest. In this approach, the beneficial mycorrhizal fungi are maintained on the site by pioneering vegetation for use by later tree crops (see Amaranthus, this volume).

Ectomycorrhizal fungi are most well known for enhancing nutrient uptake and growth of the host. Consequently, many mycorrhiza researchers have developed methods to inoculate forest tree seedlings with selected, beneficial mycorrhizal fungi (Castellano and Molina 1989, O'Dell and others 1992a, Perry and others 1987). Ectomycorrhizal fungi also perform other critical ecosystem functions, however, and it is from understanding this diversity of functions that additional ecological management tools can be developed. Management practices that encourage the healthy functioning and recovery of forest fungi and other soil microbes following disturbance will provide positive benefits to ecosystem productivity (Amaranthus and others 1990, Molina and Amaranthus 1991).

TREES, TRUFFLES, AND BEASTS: AN EXAMPLE LINKING ABOVEGROUND AND BELOWGROUND ECOLOGIES

Ecological theory recognizes that organisms do not live in isolation from other organisms. The literature is rich with examples of interdependencies among plants, among animals, and between plants and animals. But rarely do these examples include the "invisible" flora, fauna or mycota in ecosystems. The following example of ecological connections among mycorrhizal fungi, old-growth forests, and a controversial, endangered bird, the northern spotted owl *(Strix occidentalis),* in the Pacific Northwest illustrates the value and necessity of integrating aboveground and belowground ecologies.

Northern spotted owls live predominantly in old-growth forests. A primary prey of the northern spotted owl is the northern flying squirrel *(Glaucomys sabrinus* Shaw). During certain times of the year, northern flying squirrels feed on a wide variety of subterranean mycorrhizal fungus sporocarps called truffles (Maser and others 1985). As truffles mature, the interior tissue fills with spores and emits a distinctive odor. Small mammals, such as the northern flying squirrel, forage for these truffles by smell and then excavate and devour them. The spores pass through the mammals unharmed and are dispersed during defecation. The spores then re-enter the soil where they germinate and form new mycorrhizae with tree roots. This dispersal is important for young tree growth in areas where the previous forest has been destroyed by natural catastrophic events (fire, wind) or timber harvests. Hundreds of truffle fungi occur in western forests and most forest mammals consume them. Thus, in this example of tree-fungus-prey-predator connections, resource managers can view the northern spotted owl within the context of its ecosystem linkages rather than through a simple dependency on old-growth forests. Such holistic perspectives enable development of ecosystem management tools and avoid the often divisive nature of single-species conservation approaches.

BIODIVERSITY OF SOIL FUNGI

Soil harbors tremendous fungal diversity; a single gram may contains thousands of species. It is difficult to describe, let alone understand, this diversity. Most soil fungi produce only microscopic fruiting structures and require sterile culture methods for their isolation and identification. Macrofungi (species that produce macroscopic fruiting bodies), although having their cryptic aspects, can be observed without having to be cultured. Furthermore, a century of observation provides information regarding their rarity, distributions, and habitat preferences. Macrofungi include important commercially harvested species and the majority of all species covered under the survey and manage provisions of the Northwest Forest Plan (USDA and USDI (1994). Our discussion will focus on macrofungi, but many of the concepts apply equally to all fungi.

The concept of diversity encompasses many species, and relative abundancies, and genetic variation among individuals of a species. Maintenance of ecosystem function and protection of biological diversity require conservation of species and within-species variation. Diverse assemblages of species contribute to ecosystem resiliency (ability to recover after disturbance) (Tilman and Downing 1994), and of course different species may serve different functions in the ecosystem. The variation among individuals of a species is grist for the mill of natural selection and this genetic variation increases the chance for a species to survive in the face of a changing environment.

Species diversity and the intraspecific genetic diversity among individuals of a species both contribute to functional diversity in the ecosystem. Although different species may do drastically different things (for example, decompose wood vs. form mycorrhizae), individuals of a species differ more subtly, (for example, decomposing the same substrate most efficiently at different temperatures).

Two concepts, communities and guilds, are used to discuss species with similar characteristics. A community is a group of organisms sharing a piece of ground; for example, the fungi in a particular Douglas-fir stand. Communities of species commonly encountered together are often given a name: the *Pseudotsuga menziesii-Tsuga heterophyllalPolystichum munitum* plant association; fungi are too poorly known to have many named communities. A guild is a group of species that share a common function, such as fungi that form ectomycorrhizae. Increased understanding of communities and guilds will facilitate better management of fungi. If a rare fungus often occurs in a community and that community has an identified habitat requirement, we can move away from single-species management toward managing for the habitat.

Communities are not restricted to a particular spatial scale; a community could be identified that occurs on large-diameter Douglas-fir logs. Species in such a community are at risk from management strategies that fail to provide a long-term source of such logs. Succession describes how communities change over time. Successional change often results from feedback between organisms in the community and their environment. Immediately following a disturbance, for example, nutrient availability increases, and pioneer species tend to tolerate and make full use of high levels of soil N and P. As the nutrients become immobilized in biomass, late-seral species capable of using organic forms of nutrient and competing effectively for scarce resources tend to replace the pioneers. Thus, the different species that comprise early and late serai communities contribute to long-term ecosystem productivity.

POPULATION BIOLOGY OF FUNGI

What Can Genetic Studies of Fungal Populations Contribute to Management of Forest Fungi?

Genetic diversity is recognized by the World Conservation Union as one of three levels of biodiversity important to conserve (McNeely and others 1990), a task ultimately falling to land managers. A growing literature on the possibilities of linking genetics and ecology in conservation biology (Avise 1994, Avise and Hamrick 1995, Hastings and Harrison 1994, Milligan and others 1994) suggests that spatial analysis of genetic patterns can provide guidance for defining the landscape scale at which ecosystem management activities should occur to best conserve genetic variation within species (Moritz 1994). Two long-term goals of our population genetic research on ectomycorrhizal fungi are to gain some understanding of how past and current land management practices in the Pacific Northwest have altered the dynamics of fungal populations, and to use this information to predict how future land management scenarios may affect persistence of fungal populations. Achieving these goals requires an understanding of the spatial and temporal scales at which evolutionary significant processes (such as natural selection, gene flow, and genetic drift) act on fungal populations. We also need to understand which processes are most salient at spatial scales relevant to management, and how variability in landscape structure affects these processes (Wiens 1989, 1997).

Difficulties With Studying Fungal Populations

Several ecological characteristics of fungi impede our ability to select scales appropriate for quantifying the evolutionary processes important to fungal populations. Selecting an appropriate scale for population genetic studies requires an understanding of how individuals are distributed across the landscape. This presents a difficult obstacle with fungi because the mass of threadlike mycelium (thallus) that gives rise to fruit-bodies grows throughout the soil and cannot easily be measured or counted. Attempts to characterize the size and distribution of discrete thalli have identified individuals encompassing hectares (Smith and others 1992), square meters (Baar and others 1994), and square centimeters (Gryta and others 1997). Dahlberg and Stenlid (1990) also show that ecological factors such as forest age can influence the size of individuals and alter the mechanism by which new thalli are established. The range of individual size and distribution unique to each fungal species should dictate the scale at which population boundaries are encountered and set the minimum size limit for study area selection.

When fungi are sampled in the field, it is impossible to tell what proportion of the sporocarps collected represent genetically identical individuals produced by the same mycelium, and genetically distinct mycelium masses may produce intermingled sporocarps (Molina and others 1993). Discrete thalli can be established by either sexual reproduction (genets) or clonal vegetative propagation (Todd and Rayner 1980), and our understanding of populations hinges on correctly estimating the contribution of each reproductive type to the genetic diversity observed within populations (Avise 1994)

Determining the boundaries of fungal populations and identifying landscape features that impede dispersal requires the development of sampling techniques that allow us to estimate how much gene flow occurs in forest stands, in watersheds, and across regions. These sampling techniques also must account for variability in vegetation cover, disturbance type, and disturbance intensity at each scale. The ultimate goal of such a multiscale sampling regime is to ensure that the scale of our measurements and the response of fungal populations to some variable of interest (for example, disturbance) fall within the same spatial domain or area affected by the same ecological processes. Variability across fungal species in individual size and distribution, mating system, and dispersal capability makes it impossible to apply a single sampling protocol to all species. Advancement in understanding and maintaining genetic variability in fungal populations requires basic research on how species with vastly different life histories partition their variation at different spatial scales. This fundamental research will lay a general foundation for predicting how land management strategies may affect rare species depending on their life histories. Multiscale genetic studies also will help define scales potentially appropriate for future research on demographics or habitat requirements.

Current Research Example: Distribution of Genetic Variation Across Different Spatial Scales in *Cantharellus*

Building a strong knowledge base requires that basic genetic research be done on model species that will yield large sample sizes and are predictable in their fruiting from year to year. Research on such common species will allow initial studies to have the statistical power sufficient to correctly identify evolutionary important pattern-process relations (Dizon and others 1995). Pacific golden chanterelles *(Cantharellus formosus* Corner) is an economically important species that forms mycorrhizal associations with a wide range of host species over a broad geographic range (Molina and others 1993). Chanterelles also fruit predictably and abundantly and provide an ideal model species for initiating base line genetic studies.

Current genetic research on chanterelles is being conducted in collaboration with an integrated research project, the Young Stand Thinning and Diversity Study, sponsored by the Willamette National Forest, Oregon State University, and the Cascade Center for Ecosystem Management. It is located in the central Oregon Cascade Range east of Eugene, Oregon. The overall goal of the study is to determine how stand-thinning techniques and leave-tree densities affect site conditions and ecological responses. Our initial mycological goal was to determine how chanterelle fruiting respond to stand thinning (Pilz and others 1996). Our genetic population study attempts to determine the size and distribution of chanterelle genets in forest stands that differ in intensity of disturbances associated with tree harvest, and to quantify patterns of genetic variability at fine spatial scales. Results of this research will aid in the design of a sampling method that will detect genetic variation at spatial scales relevant to management. Future research efforts will examine how heterogeneity in landscape features (for example, forest stand age or patterns created by different disturbance regimes) affects rates of gene flow among chanterelle patches. Using this line of research to develop a better understanding of how fungi move across landscapes will facilitate identification of population boundaries and geographic areas important to the conservation of genetic diversity.

SURVEY AND MANAGE FUNGI IN THE NORTHWEST FOREST PLAN: NEW CHALLENGES IN CONSERVATION BIOLOGY

A challenge within the Forest Ecosystem Management Team (FEMAT) (1993) process was protecting biological diversity for all species within the master plan for protecting the northern spotted owl. Protecting all species and their ecological functions is indeed a primary tenet of the new paradigm of ecosystem management. Taxa specialist panels were convened to examine mammals, amphibians, fungi, lichens, bryophytes, vascular plants, mollusks, and arthropods with the task of listing rare taxa within the range of the northern spotted owl and taxa that required late successional forest habitat. These taxa were then run through risk assessment screens in conjunction with the various options being considered for implementation. Under option 9, the risk assessment yielded 409 species and 4 arthropod communities whose viability was not protected. The survey and manage guidelines were then developed as part of the record of decision (ROD) (USDA and USDI 1994) and serve as the basic structure for ensuring the viability of these rare taxa.

The survey and manage guidelines are organized around four strategies, each having different objectives for protecting species viability and gaining new information for use in adaptive management. The taxa were placed into these various strategies in the C-3 list (USDA and USDI 1994: C49-C61). The four strategies and their relevance to fungi are described below.

Strategy 1—Manage Known Sites

Taxa in this category receive the highest priority for protection. The strategy calls for gathering information on all extant sites, developing a Geographical Information system (GIS) data base for all species and using this information for preparing management recommendations. Management activities implemented in 1995 and later must include provisions for these known sites. In most cases, this will involve protection of relatively small sites. "For rare and endemic fungus species, areas of 160 acres should be temporarily withdrawn from ground-disturbing activities around known sites until those sites can be thoroughly surveyed and site-specific measures prescribed. For one fungus species, *Oxyporus nobilissimus,* there are only six known sites and two of these do not currently have protected status. Management areas of all usable habitat up to 600 acres are to be established around these two sites for the protection of those individuals until the sites can be thoroughly surveyed and site-specific measures prescribed. The actions to protect *Oxyporus* must be undertaken immediately" (USDA and USDI 1994: C-5). There are 147 fungal species listed under strategy 1.

Strategy 2—Survey Prior to Ground-Disturbing Activities

This strategy was designed to address the high-risk species for which survey protocols exist or could be developed reasonably soon, and for which adequate searches could be conducted in a single year. Efforts to design protocols and implement surveys would be started immediately. The information gained from the surveys would be used to develop management strategies for species protection. For fungi, these surveys must be completed prior to ground disturbing activities that will be implemented in 1999 or later. Only two fungal species are listed under strategy 2, one being *Oxyporus nobilissimus.*

Strategy 3—Extensive Surveys

The objective of this strategy is to conduct surveys to find high-priority sites for species management. "It is recommended primarily for species whose characteristics make site and time-specific surveys difficult. For example, some fungi only produce fruiting bodies under specific climatic conditions, so finding their location may take several to many years" (USDA and USDI 1994: C5-C6). Surveys under this strategy had to be underway by 1996. These surveys are likely to take several years to complete and to identify high-priority sites for protection. All strategy 1 fungal taxa also are listed under strategy 3; 87 additional fungal species are designated as strategy 3 species for a total of 234 species in this strategy.

Strategy 4—General Regional Surveys

The objective is to survey for the species to acquire additional information to determine necessary levels of protection. Although these species are not considered rare, there is only limited information regarding their abundance and distribution. The information gathered from these surveys would be used in adaptive management to refine the guidelines to better protect these species. These surveys were expected to be both extensive and expensive. They had to begin in 1996 and be completed within 10 years. There are 20 fungal species listed in this strategy.

Current Work in Progress

A primary task in implementing the survey and manage guidelines was to gather all available information on extant collections of strategy 1 taxa. For fungi, collection records and ecological information were obtained from several mycological herbaria, literature searches, and field botanists throughout the Pacific Northwest; about 1800 collections were discovered and reverified. These are now in a database and available to field managers. The database is managed and updated at the Regional Ecosystem Office in Portland, Oregon.

From the known site database and literature searches, management recommendations were drafted for use by field personnel. The management recommendations include information on species descriptions, nomenclature, known sites and geographic range, ecology, reproductive biology, habitat requirements, impacts of past disturbances, specific recommendations to maintain species presence at known sites, and research and monitoring needs. These documents will undergo formal scientific and managerial reviews before publication.

Future Directions and Challenges

Designing efficient survey protocols and conducting the extensive surveys called for under strategies 3 and 4 remain the greatest challenges in implementing the survey and manage guidelines. As part of a national effort to develop inventory and monitoring protocols for all fungal groups, members of Pacific Northwest Research Station Forest Mycology Team at Corvallis have written protocols for mushroom and truffle fungi. These protocols will be published in an upcoming book on international mycological survey protocols by the Smithsonian Institution and will serve as the foundation for developing specific regional protocols for survey and manage fungi.

A high priority is determining which survey and manage fungal species are at highest risk and thus should be surveyed immediately. Another priority is to build simple habitat-based models that will guide decisions on where to conduct surveys. For most known site records, little site-specific habitat information is recorded. Revisiting known sites to determine whether the taxon is still present (many of the known sites have been disturbed since the original collections) and gathering specific habitat information are urgent tasks prerequisite to building habitat models.

Complimentary mycological research is needed in two new areas for building a comprehensive conservation strategy for fungi. First, because the overall goal is protecting species viability, we must develop an understanding of population dynamics for forest fungi. This includes information on geographic distribution, genetic structure, dispersal capabilities, reproductive biology, and habitat fragmentation effects on population structure. As noted in the previous section, population biology is poorly understood for fungi in general, largely because of the difficulty in defining an individual and how individuals interact genetically to yield distinct populations. Many traditional approaches for defining and measuring populations used for plants and animals simply do not work for fungi. This research will require use of both field biological sampling and molecular genetic approaches (see previous section, "Population Biology of Fungi").

A second important research need is habitat modeling at the landscape and regional scale. Given the large number of survey and manage fungal species, it will be difficult to assess viability for all species across the range of the northern spotted owl. Also, because known sites occur on various public and private land holdings, it will be necessary to integrate how all available habitat will contribute to maintaining species viability. To do so will require development of predictive GIS and statistical models that examine the current and future forest conditions affecting fungal species persistence. The end product would be a working model that resource managers could use to examine how their management practices will affect viability of survey and manage species. This effort will take considerable cooperation among mycologists, statisticians, and land managers to develop a usable habitat model for decision making.

Two conditions are necessary for the long-term success of survey and manage strategies. First, communication and coordination with field units are needed to develop management recommendations and survey protocols that are attainable and efficient. Field managers are key members in the adaptive management process. They must be involved in gathering new information from the surveys and in deciding how best to use the information to refine management strategies. Second, monitoring the results of our recommendations and management decisions is essential to determining species viability. These monitoring efforts must be carefully coordinated with other Northwest Forest Plan effectiveness monitoring activities across the region.

COMMERCIALLY HARVESTED EDIBLE FOREST MUSHROOMS: OPPORTUNITIES FOR ECOSYSTEM MANAGEMENT

Edible sporocarps of many ectomycorrhizal fungus species are highly prized by different cultures and local markets for their commercial sale are common around the world. However, the decline of favorite edible species in Europe (Arnolds 1991, 1995) and Japan (Hosford and others 1997) has created a market demand for wild fungi from regions where the species remain abundant and a modern infrastructure (forest roads and nearby airports) provides quick access to and export of the fresh product. These economic forces have led to development of a multimillion dollar industry of wild mushroom harvest from the extensive forests of western North America (Amaranthus and Pilz 1996, Molina and others 1993, Schlosser and Blatner 1995).

Most of the valuable commercial species are mycorrhizal fungi. The primary tree hosts include the Pinaceae but also Fagaceae and Betulaceae. Although we have a general understanding on geographic range, host associations, and mycorrhizal characteristics of important edibles such as *Cantharellus* (Danell 1994), we poorly understand their ecology and productivity in natural forests, an understanding essential to conserving and managing the use of these fungi. The following sections discuss ecological and management implications of this commercial harvest on forest fungi and focus on current research and monitoring approaches aimed at developing management guidelines for protecting the mushroom resource and ensuring a sustainable harvest.

Commercial Mushroom Harvest in the Pacific Northwest

In the early 1980s in Oregon and Washington, a small entrepreneurial wild mushroom industry began to harvest small volumes of mushrooms and ship them to gourmet restaurants across the United States. Then, with the decline of chanterelle productivity in Europe, a new export market developed: harvested chanterelles were packed in brine and shipped to canneries in Germany. This new market vastly increased the volume of mushrooms harvested and led to development of a system of harvesters, buyers, processors, and brokers for the expanding industry. Later in the decade, the industry returned primarily to the fresh export market.

Schlosser and Blatner (1995) extensively surveyed the wild mushroom industry in Oregon, Washington, and Idaho for 1992. They report that the industry employed about 11,000 people and contributed $41.1 million to the regional economy; nearly 1,800,000 kilograms of wild mushrooms were harvested. Twenty five species are harvested commercially but the most economically important are chanterelles (mostly *Cantharellus formosus* but also *C. subalbidus* Smith & Morse), pine mushroom or American matsutake *(Tricholoma* magnivelare (Peck) Redhead), king bolete *(Boletus edulis* BulkFr.) and several morel *(Morchella)* species. Twenty-eight percent of all exports went to Japan and 25 percent to European markets (primarily France and Germany).

The most abundantly harvested ectomycorrhizal fungi are the chanterelles and American matsutake, with 454,000 and 375,000 kilograms respectively, harvested in 1992. Nearly half of all harvested chanterelles were air-shipped to Europe; chanterelles are popular throughout Europe, but productivity has declined in some regions (Arnolds 1991). For similar reasons, 70 to 90 percent of harvested American matsutake went to Japan, where they supplement the highly revered Japanese matsutake *(Tricholoma matsutake* (S. Ito et Imae) Sing.). Over the last 50, years productivity of *T. matsutake* in Japan has declined dramatically to 10 percent of previous yields as a result of insect infestations of host trees and changes in forest management (Hosford and others 1997).

Biological and Management Concerns

The magnitude of the commercial mushroom harvest in the Pacific Northwest has raised controversy about conservation of the mushroom resource, particularly regarding harvest effects on species viability and ecosystem function. As part of a comprehensive research program for managing commercial mushroom harvests, we have conducted several public workshops to gather information on the primary concerns of resource managers, the mushroom industry, and general public. Those concerns fall into four categories; we present them as a series of questions so readers can envision the scale and complexity of needed mycological research.

Production and distribution-How many fruiting bodies are being produced? How are they distributed across the landscape or within a given area? How does production vary during a season and among years? What is the actual or potential commercial productivity of a given area? What proportion of forest habitat is available and accessible for harvesting? What factors determine productivity and how might they be managed?

Mushroom harvesting-How can the sustainability of mushroom harvesting be assured? What proportion of the crop can be harvested without unacceptable impacts on the fungus itself or other resources? What techniques will mitigate those impacts; does mushroom harvesting increase or decrease subsequent production? Is spore dispersal reduced by removal of immature mushrooms, and if so, does it impair reproductive success? Are fungal mycelium and subsequent mushroom production affected by search and harvest techniques such as raking, moving woody debris, and digging? Are mushrooms harmed by numerous harvesters trampling the forest floor? How important are commercially valuable species as food for wildlife, and is human competition for the resource significant?

Land management-How do various timber harvesting methods (clearcutting, thinning to various densities, host species selection) affect subsequent mushroom production over time? What is the impact of soil compaction or disturbance from logging activities? What are the relations between fire and subsequent mushroom production, especially for morels? How does the intensity and timing of fire influence edible mushroom production? What impacts do grazing, fertilization, or pesticide application have on production? Can mushroom production be improved through habitat manipulation; for example, planting tree seedlings inoculated with specific fungi, thinning understory brush for sunlight and rainfall penetration, prescribed burns, and irrigation? Can production be increased across the landscape by managing forests to attain tree age class, structure, and composition optimal for fruiting?

Biology and ecology-What are the important reproductive events in the life cycle of a particular fungus species? How are new colonies or populations established and maintained? What causes them to diminish or perish? How important is spore dispersal to reproductive success, population maintenance, genetic diversity, or adaptability to unique microhabitats? How much genetic diversity exists within and among populations? Are there endemic, narrowly adapted, or unusual populations of otherwise common species? What are the growth rates of fungal colonies in soil and degree of mycorrhizal development by specific fungi on root systems? To what degree do other mycorrhizal or saprophytic fungi compete with desired fungi for colonization sites on host roots or space in the forest soil?

Answering these questions will require scientific investigations on an array of ecological scales (soil microniches to regional landscapes) and using a variety of investigative methods.

Monitoring Needs and Methodological Considerations

Numerous biotic and abiotic factors influence fruiting of ectomycorrhizal fungi, and sporocarps of different species differ in abundance and distribution from year to year (Vogt and others 1992). Sporocarps are typically clustered and associated with particular substrates. Fruiting is generally nonuniform and frequently occurs in arcs or patches of a few to numerous sporocarps. The distribution of patches also can range widely from a few scattered groups to concentrated clusters. Commercially harvested species such as American matsutake, *Cantharellus* species, and *Boletus edulis* also associate with a broad range of host tree genera in the Pacific Northwest *(Abies, Arbutus, Lithocarpus, Pinus, Pseudotsuga, Quercus, Picea,* and *Tsuga)* and occur over a range of forest habitats and tree age classes. This broad spatial and temporal variability of sporocarp occurrence, combined with insufficient ecological knowledge of the mycorrhizal fungi, presents a formidable challenge for mycological research.

The first step to meeting this challenge is establishing long-term monitoring of the fungal resource over the regional land base. Three types of monitoring are required: detection, evaluation, and research. Each type addresses different concerns and provides data to meet specific management objectives.

Detection monitoring addresses questions of productivity and distribution. It documents the current production of commercial fungi and variability with space and time. This baseline information is essential to assess whether production is declining, increasing, or stable. Because annual fruiting typically occurs over a short period and varies from year to year, sampling must be repeated at least weekly throughout the fruiting period and over several years to assess seasonal production. Total seasonal production must be tracked for years to detect trends among high levels of annual variation. Numbers of mushroom and their weights must be recorded as well as commercial quality and current market prices, so that total commercial value can be determined. Detection monitoring also requires establishment of control areas where mushroom harvest is restricted.

The scattered distribution of fungal sporocarps in forest stands and the extensive land area needing to be sampled present the greatest difficulty for establishing a regional monitoring program. Most mushroom-detection sampling designs use either transects (long, narrow strip plots) or quadrats (square or circular plots); each approach has strengths and weaknesses (Vogt and others 1992). We use a variety of transect methods. Some transects serve as permanent plots and are repeatedly sampled throughout the fruiting season for several years. Others are temporary, with either randomly chosen locations, or locations chosen to systematically sample a given land area; for example, numerous parallel transects. They allow search of extensive areas for sporocarps. Once located, sporocarp distributions can be mapped for later ecological study of the fungal colonies. Compared to square or circular quadrat sampling plots, transects increase the likelihood of detecting mushrooms in areas where fungal fruiting is patchy or is responding to fine-scale changes in abiotic or biotic conditions within a stand. Narrow transects 1 to 2 meters wide reduce trampling effects and human error in detection, because the harvester can easily see and reach into the plot without disturbing the soil. We are testing transects of variable width and length to determine which best assess mushroom productivity and distribution in different forest habitats and topographic conditions.

Evaluation monitoring addresses questions about the effects of mushroom harvest and forest management practices. It relies on trends in data from detection monitoring. For example, if detection monitoring indicates declining levels of mushroom harvest, additional evaluation monitoring is needed to determine the extent and cause of the impact. Evaluation monitoring focuses on specific concerns such as mushroom harvest level, type and intensity of site disturbance and changes in forest structure and composition. Forest managers can use results from evaluation monitoring to assess impacts of these activities and then modify management approaches accordingly. Evaluation monitoring also can include studies that evaluate strategies for increasing production of commercial mushrooms.

As an example, to evaluate the effects of various mushroom harvest techniques on future mushroom productivity of American matsutake, we are conducting evaluation monitoring studies in four areas in Oregon. Harvesters sometimes disturb soil layers looking for the more valuable immature matsutake, which causes concern for future fruiting. Specific treatments in order of increasing soil and mycelium disturbance include (1) control plot - no mushroom harvest; (2) mushroom harvest with minimal disturbance of soil and fungus mycelium - individual mushrooms are located and gently pulled from the soil; (3) after a matsutake colony is located, the litter and humus are removed over the entire colony by raking the surface organic material to the depth of the mycelium and pulling it to the side of the colony - the mushrooms are then pulled from the soil and the litter and duff replaced over the colony; (4) same procedure as treatment three, but the litter and duff are not replaced over the colony; (5) same procedure as treatment four, but deep raking occurs throughout the mycelium, thus completely disrupting the roots and fungal network - disturbed layers are replaced; and (6) deep raking but soil layers are not replaced. In another study, 5 liters of water per square meter of fruiting area was added at 2-week intervals throughout the fruiting season as a fruiting enhancement technique.

Research monitoring examines basic biological and ecological phenomena and presents a myriad of investigative opportunities for mycological research. In addition to specific studies on their mycorrhizal ecology, research would examine the functional roles of these fungi in forest ecosystems. For example, how do these fungi contribute to nutrient cycling, soil aggregation, and overall site productivity? These investigations can be conducted concurrently within detection and evaluation monitoring sites where environmental and forest stand data are available. Modern methods and techniques, such as molecular DNA tools and *in vivo* root observation chambers, can be used to great advantage in these studies to better understand mycorrhiza dynamics.

Future Challenges

The difficulty in assessing cause and effect for the decline for some ectomycorrhizal fungi in Europe emphasizes the need for establishing long-term fungal inventory and monitoring programs. The intense commercial harvest of edible ectomycorrhizal fungus sporocarps heightens this need in the Pacific Northwest. Long-term monitoring is essential to assess the "carrying capacity" of the land and to develop ecological models to predict future mushroom productivity. Changes noted in mushroom productivity also can serve as biological indicators of large-scale changes in forest health due to management practices, pollution, or global climate change.

The greatest challenge in this endeavor for mycologists and forest managers is dealing with broad landscape, regional-scale, and long-term questions. Most field studies of mushroom production and fungal species diversity focus at the stand level and are of short duration (Pilz and Molina 1996, Vogt and others 1992). Few fungal community studies address questions of habitat disturbance or effects of mushroom harvest on future sporocarp production, and available data thus relate little to managing widespread commercial harvesting. To meet these challenges and provide the essential information needed to wisely manage fungal resources, mycologists must work closely with other scientists, forest managers, and interested publics to conduct cooperative studies within an ecosystem framework. Several such integrated studies are underway in the Pacific Northwest (see Pilz and Molina 1996).

QUESTIONS FROM THE SYMPOSIUM FLOOR

Q: Can we ever hope to characterize system health from the fungal diversity that would be expected at different times over succession of a forest?

A: Yes, I think this is a realistic goal and we are conducting research on that topic. We have found that several species of fungi occur during different periods of forest community development. Some are only found in old, mature forests and often associate with legacy structures such as buried wood from fallen trees or deep organic matter. The bright yellow ectomycorrhizal fungus, *Piloderma croceum,* is one such fungus. We believe the presence of this fungus during later stages of forest community development could serve as an indicator of a healthy, functioning forest ecosystem. One of our goals over the next several years is to build habitat based models of fungal diversity. Such models would provide specific habitat characteristics that predict presence and function of particular fungal species or species guilds. If used at a broad landscape scale, such models could provide valuable information to managers and enable them to select management options that maintain or create critical fungal habitat.

Q: What is the health and functionality of mycorrhizal mats in moderate to heavily compacted skid trails? If these mats are still functionally, active, does subsoiling negatively impact these mats?

A: Ectomycorrhizal fungi are strongly aerobic so soil compaction can have a negative effect on presence and function of ectomycorrhizal fungi. We have studied the production of ectomycorrhizal fungus sporocarps in compacted vs. noncompacted soils and production is less in compacted soils. Also, fungal diversity differs between these two soil types and is typically lower in compacted soils. Those fewer species found in compacted soils are likely adapted to such disturbed conditions. Although we have not conducted quantitative studies on ectomycorrhizal root tip abundance in compacted soils, other studies have shown diminished rooting of tree seedlings in compacted soil.

It follows that ectomycorrhizae would also be diminished and subsequently the activity of mycorrhizal fungus hyphae. We have not seen typical production of ectomycorrhizal fungal mats in compacted soil as is common in most forest soils. Subsoiling could have a direct negative effect on fungi that are trying to grow in compacted soil. But more likely, subsoiling would be beneficial in the long run by providing better soil aeration. Specific studies are needed to address long-term effects of soil compaction and subsoiling treatments on mycorrhizal functioning.

Q: What is the relationship, if any, between the decay of coarse woody debris, the formation of humus, and the health of mycorrhizal fungi?

A: The presence of coarse woody debris and humus formation is particularly critical to the health and function of ectomycorrhizal fungi. Many ectomycorrhizal fungi (and their ectomycorrhizae) develop exclusively or fruit extensively in well-rotted, buried wood or deep humus. More importantly, work in Idaho and southern Oregon (see chapters by Al Harvey and Mike Amaranthus, this proceedings) shows that in arid forest ecosystems, ectomycorrhizae are most abundant in buried wood compared to mineral soil. Such substrates have strong moisture holding capacity so they may serve as critical water resources during times of drought. Also, recent studies show that ectomycorrhizal fungi have greater enzymatic capabilities to degrade organic nitrogen and carbon than was previously thought. Thus, coarse woody debris and humus material provide a direct food source for mycorrhizal fungi and a nutrient source for their associated host trees. Maintaining such coarse woody debris is critical for sustaining the healthy function of the diverse forest mycoflora.

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SOIL BACTERIA: A DYNAMIC POOL OF SOIL ORGANIC MATTER AND CATALYSTS OF KEY BELOWGROUND PROCESSES

Jeanette M. Norton[1]

ABSTRACT

Bacteria are key components of the soil ecosystem forming the basis for the soil food web and mediating important biogeochemical reactions. Bacteria are the most numerous soil organisms in terms of numbers of individuals, but in most wildland ecosystems bacteria comprise a smaller portion of the microbial biomass than the fungi. The bacterial biomass is a portion of the soil organic matter that has a relatively rapid turnover time and therefore has the potential for releasing quantitatively important plant available nutrients during turnover (death). The active soil bacteria can be distinguished from inactive by their ability to respire and process carbon, but microscopic methods for this differentiation are too labor intensive or expensive for most ecosystem level (field) studies. The active bacteria have an incredible metabolic diversity and their metabolic types may be classified on the basis of their sources of energy, carbon and reducing power. The types of bacterial metabolism present in the soil are dependent on the oxygen status (redox potential) in the soil environment. Specific bacterial metabolic products are indicators of anaerobic (oxygen deprived) soil conditions. The presence of active bacteria with a specific metabolic potential combined with the appropriate environmental conditions results in the activity of bacteria as catalysts for key soil processes. The chemolithotrophic bacteria are especially important for their major role in the biogeochemistry of nitrogen, sulfur and iron.

Keywords: soil bacteria, bacterial biomass, microbial biomass, diversity, redox potential, biogeochemistry

INTRODUCTION

Bacteria are the most numerous of the living organisms on the surface of the earth and are the most diverse. In a single gram of surface soil there are generally in excess of a billion individuals (Metting 1993), potentially representing more than 1000 different types or species (Torsvik and others 1990). Bacteria and fungi together comprise the soil microflora and are the foundation for the soil food web (Bloem and others 1997). The products of primary production, both above and below-ground plant debris, must pass through the soil microflora before entering the soil organic matter. Jenkinson (1977) described the microbial biomass as the "eye of the needle through which all organic material that enters the soil must pass." The soil microbial biomass carbon comprises approximately 2-5 percent of the soil organic carbon in a wide range of surface soils (Smith and Paul 1990).

The soil bacteria are incredibly diverse both in their types and their metabolic capabilities. The bacteria can use a wider range of compounds for the production of energy and biomass than any other group of organisms. Soil bacteria can be active and mediate the transformations of carbon and nutrient elements under environmental conditions that restrict the activities of other organisms. Therefore, the bacteria are both a significant portion of the soil microbial biomass and the catalysts of key belowground processes in carbon and nutrient cycling.

BACTERIA AS A POOL OF SOIL ORGANIC MATTER

The soil organic matter (S0M) is comprised of both living and non-living components and varies widely in amount and quality, depending on the soil type and location. On a broad scale, the amount of soil microbial biomass correlates to the amount of SOM, with the microbial biomass carbon accounting for 2-5 percent of the soil organic C (Smith and Paul 1990, Martens 1995). Bacteria comprise only a portion of this microbial biomass and the dominance of bacteria versus fungi varies with soil and ecosystem type, location and depth and previous management history.

Quantifying Soil Bacteria

The numbers of bacteria in the soil varies widely in different ecosystems but is grossly correlated with the level of organic C in the soil. Numerous attempts to compare total microscopic counts of bacteria to viable counts on media plates have shown that most of the

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[1] Jeanette M. Norton is an Assistant Professor of soil microbiology in the Department of Plants, Soils and Biometeorology at Utah State University, Logan UT 84322-4820.

bacteria in soils are not recoverable on standard microbiological media (Torsvik and others 1990, Bakken 1997). Therefore direct microscopy is the preferred method for determining total numbers of bacteria in any given soil, and plate counts are of very limited value. Epifluorescence microscopy has the advantage of allowing the visualization of bacteria against the opaque background of soil particles and allowing the visualization of bacteria in the smaller ($<0.1\ \mu m^3$) size classes. The currently recommended fluorescent stains and procedures have been summarized (Bottomley 1994, Bloem and others1995). The numbers of bacteria in defined size classes can be used to convert bacterial numbers to biovolume and biomass estimates. Recent advances in image analysis and confocal microscopy may make direct counting and size analysis of fluorescently stained bacteria more efficient and less subject to microscopist bias (Bloem and others 1995).

Techniques are available for differentiating active from inactive bacterial cells in soils (Norton and Firestone 1991, Bottomley 1994, Hartmann and others 1997). Using these methods one can estimate the portion of the bacterial biomass that is considered active using an operational definition. Typical values vary around 50 percent but are dependent on the soil type, organic matter availability and proximity to roots (for example see Norton and Firestone 1991). The complexity of the methods available and the high spatial and temporal variability of active bacteria means that determination of the quantity of active bacteria is currently too laborious and expensive for most field studies.

As an alternative to microscopic methods, physiological methods have been used to examine the quantity and activity of soil bacteria. In the widely used substrate induced respiration (SIR) method, the respiratory response of soil microorganisms to glucose substrate addition, in combination with selective antibiotics, is measured and related to the contribution of bacteria and fungi to soil respiration (Anderson and Domsch 1973, 1975). SIR values are also typically converted to microbial biomass C and used to derive fungal to bacterial ratios. Discrepancies between values determined by microscopy and SIR techniques (Bardgett and others 1996, Velvis 1997) and the numerous assumptions typical of both microscopic and SIR determinations has made cross site comparisons and interpretations of active bacteria values extremely difficult. Selected values for bacterial biomass C as determined by fluorescent microscopy and the SIR method are shown in table 1.

Turnover of the Bacterial Biomass Releases Nutrients

The death and decomposition of microbial cells and their incorporation into new microorganisms or into the SOM is known as microbial turnover. The nutrient content of living microorganisms is generally higher than that of the total SOM, and as these microorganisms die the nutrients released become available for plant uptake. Conversely, the growth of the microbial biomass can incorporate or immobilize nutrients, making these unavailable for plant uptake. Estimates of the size of the microbial biomass and its nutrient content, together with calculated turnover times, reveal that the release of nutrients from microbial turnover is large enough to meet plant demands in many ecosystems (Smith and Paul 1990). The microbial biomass is estimated to turnover approximately 2-5 times per year (Smith and Paul 1990) although the bacterial turnover rate is thought to be significantly more rapid. For example, in an agricultural and a forest soil the bacterial population was calculated to turnover between 14-28 times annually (Baith 1990). These turnover values emphasize that the bacteria in soil are a significant source and sink for plant nutrient elements.

Turnover of bacterial cells in soil is caused by both biotic and abiotic factors. Grazing or predation by soil fauna such as protozoans and nematodes plays an important role in releasing the nutrients found in the microbial biomass (Bloem and others 1997). When grazers and predators consume the relatively nutrient rich bacteria, excess nutrients are released in plant available forms, such as ammonium and phosphate. Abiotic factors, such as wetting and drying cycles and physical soil disturbances (for example tillage, timber harvest, fire), cause various levels of microbial turnover. Soil wetting and drying events have been shown to affect bacterial numbers and biomass values, with moist soils favoring bacteria growth (Clarholm and Rosswall 1980, Lundgren and Soderstrom 1983, van Veen and others 1985). For example, in the humus layer of a pine forest, a peak in bacterial numbers followed within 3 days of wetting rainfall events (Clarholm and Rosswall 1980). Freeze-thaw cycles may also release some of the plant available nutrients contained in bacterial cells. Soil disturbance which incorporates plant residues such as tillage or those accompanying timber harvesting may cause rapid growth of the soil microorganisms and then subsequent death and release of nutrients to the soil.

Table 1 —Bacterial biomass and fungal/bacterial (F/B) ratios in surface soils.

System type	Treatment or soil type	Location	Method[a]	Bacterial biomass (dry wt) mg kg^{-1} soil	F/B biomass
Agricultural[b]			DM		
	conservation reserve	WA, USA		29	2.9
	wheat fallow			25	2.1
Mixed Conifer Forest[c]		CA, USA	DM		
	old growth H-layer			590	2.2
	clearcut mineral soil			80	7.9
Pacific NW Riparian[d] (summer)		OR, USA	DM		
	mixed forest			1200	8.8
	pasture			800	3.3
Scots Pine Forest[e] (seasonal mean)		Wekerom, NL	DM		
	L-layer			302	NA[f]
	F-layer			308	
	H-layer			252	
Desert[g]		Negev, Israel	SIR		
	wet season			200	0.6
	dry season			30	1.2

[a] Methods: direct microscopy (DM) or substrate induced respiration (SIR).
[b] Staben and others (1997).
[c] Norton (1987) unpublished data.
[d] Griffiths and others (1997).
[e] Berg and others (1998).
[f] Not available.
[9] Vishnevetsky and Steinberger (1997).

BACTERIA AS CATALYSTS OF KEY SOIL PROCESSES

Energy and elemental cycling through the microbial biomass is the basis for plant residue decomposition and biogeochemical nutrient cycling. The portion of the microbial biomass active in the transformation of a substrate can be described as the catalyst for the specific process. In enzyme kinetic theory the dependence of the rate of substrate depletion on both the substrate concentration and the microbial catalyst would be described as a second-order reaction according to the following equation:

$$\frac{dS}{dt} = -k[B][S]$$

where $\frac{dS}{dt}$ is the rate of change of the substrate (S), k is the rate constant and B is the microbial catalyst concentration. If the microbial biomass concentration is constant over time then the above equation reduces to:

$$\frac{dS}{dt} = -k^1[S]$$

where k^1 is the apparent rate constant and the reaction is a pseudo-first-order reaction.

In the soil environment, the microbial catalyst may be considered constant only over relatively short time periods, and annual cycles in the size of the microbial catalyst population should be considered for reliable estimates and models (Smith and Paul 1990). The reactions catalyzed by the soil bacteria include a wide diversity of processes which cycle carbon from plant primary production into the SOM and transform nutrient elements. While many bacteria are generalists and are capable of varied processes, some bacterial groups have specific metabolisms and a restricted range of transformation which they mediate. The next section classifies the metabolic types found in the soil bacteria.

Classification of the Metabolic Diversity of Bacteria

The systematic classification of metabolic types of organisms is based on three basic biochemical requirements: 1) an energy source, 2) a source of carbon and 3) a source of reducing equivalents. This classification scheme is summarized in table 2. Each of these categories has a specific prefix that is amended to the root, troph (from the Greek trope meaning nourishment) to yield combinatorial names for the specific metabolic types. For example, many common soil bacteria use organic materials as a source of energy, reducing equivalents and cell carbon. These organisms are then classified as chemoorganoheterotrophs which is often shortened to simply heterotrophs. The cyanobacteria important in the formation of microbiotic crusts are generally photolithoautotrophs, using photosynthesis and $C0_2$ fixation to colonize their harsh environment. Some important bacteria in biogeochemical cycling are chemolithotrophs which use chemical oxidation as the source of energy and inorganic compounds as the source of reducing equivalents. Some representative genera of bacteria important in the cycling of nitrogen, iron, sulfur and methane are listed in table 3. Many of these chemolithotrophs are autotrophs and capable of fixing CO_2 for their C source. The chemolithoautotrophic bacteria include the ammonia oxidizing bacteria such as *Nitrosomonas* important in the process of nitrification. The chemolithotrophic bacteria are of crucial importance to ecosystem processes and control the abundance and form of major nutrient elements, such as N, S, Fe and Mn through their oxidation and reduction reactions (Haack 1996). Examples of these bacterial processes are given in the following sections.

Table 2 —Classification of Organisms based on Energy Source, Carbon Source and Source of Reducing Equivalents

Energy Source:

Light = phototroph
Oxidation of organic or inorganic compounds
chemotroph

Carbon Source:

Inorganic = autotroph
Organic = heterotroph

Source of Reducing Equivalents:

Inorganic = lithotroph
Organic = organotroph

Bacteria may also be categorized based upon their requirement for oxygen for growth and the production of ATP. Bacteria which require oxygen are aerobes and have respiratory metabolisms with O_2 as the terminal electron acceptor. Anaerobic respiration uses other inorganic oxidized compounds such as nitrate or sulfate as alternative electron acceptors, while fermentation uses internal electron transfer between organic compounds. The facultative anaerobes can grow with or without oxygen and may be particularly important in controlling the oxygen availability in soil environments. While the metabolic classification of bacteria has proven useful, it is important to remember that some organisms in nature do not respect these rigid categories and switch from one type of metabolism to another, dependent on environmental conditions.

Environmental Constraints on Bacterial Metabolism

The types of bacterial metabolism that are active in a soil are highly dependent upon the availability of oxygen, which is primarily controlled by the water status of the soil. As O_2 is used by microbial metabolism it is replaced by diffusion from the atmosphere a process which is extremely slow through water filled pores. The intensity of a soil's reduction or oxidation is known as the redox potential and is a measure of the availability of electrons. Aerated soils have positive redox potentials varying from around +400 to +700 mV, while waterlogged reduced soils have negative redox potentials typically as low as -200 to -300 mV. The redox potential of soils interacts with soil pH and sets limits on the redox and pH values found in soil systems (fig. 1, Bohn and others 1985). The redox potential decreases as microbial metabolism shifts from aerobic to anaerobic respiration (that is denitrification, sulfate respiration) and eventually to fermentation. A representative series of microbial reactions and their reference redox potentials is shown in table 4. The bacterial groups responsible for a wide variety of transformations in soil are active in different ranges of redox potential (Eh) and pH as shown in figure 2. Some of these processes are discussed individually in the following section. The abiotic controlling factors of temperature and water potential on the transformation of organic matter and on microbial metabolism in general are outside of the scope of this report but are summarized by Paul and Clarke (1989).

Examples of Key Soil Processes Unique to Bacterial Metabolism and their Relevance to Ecosystem Management

The following examples have been chosen as examples of processes mediated by bacteria that may be of key

Table 3 —Examples of chemolithotrophic bacteria and their functions in the soil.[a]

Element	Active under aerobic (oxidizing) conditions	Active under anaerobic (reducing) conditions
N	Nitrifiers	Denitrifiers
	Ammonia oxidizers: *Nitrosomonas, Nitrospira* Nitrite Oxidizers: *Nitrobacter*	*Paracoccus denitrificans,* *Thiobacillus denitrificans*
Fe	Iron Oxidizers	Iron Reducers
	Gallionella, Sulfobacillus *Thiobacillus ferrooxidans*	*Geobacter*
S	Sulfur Oxidizers	Sulfur Reducers
	Thiobacillus, Thiothrix	*Desulfovibrio, Desulfobacter*
C	Methane Oxidizers (C1 only)	Methanoaens and Acetogens
	Methylococcus, Methylocystis, Methylosinus	*Methanobacteriaceae, Acetobacterium*

[8] from Haack 1996.

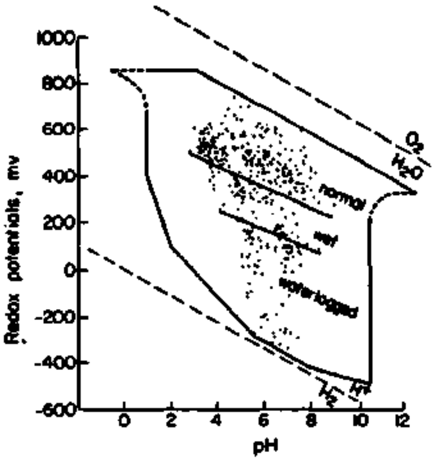

Figure 1 —The range of redox potentials and pH values in soils. From Bohn and others 1985, Soil Chemistry based on Bass Becking and others 1960, J. Geology 68: 243, 1960.

importance to ecosystem function and management. The role of bacteria as generalized decomposers of plant residues is not discussed here, but see Bloem and others (1997) for a discussion of the soil food web. Several of the processes described are involved in the N cycle. Since N is the most often limiting nutrient to plant growth, bacterial N transformations are of particular importance.

Chemolithotrophic nitrification —Nitrification is defined as the biological conversion of reduced nitrogen in the form of ammonia (NH_3) or ammonium (NH_4^+) to oxidized N in the form of nitrite (NO_2^-) or nitrate (NH_3^-).

The conversion of a cation, NH_4^+, which is retained by the negatively charged soil matrix to an anion (NO_2 or NO_3), which is mobile in the soil, strongly influences the fate of N in the ecosystem. In most soil environments nitrification is mediated primarily by chemolithotrophic bacteria which gain energy from the oxidation of N. The oxidation of N takes place in two steps: the ammonia oxidizing bacteria such as *Nitrosomonas* and *Nitrosospira* convert NH_3 to $N0_2$ according to:

$$NH_3 + O_2 + 2H^+ + 2e^- \quad NH_20H + H_20 \quad N0_2^- + 5H^+ + 4e^-$$

While the nitrite oxidizing bacteria such as *Nitrobacter* convert $N0_2$ to NO_3 :

$$NO_2 + H_2O \quad NO_3 + 2H^+ + 2e^-$$

Note that both reactions require O_2 and produce acid in the soil environment. The population of nitrifying bacteria and their activity is generally limited by the availability of their substrates, particularly NH_4^+ but also O_2. In systems where vegetation has been removed (for example clearcuts, overgrazed range), excess NH_4 which was formerly taken up by plants or heterotrophic microorganisms may become available for nitrification. This stimulation of nitrification in conjunction with diminished $N0_3^-$ use can lead to accumulations of NO_3^- in soils (Vitousek and others 1982, Stark and Hart 1997). The potential for N loss from the system by leaching and denitrification (see below) increases under conditions of high NO_3^- availability and may have detrimental effects on water quality and atmospheric chemistry. Maintaining the N

Table 4 — Thermodynamic sequence for reduction of inorganic substances at pH 7.0 and reference redox potentials.[8]

Reaction	E_h (Volts)
Disappearance of O_2 (aerobic respiration)	
$O_2 + 4H^+ + 4e - 2H_2O$	0.816
Reduction of NO_3^- (1st step of denitrification)	
$NO_3^- + 2H^+ + 2e - NO_2^- + H_2$	0.421
Reduction of Mn(IV) to Mn (II)	
$MnO_2 + 4H^+ + 2e- - Mn^{2+}\ 2H_2O$	0.396
Reduction of Fe(III) to Fe(II)	
$Fe(OH)_3 + 3H^+ + e^- - Fe^{2+} + 3H_2O$	-0.182
Reduction of sulfate to H_2S gas	
$S0_4^2 + 10H^+ + 8e - H_2S + 4H_2O$	-0.215
Formation of CH_4 (methanogenesis)	
$C0_2 + 8H^+ + 8e^- - CH_4 + 2H_2O$	-0.244

[a] From Stevenson (1986).

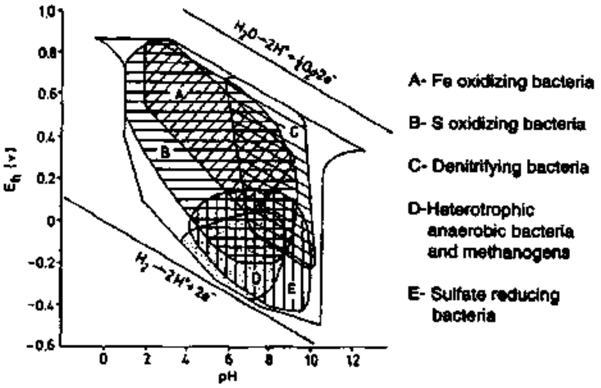

Figure 2—Environmental limits of Eh and pH for some bacterial groups. From Ehrlich 1990, Geomicrobiology based on Bass Becking and others, J. Geology 68: 243, 1960.

fertility of a wildland site over the long-term will also require management to retain N on the site or to replace it by fertilization. In agricultural systems, nitrification inhibitors such as nityrapyrin (trade name N-serve, Dow Chemical Co.) are used to inhibit nitrification for a relatively short time period (approximately 4 to 8 weeks) and retain added fertilizer N in the NH_4^+ form (Paul and Clark 1989). In wildland systems, it is reasonable to control the accumulation of excess $N0_3^-$ by reducing the NH_4^+ available as substrate or by encouraging the use of NO_3^-. Management practices which maintain a high microbial and plant demand for inorganic N (NH_4^+ and $N0_3^-$) include: 1) leaving woody residues on the soil surface , 2) leaving adequate vegetation which can assimilate N, and 3) managing grazing to prevent waste accumulation in sensitive areas such as riparian zones and to maintain plant cover. The goal of ecosystem N management is to keep N onsite, in the NH_4^+ or organic N forms, where it can be available for future plant uptake.

Denitrification—Denitrification is defined as the bacterial respiratory reduction of nitrate ($N0_3^-$) or nitrite (NO_2) to the gaseous end products nitrous oxide (N_2O) and dinitrogen (N_2). The denitrification process results in the net loss of N from the ecosystem and is the primary route by which N is returned to the atmosphere from terrestrial systems. Denitrification occurs when soils containing NO_3 become depleted in O_2 primarily due to excess moisture. Under these conditions, certain bacteria have the ability to use NO_3^- as an alternative electron acceptor for anaerobic respiration. The capacity for denitrification has been found in at least 23 genera of bacteria, most of which are chemoheterotrophs (for example *Pseudomonas, Alcaligenes)* although there are several chemolithotrophs (for example *Thiobacillus denitrificans)* which also have this capacity (Firestone 1982, Haack 1996). The general requirements for rapid denitrification are 1) lack of O_2, 2) supply of NO_3, 3) available organic substrates (electron donors), 4) biological temperature range, and 4) presence of denitrifying bacteria. The management of denitrification in order to maintain N in the soil system should focus on maintaining the O_2 supply (aerobic soil) and limiting the accumulation of NO_3 (see section of nitrification). Management decisions should be focused on avoiding soil compaction and excess water which will promote the anaerobic conditions required for denitrification. It should be noted that in situations where there is excess N in the system (for example wastes, sewage) denitrification is often used as a way to eliminate excess N and return it to the atmosphere.

Sulfur oxidation and reduction-A summary of the microbial cycling of sulfur in soils is shown in figure 3. The oxidation and reductions of sulfur in soil are highly dependent on O_2 availability. In a transformation similar to nitrification, chemolithotrophic bacteria can use the oxidation of reduced sulfur compounds such as FeS and FeS_2 (iron sulfides and pyrite) and elemental S as a source of reducing equivalents and energy. This reaction generally requires available O_2 and produces an extremely acidic end product, H_2SO_4 (sulfuric acid) and frequently associated with heavy metal contamination. Bacteria in the genus *Thiobacillus* are examples of bacteria which mediate and accelerate this process. Sulfur oxidation can be devastating to the environment when reduced S containing ores or sediments are exposed to O_2 by being brought to the surface, causing acid drainage. Some examples include the exposure of sulfide containing sediment layers in road cuts and the activities associated with mining. Management implications are to ensure that mine spoils containing pyrite and others metal sulfides are properly managed in designed waste dumps to prevent exposure to air and acid drainage into surface waters. The BLM and the U.S. Forest Service require that companies assess the potential for acid mine drainage as part of the permitting process (White and Jeffers 1994). The other situation where sediments are rich in reduced S is found in coastal regions with sediments previously exposed to salt or brackish water. If these sediments are drained and exposed to aerobic conditions, the sulfide will oxidize and acid will be produced. Acid drainage often has an orange color typical of the oxidized iron compounds formed.

Under anaerobic conditions the opposing process of sulfate reduction may become significant. Certain bacteria (for example *Desulfovibrio)* can use sulfate (SO_4^{-2}) as an alternative electron acceptor when O_2 and $N0_3$ have become depleted (table 4). The reduction of SO_4^{-2} produces the sulfide ion (S^{-2}), which may be released from the soil as hydrogen sulfide gas (H_2S) or combine with Fe to form FeS. The presence of the "rotten egg" smell of H_2S and the black color associated with FeS are both strong indicators of anaerobic soil conditions. These are useful indicators of the hydric soils typical of wetlands (see following section also).

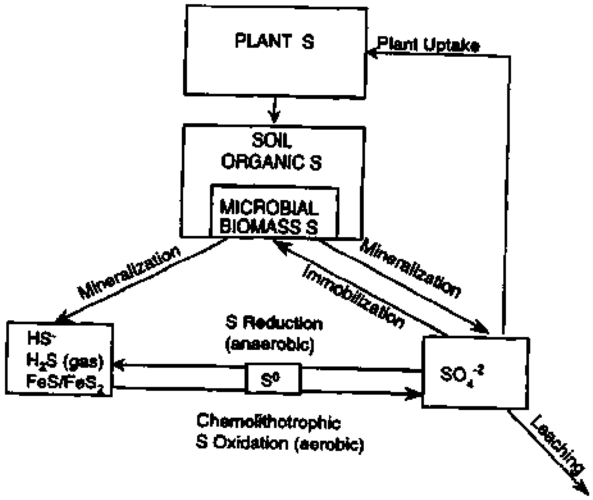

Figure 3—Microbial sulfur transformations in the soil environment.

Fe and Mn oxidation and reduction—The soil redox chemistry of Fe and Mn are complex with many reactions capable of occurring without microbial intervention. However, these same reactions often occur more quickly when the microbial catalyst is active (Loveley 1995). Certain chemolithotrophic bacteria have been implicated in the oxidation of Fe (II) to Fe (III); an example of a chemolithotrophic aerobic Fe oxidizing bacteria is *Thiobacillus ferroxidans.* Manganese oxidizing bacteria have been implicated in the formation of desert varnish, the dark coloring on desert rocks containing the brown MnO_2. Conversely, bacteria are also involved in the reduction of Fe and Mn under anaerobic conditions (table 4). Both Fe (III) and Mn (IV) are capable of acting as terminal electron acceptors in anaerobic respiration (Lovely 1995). The reduced products Fe (II) and Mn (II) give anaerobic soils their dark, low chroma or gleyed appearance. These reduced forms are also more mobile in soils and may be translocated, forming the redox depletions and concentrations that are indicators for hydric soils in wetland delineation.

SUMMARY

Bacteria have a crucial role in ecosystem processes both as a source and sink of carbon and nutrients and as catalysts for key ecosystem processes. Their incredible metabolic diversity allows them to transform carbon and nutrients under a wide variety of environmental conditions. In contrasts to plants and animals, the true extent of the diversity of bacteria in the soil environment is only beginning to be explored. The varied roles of bacteria in biogeochemistry are integral to the understanding and management of nutrient cycling, wetland geochemistry and C cycling in terrestrial ecosystems.

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DECOMPOSITION OF WOODY MATERIAL: NUTRIENT DYNAMICS, INVERTEBRATE/ FUNGI RELATIONSHIPS AND MANAGEMENT IN NORTHWEST FORESTS

Robert L. Edmonds[1] and James L. Marra[2]

ABSTRACT

Coarse woody debris (CWD) is being actively managed in many Pacific Northwest forest ecosystems because of its ecological importance. This paper discusses: (1) the source, amount and type of CWD present in ecosystems relative to their fire regime, (2) decomposition rates of CWD, (3) relationships among invertebrates, fungi and fire in the decomposition process, (4) nutrient dynamics in CWD, and (5) management of CWD. Amounts of CWD have decreased as a result of forest management west of the Cascade crest, but increased in the drier areas east of the Cascade crest as a result of fire suppression, defoliator and bark beetle attacks and diseases. Logs decay slowly, but this depends on their species and size and the environmental conditions. Coarse woody debris provides a considerable amount of soil organic matter, but lower amounts of nutrients. However, it can be both a source and sink for nitrogen. Invertebrates and fungi are intimately related in the decomposition process and CWD is a source of ecosystem biodiversity. Understanding the natural ecology of CWD in various ecosystems is important in determining how much CWD to leave and recruit. Long-term field experiments and simulation modeling efforts are being conducted to determine the role of CWD in ecosystem sustainability and in maintaining long-term productivity.

Keywords: logs, snags, coarse woody debris, decomposition, nutrients, invertebrates, fungi

INTRODUCTION

Until relatively recently coarse woody debris (CWD) was considered to be a nuisance for forest managers, interfering with plans for planting seedlings and regenerating sites. It was commonly yarded to logging landings, a practice known as YUM (yarding unmerchantable material), where it was usually burned. If it could not be yarded, it was piled and burned, or broadcast burned. However, since the 1980s scientists and forest managers have become increasingly aware of the need to retain intact CWD in ecosystems because of its ecological importance. Coarse woody debris is an important component of the concept of ecosystem management (Kohm and Franklin 1997). In terrestrial ecosystems CWD provides habitats for plants, small mammals, birds, bats, invertebrates, mycorrhizal and decomposer fungi and bacteria; improves slope stability and prevents erosion; stores water, carbon and nutrients; is a site for N fixation; helps maintain site productivity; and is an important site for biodiversity (Maser and Trappe 1984, Harmon and others 1986, Jurgensen and others 1987, Carpenter and others 1988, Franklin and others 1989, Harmon 1992, Caza 1993, Griffith and others 1993, Harmon and others 1994, Harmon and Sexton 1995, Bull and others 1997). It is also important in forest streams where it creates pools for fish and stabilizes stream banks (Maser and Trappe 1984). Some researchers, however, are still skeptical about the role of CWD, particularly with respect to its role in maintaining forest productivity. For example, Johnson and Todd (1998) suggested that dead logs in southeastern U.S. oak forests appear to be an ephemeral and rather unimportant ecosystem component. Respiration from logs is also considerable (Marra and Edmonds 1994), and this contribution to atmospheric CO_2 and global warming has been widely debated (Harmon and others 1990; Johnson and Todd 1998).

Harmon and Chen (1991) and Harmon and Sexton (1996) defined CWD as material greater than about 10 cm in diameter at the large end and 1.5 m in length. This is roughly comparable to the 7.6 cm diameter (the 100-hour fuel size break) used for fuel inventories. Coarse woody debris is now being actively managed in many forest ecosystems and sound, fresh logs as well as decaying logs and snags are left on site after harvesting. Fresh snags are created by cutting tree tops with chain saws or blowing them off with explosives and green trees are left as future sources of snags and eventually logs. These are considered to be biological legacies for the next forest and most state forest practices acts now include provisions for managing CWD. In Washington typical state provisions require managers to leave 5 logs greater than 30 cm in diameter and 12 green trees/ha (Washington Forest Practices Board 1995), but this varies from organization to organization. The Federal Northwest Forest Plan requires 15%

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[1] Robert L. Edmonds is a professor of soil microbiology and forest pathology. University of Washington, Seattle, WA 89195
[2] James L. Marra is a research associate in soil microbiology, University of Washington, Seattle, WA 89195

retention of the area in green trees where harvesting is allowed with tree densities ranging from 15-60 trees/ha (USDA Forest Service and USDI Bureau of Land Management 1994). Guidelines are also given for CWD; for most of western Oregon and Washington leave 180 linear meters of logs/ha greater than 51 cm in diameter, but logs less than 6 m in length are not credited towards the total. In eastern Oregon and Washington and southwestern Oregon a minimum of 90 linear meters of logs per ha greater than or equal to 41 cm in diameter and 5 m long should be retained. But should these recommendations for CWD apply to all forest ecosystems? We would argue no; CWD should be managed relative to its natural ecology. The Northwest Forest plan, however, does distinguish between moist and dry ecosystems.

We still have a lot to learn about the ecology and management of CWD in Pacific Northwest forest ecosystems. Coarse woody debris does not behave the same in all ecosystems and the functioning of CWD is largely controlled by the climate, tree species and fire regime occurring in a given ecosystem. Fire regimes are extremely important in the Pacific Northwest so they will provide the focus for this discussion. Agee (1993) delineated three distinct fire regimes defined by temperature and moisture conditions (fig. 1): (1) high intensity, low frequency fires that occur in western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) /Douglas-fir *(Pseudotsuga menziessi* (Mirb.) Franco), Pacific silver fir *(Abies amabilis* (Dougl.) Forbes) and subalpine ecosystems, (2) moderate intensity, frequency fires that occur in dry Douglas-fir, mixed evergreen, lodgepole pine *(Pinus contorta* var. *murrayana* (Grev. and Balf.) and red fir *(Abies magnifica* var. *shastensis* Lemm.) ecosystems, and (3) low intensity, high frequency fires that occur in mixed conifer, ponderosa pine *(Pinus ponderosa* Dougl. ex Laws) and oak woodland ecosystems.

The objectives of this paper are to discuss: (1) the source, amount and type of CWD present in ecosystems relative to their fire regime, (2) decomposition rates of CWD in representative ecosystems, (3) relationships among invertebrates, fungi and fire in the decomposition process, (4) nutrient dynamics in CWD, and (5) management of CWD.

SOURCE, AMOUNT AND TYPE OF CWD

Unlike fine litter, such as needles, leaves and small branches, inputs of CWD are pulsed and related to the events listed in table 1, such as fire, wind, insect attacks and management activities, that occur infrequently. Large wind storms such as the 1921 blow and the 1962 Columbus day storm in coastal Washington produced huge quantities of CWD. Coarse woody debris is also unevenly distributed spatially. A good example of this is provided by Agee and Huff (1987) who presented detailed maps of the position of large logs and snags in plots on the Olympic Peninsula of Washington. Logs may cover a considerable portion of the forest floor.

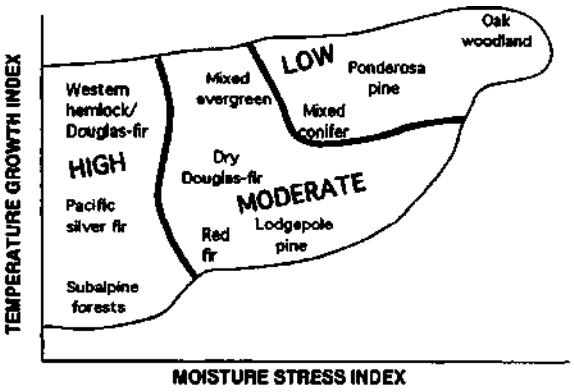

Figure 1 —Natural fire regimes in the Pacific Northwest (adapted from Agee 1993).

Table 1 —Factors influencing inputs of CWD into forest ecosystems.

Fire
Insect attacks (especially defoliators and bark beetles)
Disease
Wind
Interactions of disease and wind, fire and insects and fire, insects and diseases
Volcanic eruptions
Landslides and erosion
Floods
Avalanches
Competition among trees
Human activity - clearcutting, thinning, etc.

In the western Olympic Peninsula Edmonds and Lebo (in press) and Graham and Cromack (1982) reported that the average surface area occupied by dead boles was 9.8 and 11.6 percent, respectively. Franklin and Waring (1980) reported an even higher value of 16 percent for the Oregon and Washington Cascades. There is also a considerable amount of buried wood in the soil in cool, moist ecosystems. In drier east slope environments the surface area covered is generally smaller and buried wood is less common, especially in ecosystems with high fire frequency. The soil surface area occupied by logs is important because many tree species, such as western hemlock and Sitka spruce

(Picea sitchensis (Bong.) Carr.) regenerate almost solely on rotted wood. Rotted wood can also act as refugia for roots and mycorrhizal fungi, as well as invertebrates and other animals.

Coarse woody debris is an extremely dynamic component of forest ecosystems. In the Douglas-fir/western hemlock ecosystems in the Cascades of Oregon and Washington large high intensity stand replacement fires naturally kill large numbers of trees and produce large amounts of CWD as shown in figure 2. This CWD decomposes, but as the stand develops new inputs from competition mortality, insects, diseases and wind tend to increase the biomass of CWD until it is ready to burn again in the next high intensity fire 500 years after the initial fire, repeating the cycle.

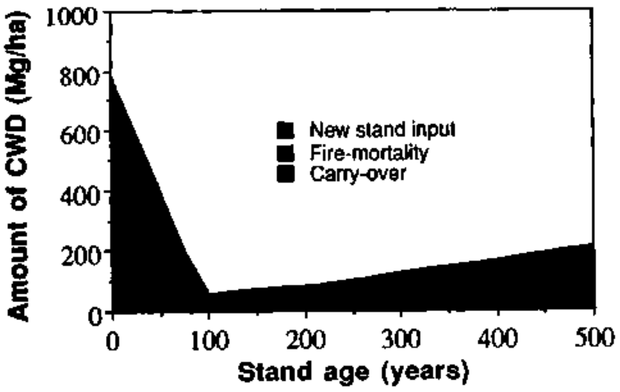

Figure 2 —Amount of coarse woody debris (CWD) in Douglas-fir/western hemlock ecosystems in the Oregon and Washington Cascade Mountains relative to time after a natural catastrophic stand replacement fire (adapted from Spies and others 1988).

Large wind storms such as the 1921 blow and the 1962 Columbus Day storm on the Olympic Peninsula of Washington also produce large areas of downed trees. Smaller gaps may develop with less intense storms. For example, on December 31, 1996 a storm created many gaps that were 1 ha or smaller in the Hoh rain forest in Olympic National Park. On closer examination we found that many of the blowdown trees in these gaps were suffering from Armillaria root disease. Interestingly, all of the trees were western hemlocks ranging in age from about 40 to 110 years. Larger and older Douglas-fir and western redcedars in the area were not blowdown. Wind and root diseases are intimately related in creating CWD in this case.

Table 2 shows the amount of CWD occurring in old-growth forests on the Olympic Peninsula with total amounts of logs and snags ranging from around 100 Mg/ha to more than 500 Mg/ha. Forest management, with YUM yarding, slash burning and 60-year rotations has short-circuited this process and as a result amounts of CWD in most managed west-side stands are now considerably lower and of smaller diameter than those in natural stands. Edmonds (1991) estimated that log biomass was <10 Mg/ha in third rotation Douglas-fir stands in the Puget Sound region while stumps contributed only 3 Mg/ha.

Table 2 —Biomass (Mg/ha) of logs and snags (coarse woody debris) in contrasting cool, moist western hemlock/Douglas-fir ecosystems on the Olympic Peninsula of Washington and hot, dry mixed conifer ecosystems in the Sierra-Nevada Mountains of California.

Western hemlock/Douglas-fir		Mixed conifer	
Logs	Snags	Logs	Snags
442[a]	95	20.2 - 43.3[b]	-
94-121[c]	26-40	28.0-48.74[d]	0.7-52

[a] Agee and Huff (1987)
[b] Kauffman and Martin (1989)
[c] Graham and Cromack (1982)
[d] Harmon and others (1986)

In contrast to the large amount of CWD in the moist forests, the amount of CWD in the low intensity fire mixed conifer forests of California is much less (< 100 Mg/ha and more usually near 50 Mg/ha) (table 2). However, in many dry forest types in the inland west, the amount of CWD is higher than natural levels, due to fire suppression, selective species logging, increases in stand density, bark beetles, and diseases such as white pine blister rust and Armillaria root disease. This has given forest managers a problem; should they remove this additional CWD by prescribed burning or salvage beetle killed trees to prevent future large fires? Many environmentalists strongly oppose salvage logging, but in some cases it may be justified. The season of burning controls the amount of CWD removed. Prescribed burns in mixed conifer forests in California in late fall can essentially consume all the CWD, especially rotten logs (table 3). Cooler fires in spring typically do not reduce the amount of CWD to the same extent and in some cases can actually increase CWD biomass due to tree mortality; for example, at the Challenge Experimental Forest (table 3). In some cases CWD may need to be protected during burning if there is not enough on the site.

DECOMPOSITION RATES OF CWD IN DIFFERENT ECOSYSTEMS

Decomposition rates of CWD vary according to species, diameter and stage of decay. Substrate chemistry is a major factor controlling decomposition. Extractives, or non-cell wall chemicals that convey decay resistance strongly control wood decomposition rates. Species with colored heartwood, such as Douglas-fir and western redcedar *(Thuja plicata* D. Don) are generally more decay resistant than white wood species such as western hemlock and true firs. Environmental factors such as temperature and moisture also control decomposition rates.

Table 3 —Percent consumption by prescribed fire of greater than 7.6 cm diameter logs in Sierra Nevada mixed conifer forests in California (from Kauffman and Martin 1989).

Season	Location	Log type	
		Sound	Rotten
Early fall	Blodgett Experimental Forest	40.3	96.1
	Challenge Experimental Forest	78.6	100.0
	Quincy Experimental Forest	83.7	100.0
	Average	67.5	8.7
Early spring	Blodgett Experimental Forest	37.3	33.4
	Challenge Experimental Forest	+ 35.6	+ 35.2
	Quincy Experimental Forest	48.0	81.5
	Average	16.6	26.6

Figure 3 shows the typical course of mass loss of Douglas-fir logs in old-growth forests in the Cascades of Washington and Oregon in relation to time. Four phases are involved. Phase 1 is a lag period before mass loss can be detected lasting 5 or so years. Following the lag period there is a period of fairly rapid decay involving fragmentation, leaching and microbial mineralization (Phase 2). Phase 3 is slightly slower and involves cellulose loss. The final stable phase involves very slow decomposition and lignin degradation. This is typical for brown rotted logs. The difference between brown and white rots is discussed in the next section.

Log decomposition is typically expressed as a series of negative exponential curves. A 3-exponential model fits the data in figure 3 representing phases 2, 3 and 4. Schowalter and others (1998) suggested that a 3-exponential model might also be suitable for oak log decomposition. The first phase represents an initial rapid loss from bark substrates followed by slower sapwood decay (phase 2). Phase 3 is the very slow heartwood decay. Logs, however, do not always decompose from the outside in. Insects are important in the initial stages of decay and wood borers may introduce decay fungi into logs allowing them to decompose rapidly from the inside (Edmonds and Eglitis 1989).

Table 4 shows CWD decomposition rates, expressed as half-lives, for both snags and logs of different tree species. Half-lives, or time to 50% exponential mass loss, for both mineralization and fragmentation are shown. Snags tend to decompose faster than logs, although some large Douglas-fir snags may slowly mineralize and may have half-lives as long as 230 years. Half-lives for snags vary from 5-55 years for fragmentation and 18-230 years for mineralization. Some standing dead trees simply fall after a period of time. In lodgepole pine ecosystems in Oregon, beetle killed trees mostly fell in the first 7 years (Mitchell and Preisler 1998).

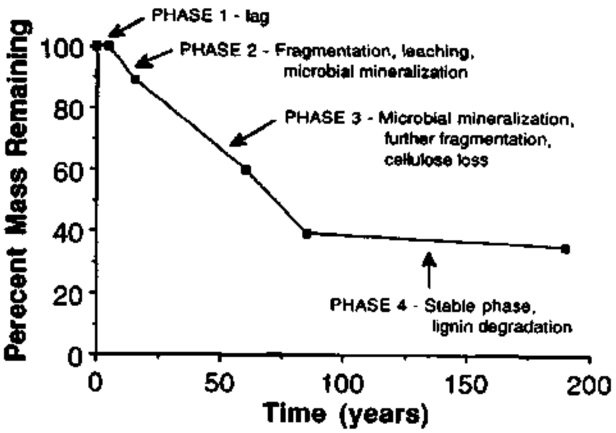

Figure 3 —Phases of decomposition of old-growth Douglas-fir logs in the Oregon and Washington Cascades. Data from Sollins and others (1987)..

Table 4—Decomposition rates (half-lives) of snags and logs of different tree species (from Harmon and others 1 986)

Species	Half-lives (years) Snags	
	Fragmentation	mineralization
Ponderosa pine	5-18	-
lodgepole pine	4-37	-
Douglas-fir	6-55	25-230
western hemlock	12	18-43
	Logs	
Ponderosa pine	-	-
lodgepole pine	-	57
white fir	36	14
Douglas-fir	166	98-172
western hemlock	-	29-88

Half-lives for logs vary from 36-150 years for fragmentation and 14-172 years for mineralization. Note that both Douglas-fir snags and logs decompose less rapidly than western hemlock snags and logs (table 4). Logs of white fir (*Abies concolor* (Gord & Glend.) Lindl. ex Hildebr.), a white wood species, and even lodgepole pine (Busse 1994), decompose very rapidly despite the dry environments in which they occur. Insects play an important role in the decomposition of white fir logs. In the dry mixed-conifer forests in Sequoia National Park in California, wood volume excavated by insects increased with the age of white fir logs (Harmon and others 1987). Logs less than 6-years-old were rarely attacked by carpenter ants *(Camponotus* spp.) or termites *(Zootermopsis nevadensis),* but in older logs insects excavated wood volume at a rate of about 0.7 percent per year. Relationships between insects, fungi and fire are discussed further in the next section.

Unfortunately, we could find no data for decomposition rates of large ponderosa pine logs. Erickson and others (1985), however, examined the decomposition rates of small 8-12 cm diameter sections of ponderosa pine in eastern Washington and found them to have an average half life of 53 years on the ground and 58 years when suspended above ground (table 5). Decomposition rates of the ponderosa pine sections were considerably slower than those for the Douglas-fir and western hemlock sections in western Washington. Table 5 also indicates that decomposition rates for the Douglas-fir, western hemlock and ponderosa pine sections were generally greater when the wood was in contact with the ground surface. Logs do not decompose uniformly and sections suspended above ground usually decompose slower than those in contact with the forest floor and soil because of more favorable moisture conditions. Interestingly, the slowest decomposition rates occurred in Pacific silver fir sections which had a half-life of 78 years whether suspended or not. In cold, moist, high elevation Pacific silver fir ecosystems, deep, long-lasting snow packs keep moisture conditions above ground similar to those on the soil surface for most of the year.

Table 5—Half-lives of 8-12 cm diameter wood sections situated on or suspended above the soil surface in different ecosystems in Washington (from Erickson and others 1985).

Species of wood and location	Position	Half-lives (years)
Pacific silver fir	On soil	77
Findley Lake	Suspended	77
Ponderosa pine	On soil	58
Eastern Washington	Suspended	53
Douglas-fir	On soil	19
Pack Forest	Suspended	43
Western hemlock	On soil	19
Olympic Peninsula	Suspended	29

RELATIONSHIPS BETWEEN INVERTEBRATES, FUNGI AND FIRE

Invertebrates, fungi and fire typically interact in the decomposition of CWD, although in cool, moist ecosystems fire plays a smaller role because of the long time periods between fires and the small average annual area burned. In these areas invertebrates and fungi dominate. In dry ecosystems fire and insects may dominate the decomposition process. Table 6 shows fire data for different forest types in Oregon, including areas in each type, fire severity, fire periodicity, average annual area burned and the percentage of area burned annually. As much as 6.7 percent of the ponderosa type burned historically every year, while less than 1 percent of the Douglas-fir, cedar/spruce/hemlock and subalpine types burned.

Table 6—Fire periodicity, severity, area, and annual historic area and percentage of area typically burned in Oregon (data courtesy of James Agee, College of Forest Resources, University of Washington).

Forest type	Fire periodicity (years)	Severity	Area in type (thousands of ha)	Average annual historic area burned (thousands of ha)	Percentage of area burned
Ponderosa pine	15	Low	3,142	209.4	6.7
Oak woodland	25	Low	1,002	40.1	4.0
Mixed conifer	30	Low	399	13.3	3.3
Lodgepole pine	80	Moderate	757	9.4	1.2
Douglas-fir	150	Moderate-High	4,446	29.6	0.7
Cedar/spruce/ hemlock	400	High	292	0.7	0.3
Subalpine	800	High	1,076	1.3	0.1
Other	-	--	2,398	18.0	0.8

An excellent example of interactions between fire, insects and fungi is provided in the moderate fire regime lodgepole pine forests in central Oregon (Gara and others 1985). In their study area they determined that a new lodgepole pine forest was established after a stand replacement fire in 1839. As the forest developed competition for light and moisture caused considerable suppression mortality. Over the next 60 years these small dead trees provided fuels that lay on top of the more decayed logs remaining from the 1839 fire. In 1989 a slow-moving-smoldering fire slowly burned the logs away to ash, killing trees and wounding major lateral roots and boles of residual trees where they contacted the burning logs. *Ips* spp. beetles attacked the killed trees and a succession of fungi entered the wounded trees, especially *Poria asiatica.* In 1970, the largest trees with advanced butt rot were preferentially attacked by the mountain pine beetle *(Dendroctonus ponderosae).* In subsequent years the largest of the remaining trees were attacked setting up the forest for another stand replacement fire 150 years after the initial fire.

Bark beetles and wood borers are among the earliest colonizers of wood (Edmonds and Eglitis 1987; Harmon and others 1987; Carpenter and others 1988). Edmonds and Eglitis (1987) found that the Douglas-fir beetle quickly attacked freshly downed Douglas-fir logs in the Cedar River Watershed 60 km southeast of Seattle, but had little influence on log decomposition. On the other hand, the wood borer *Monochamus scutellatus* introduced fungi deep into wood speeding up the decomposition process. The two most common fungi observed were *Oligoporus placentus* and *Fomitopsis pinicola,* both brown rotters. Logs that were screened to prevent insect attack had much less decomposition. Log diameter was an important variable; small diameter logs had less insect attack, perhaps because they could not establish in the bark or phloem. As a result large diameter logs had a faster decomposition rate than small diameter logs, which is counter to conventional wisdom.

Wood borers and bark beetles are not the only invertebrates associated with logs, and as decomposition proceeds a wide variety of invertebrates are found. Mites, Collembola, beetles and fly larvae commonly occurred in 10-30 cm diameter decay class 3 Douglas-fir and western hemlock logs in 50-70 year-old stands on the Olympic Peninsula (table 7). Logs are typically classified in 5 decay class from 1 (least decayed) to 5 (most decayed) (Maser and others 1979). Decay class 3 logs are the most common logs on the forest floor (Harmon and others 1986), and this is clearly illustrated in figure 4 for an old-growth forest in the Hoh River Valley in Washington for both log biomass and numbers per ha. Populations of mites and Collembola were much higher than those for beetles and fly larvae in both brown and white rotted wood (table 7). However, brown rotted wood had significantly higher populations of both mites and beetles than white rotted wood. Collembola were also higher, but not significantly. Brown rot is produced by fungi that decay only the cellulose, leaving a lignin residue that remains for hundreds of years contributing to soil organic matter. On the other hand, white rotted wood is produced by fungi that decompose both cellulose and lignin and thus has a much shorter residence time. White rotted wood may less favorable for invertebrates because it is thought to have a higher moisture content than brown rotted wood, although this is not always the case (table 8).

Table 7—Invertebrate density in brown and white rotted wood in 10-30 cm diameter decay Class 2-3 Douglas-fir/western hemlock logs on the Olympic Peninsula, Washington.

Invertebrate	Density (No. m^{-3}) Brown rot	White rot
Mites	177,231	112,716[a]
Collembola	80,801	54,117
Beetles	2,141	889[a]
Fly larvae	1,959	3,854

significantly different $p<0.05$.

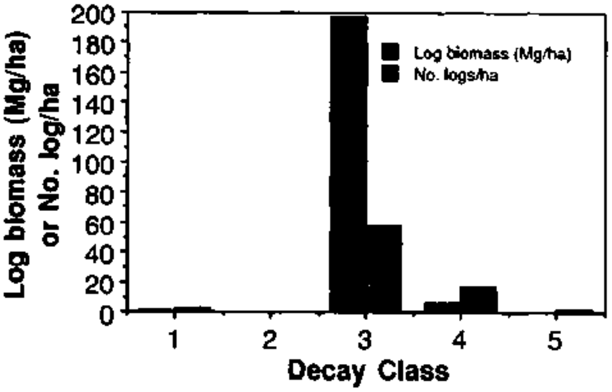

Figure 4—Log biomass and number of western hemlock and Sitka spruce logs per ha in various decay classes in an old-growth forest in the Hoh River Valley, Olympic National Park (from Edmonds and Lebo in press).

Decaying logs provide a considerable amount of biodiversity in forest ecosystems and to date we have found an average of 142 species of invertebrates in old-growth logs on the Olympic Peninsula and 112 species in logs in clearcuts. Interestingly, we have found a species of beetle in the Family Throscidae in logs young-growth stands that did not occur in logs in old-growth stands (Marra 1995). In general beetles appear to respond to changes in specific characteristics of CWD such as log species, diameter and species of fungal sporocarps more than other invertebrate groups, suggesting that they may be good indicators of ecosystem change. Carpenter ants and termites are also heavily involved in the wood decomposition process, but are more important in drier environments.

Table 8—Percentage of 10-30 cm diameter decay class 2-3 Douglas-fir/western hemlock logs on the Olympic Peninsula, Washington with brown and white rot and related moisture contents in spring 1995 and 1996.

Sampling Season	Percentage of decay type			
	Brown	White	Both	No decay
Spring 95	52	32	9	17
Spring 96	26	42	14	18
	Percent moisture			
	Brown	White	Both	No decay
Spring 95	169	157	153	102
Spring 96	168	206	260	137

Carpenter and others (1986) examined the early pattern of heterotroph activity in four species of logs in a 200 year log decomposition study established in 1985 in the H.J. Andrews forest in the Oregon Cascades and described in Harmon (1992). The foodweb during the early stages of decomposition includes nitrogen-fixing and other bacteria, fungi, protozoa, nematodes and arthropods. Fungi play an extremely important role in the wood decomposition process. Harmon and others (1994) found 13 species of fungi fruiting on class 1 logs in the first 7 years with maximum production of fruiting bodies at age 5. None of the species were mycorrhizal fungi. Edmonds and Lebo (in press) noted considerably more taxa (82, including 18 mycorrhizal species) in decayed logs on the Olympic Peninsula (table 9). Some species found by Harmon and others (1994) were not observed by Edmonds and Lebo (in press). Species common to both sites included *Naematoloma capnoides* and *Fomitopsis pinicola.* *Naematoloma capnoides* was the most common species on class 1 logs in Oregon. Logs are a considerable source of ecosystem biodiversity for both invertebrates and fungi in forest ecosystems.

Large diameter CWD in old-growth forests west of the Cascade crest appears to be largely decayed by brown rot fungi, particularly by *Fomitopsis pinicola.* Is the smaller diameter CWD associated with managed stands decayed mostly by brown or white rot fungi? We hypothesized that white rot fungi might predominate because of the higher sapwood component of small diameter logs. However, table 8 shows no consistent trend for small diameter Douglas-fir and western hemlock logs on the Olympic Peninsula. Samples of 30 decay class 2-3 logs revealed a predominance of brown rot in Spring 1995, but the opposite trend in Spring 1996. More data need to be obtained before we can come to a conclusion on this subject.

Table 9—Numbers of fungal taxa occurring on logs in an old-growth western hemlock/Sitka spruce forest in the Hoh River valley, Washington (from Edmonds and Lebo in press).

Type of fungus	Number of taxa
Decomposers/pathogens	64
Mycorrhizal	18
Total	82

Fire, invertebrates and fungi all operate in the log decomposition process. However, we still need to learn more about their roles and relationships, especially in dry environments. We know very little about fungi and invertebrates associated with charred wood and the decomposition rate of charred wood. Hadfield and Magelssen (1998), however, recently examined changes in trees killed by the 1994 fires in eastern Washington and found considerable stain, decay and insect development in many trees after only 3 years, depending on the tree species. The pouch fungus *(Cryptoporus volvatus)* was most commonly observed.

NUTRIENT DYNAMICS IN CWD

Coarse woody debris is regarded as a source of organic matter and nutrients for forest soils leading to the argument that loss of CWD debris from ecosystems will result in a loss of productivity. Johnson and Todd (1998) found that removing oak CWD on a harvested site in Tennessee had no effect on the C contents of either vegetation or soils after 15 years harvesting. The connection between CWD and forest productivity, however, still needs more research. Coarse woody debris contributes a large amount of organic matter to the soil in moist ecosystems in the Pacific Northwest, but only a small amount of nutrients. In the Hoh River Valley of Washington, the biomass of logs in all decay classes totals 205,000 kg/ha or 205 Mg/ha (table 10). The nutrient content of these logs, however, is relatively small (180 kg/ha for N, 20 kg/ha for P and 64 kg/ha for K). Fine litter contributes considerably more nutrients to soil than CWD (Keenan and others 1993).

Because of the high C/N ratio of logs (> 500:1) it has been suggested that logs are sinks for N during the decomposition process and Grier (1978) found strong immobilization of N in western hemlock logs in coastal Oregon during the first 24 years of decomposition. Nitrogen contents of logs can increase as a result of oatmospheric inputs, fungal hyphae transporting N from the surrounding litter, and internal N fixation by bacteria. Decomposing logs could prevent nitrate leaching losses from ecosystems by immobilizing N. Nitrogen losses from logs occur through fire, leaching, invertebrates and the production of fungal fruiting bodies. Even during the early stages of decomposition some N might be released from logs through leaching and the production of fungal fruiting bodies. Harmon and others (1994) found that from 0.9-2.9 % of the initial N, 1.9-6.6% of initial P and 1.8-4.5% of the initial K was released from logs in the first 7 years of decomposition in the Oregon Cascades. However, as decomposition proceeds, the amount of N, P and K released in fungal fruiting bodies seems to get smaller and in decay class 3 logs Edmonds and Lebo (in press) found that only 0.009 percent of the log N capital, 0.023 percent of the log P capital and 0.029 percent of the log K content was released annually. Both these studies illustrate that logs not only function as sinks for N but also as sources.

Table 10 —Log biomass and N, P and K content, annual sporocarp production and percentage of log nutrient capital in an old-growth western hemlock/Sitka spruce forest in Hoh River valley, Washington (from Edmonds and Lebo in press).

	Biomass	N	P	K
Logs (kg/ha)	205,049	180	20	64
Annual Sporocarp production (g/ha)	6.3	0.21	0.06	0.24
Percentage of log nutrient capital	0.0002	0.009	0.023	0.029

MANAGEMENT OF CWD

There is strong evidence that CWD plays important structural and functional roles in many forest ecosystems. However, the exact connection between the amount of CWD, expressed either as numbers of logs or biomass per ha, and forest productivity is not known. The diameter of CWD, contact with the soil surface, decay class, species, orientation on slopes, climatic regime and whether the CWD is located in upland or riparian forests or in a high, moderate or low fire severity regime are variables that have to be taken into account.

Very general guidelines have been given to forest managers with respect to leaving logs and snags and green trees from which new snags and logs can be recruited. How can we better refine these guidelines and make them more specific for each forest type? Several approaches have been taken; long-term experiments and modeling. There are a number of examples of long-term experiments including: (1) Mark Harmon's 200 year study at the H.J. Andrews Forest in Oregon (Harmon 1992), (2) the Long-Term Ecosystem Productivity (LTEP) Study of the U.S. Forest Service, and (3) the Habitat Development Project of the U.S. Forest Service on the Olympic Peninsula. The 200-year study involves 4 species (Douglas-fir, western hemlock, white fir and western redcedar) and 530 logs 5 m in length and 50 cm in diameter placed in 6 replicate locations on the H.J. Andrews. The LTEP Study is located at 6 sites; Sappho, on Washington State Department of Resources land and on the following national forests; Willamette, Umatilla, Siskiyou and Siuslaw in Oregon and Wenatchee in Washington. The study involves the following treatments; untreated controls in 50-100 year-old forests, 3 levels of CWD (low, moderate, and high) and 3 successional stages (early - clearcut with Douglas-fir and red alder, mid - clearcut with Douglas-fir, and late - thinned to promote late successional species). Treatment blocks are 6 ha with 3 replicates of each treatment. More details on the LTEP study are available on the following world wide web site - http://www.cof.orst.edu/research/ltep.

The Habitat Development Project is being conducted in Adaptive Management areas on Olympic National Forest as part of the Northwest Forest Plan. One objective of this study is to determine if piling small diameter CWD into structures resembling large logs provides better habitat for small mammals in thinned 50-70 year-old stands than scattered individual logs. As a component of this study we have been examining invertebrates and fungi and the proportion of brown and white rot in small diameter logs (tables 8 and 9). If there is a very high proportion of white rot then the logs will not last long and they will not function like large logs which tend to last longer because they are mostly brown rotted. One solution to this potential problem may be to inoculate fresh logs with brown rot fungi.

There are a number of computer models incorporating CWD that can be used to simulate removal or addition of CWD on forest productivity. An example is FORECAST (FORestry and Environmental Change Simulator) which is an ecosystem-level model designed to analyze the consequences of forest management on ecosystem function, sustainability and harvestable productivity (Kimmins 1997). Chapter 17 in Kimmins (1997) provides an analysis of models and their role in ecology and resource management.

While we wait for the results of long-term experiments and simulation runs to be completed, the best advice we can give is: 1. Inventory the CWD you have on a site and see if it falls within the natural range for that particular ecosystem. If not, then a decision needs to be made to add new logs or snags or even reduce CWD. Coarse woody debris levels should be related to habitat type and east- and west-side ecosystems should be managed differently. In moist ecosystems, it should be recognized that a large number of snags and logs would have to be added to many ecosystems to reach historical levels. If there were typically 50 or more logs per ha then adding 5 would make little difference to soil organic matter, but they might provide habitat for small mammals and salamanders. In drier ecosystems burning might be conducted to reduce CWD to historical levels. Salvage logging should be considered carefully with respect to potentials for future beetle epidemics and large wildfires. Maintaining a supply of suitable snags may be more difficult to accomplish than logs. Experiments are currently being conducted where a variety of fungi have been inoculated into green trees to prepare them for cavity nesting birds and other wildlife (Bull and others 1997). 2. Management objectives are very important to take into account. Is the site to be managed primarily for timber production or for other values, such as wildlife habitat and how does the site fit within the objectives for landscape? Understanding the ecology of CWD in a particular ecosystem is very important.

CONCLUSIONS

1. CWD plays an important role in the functioning of ecosystems. Its functional role in stream ecosystems has been well established and many stream restoration projects are underway. Its role in terrestrial ecosystems is still not completely understood. The sources, amounts, decomposition rates and perhaps the roles of CWD vary from one ecosystem to another. The amount of CWD varies by an order of magnitude from the cooler, wetter ecosystems to the hot, dry ecosystems in the Pacific Northwest.

2. Fire, fungi and invertebrates are all heavily involved in the creation and decomposition of CWD. Wind and fungi commonly function together to create CWD.

3. Amounts of CWD have decreased as a result of forest management in the cooler moister forests of the west slopes of the Cascades, Olympics and Coast ranges. However, it has increased in the drier, hotter east slopes of the Cascades as a result of fire suppression and bark beetle attacks.

4. Inputs of CWD are pulsed, which makes its management difficult. We still don't know exactly how much CWD to keep and add in terrestrial ecosystems and how to arrange it. Interesting questions still need to be answered, such as, what species is best to leave, should small logs be in bundles or left singly and how much brown rot versus white rot do we need? Do small log lengths (1.5 m) functions as well as long lengths (>6 m)?

5. Coarse woody debris is both a source and sink of carbon and nutrients in ecosystems even in the early stages of decomposition.

6. Coarse woody debris is a source of biodiversity in ecosystems, especially fungi and invertebrates.

7. We have a better understanding of the role and functioning of CWD in moist ecosystems than dry ecosystems. More research needs to be done in dry ecosystems.

8. We still don't know the exact relationship between CWD and the sustainability and long-term productivity of Pacific Northwest forests. The long-term log decomposition study at the H.J. Andrews and the LTEP study of the U.S. Forest Service are addressing this study, but results will be a long time in coming. The best short-term solution for examining management strategies is to be conservative and use simulation models which include CWD as a component.

QUESTIONS FROM THE FLOOR

Q: Could you speculate on why invertebrate numbers are higher in brown rotted logs than in white rotted logs?

A: We think that the moisture environment in brown rotted wood may be more favorable than that in white rotted wood. Typically white rotted wood is stringy and wetter than brown rotted wood. During certain stages of the decay process you can actually wring water out of white rotted wood. If the environment gets too low in oxygen then invertebrates would probably leave. There are probably other reasons to do with the food chain in decaying wood and the food source for invertebrates.

Q: If fire is the main decomposition agent in dry systems what difference does it make to have a fall burn? Isn't that when fires naturally happened?

A: Yes, most fires in dry ecosystems in the west naturally occur in the fall. What we were trying to point out was that you get more complete combustion of CWD in the fall than the spring. So if you wanted to reduce the fire danger from fuel accumulation, but not reduce the CWD completely, then spring would be time to burn, even though this may not have happened naturally.

Q: I don't understand how logs tied together replicate a natural CWD system? Can you explain?

A: The rationale behind this is that a large proportion of the CWD in old-growth forests is of large diameter. We obviously can't grow trees of this size in managed forests, so why not tie smaller diameter logs together in a bundle and see if they function like large logs. Small diameter logs are readily available in managed stands. The emphasis of the studies in the Forest Service Adaptive Management Areas in Olympic National Forest is to see if wildlife, particularly small mammals and salamanders, find bundled logs to be suitable habitat.We are looking to see if the decay in these small logs, i.e., the proportion of brown to white rot, is similar to large logs. If the decay is predominantly white rot then they will not last long and won't provide suitable habitat for small mammals and probably invertebrates.

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INVERTEBRATE BIODIVERSITY, FORESTRY AND EMULATION OF NATURAL DISTURBANCE: A DOWN-TO-EARTH PERSPECTIVE

John R. Spence[1], Christopher M. Buddie[2], Kamal J. K. Gandhi[3], David W. Langor[4], W. Jan A. Volney[5], H. E. James Hammond[6] and Greg P. Pohl[7]

ABSTRACT

A fire-based conceptual model of forest spatial dynamics is widely embraced as the way to make boreal forest management more ecologically friendly and to conserve biodiversity. However, use of the term "ecosystem based management" does not automatically confer either wisdom or naturalness to resource management tactics. We examine the logical structure of recently invoked arguments and summarize recent work to determine whether this conceptual model is necessary, sufficient and adequately developed to generate specific tactics for management of the western boreal forest. In particular, we show that biotic elements involved in both the early phases of natural succession and in the breakdown of coarse woody material will be at risk if only landscape level processes like the large-scale spatial dynamics of wildfire are considered in mangement. Development of complex stand structure associated with gap dynamic processes that are characteristic of post-rotational age forest should be accommodated in extensive forest management to conserve the biota and the processes that ensure long-term maintenance of site productivity. We preview developing efforts under the Canadian EMEND project to understand how the situation might be improved.

Keywords: biodiversity, invertebrates, boreal, natural disturbance, wildfire, spatial patterns

INTRODUCTION

Humans generally are impressed by big things, and trees are the biggest living things that most of us encounter day to day. Likewise large stands of trees, comprising primeval forests, intrigue us and provide comfort and solace to many. The Canadian boreal forest, as it presently exists in northern Alberta, is among the last of the Earth's large, wild forests, and this ecosystem is tightly linked to the identity of many Canadians. However, the western boreal forest is being cut at an unprecedented and accelerating rate (Pratt and Urqhart 1994). By the end of a projected 80 year rotation period started in the present decade, much of the remaining primeval timber will have fallen to the saw in Alberta. Never-cut forests of merchantable volume will remain only on inaccessible land or in a few scattered parks and reserves, but large tracts of regenerated forested land will remain to possibly satisfy our manifold non-timber interests. Nonetheless, natural dynamics on many scales, which have heretofore patterned the Canadian boreal landscape, will be profoundly altered by human activity. Will it matter? How will we know? Should we do anything about it? Can we do anything to guarantee a more favourable outcome? Although we are not in a position to answer these questions confidently with respect to many components of unmanaged forests, including their invertebrate faunas, ongoing research suggests answers that can be built into adaptive forest management.

Western societies have started to feel uneasy about the depth of our imprint on the planet's forests. In developed countries we increasingly consider forests as more than a collection of harvestable trees — first as habitats for charismatic wildlife, and now after the Rio Summit, as repositories for 'biological diversity'. In fact, conservation of 'biodiversity' is now widely, and perhaps somewhat uncritcally, accepted as representing whole forest values (fig. 1). Land-use policy makers are increasingly adopting biodiversity

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[1] John Spence, Professor, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9.

[2] Chris Buddie, graduate student, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9.

[3] Kamal Gandhi, graduate students. Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9.

[4] David Langor, Research Scientist, Canadian Forest Service, Northern Forestry Centre, 5320-122nd St., Edmonton, Alberta, Canada T6H 3S5.

[5] Jan Volney, Research Scientist, Canadian Forest Service, Northern Forestry Centre, 5320-122nd St., Edmonton, Alberta, Canada T6H 3S5.

[6] James Hammond, Biologist, Canadian Forest Service, Northern Forestry Centre, 5320-1 22nd St., Edmonton, Alberta, Canada T6H 3S5.

[7] Greg Pohl, Biologist, Canadian Forest Service, Northern Forestry Centre, 5320-1 22nd St., Edmonton, Alberta, Canada T6H 3S5.

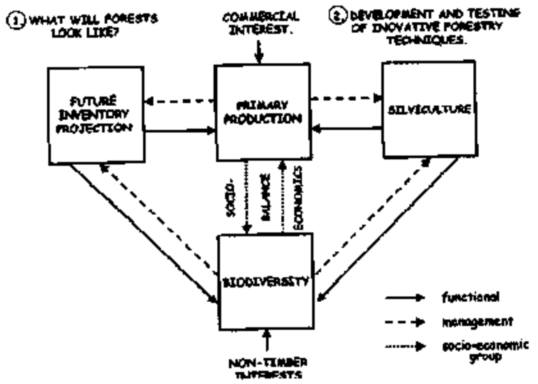


Figure 1-Forces that guide development of forest management. Since the Rio Convention on Biodiversity, both long- and short-term effects on biodiversity have entered the forest planning domain.

measures to indicate whether ecosystems are being maintained in a 'functionally integrated state'. In many countries, some version of the biodiversity criterion is being explored as a possible addition to those of regeneration standards and future inventory projection that have been used to support a sustained yield approach to allocating harvests (Probst and Crow 1991, Franklin 1993, Angelstam 1997). The new suite of evolving protocols proposed to regulate harvest and evaluate forest management plans is termed "sustainable forest management". Incorporation of the biodiversity criterion broadens the focus beyond fiber yield.

The general rationale for the approach adopted under sustainable forest management is that "nature knows best". Simply put, forest communities with biodiversity measures in the range of natural variation, as established from undisturbed areas used for baseline studies, are judged to be "healthy", whether or not we understand the ecological functions of the component species. This approach to managment of complex ecosystems acknowledges our ignorance. It prompts us to tread more gently with respect for the whole system, rather than insist on solid functional or economic evidence for retaining any particular component. Thus, more than a half century after it was penned, land use policies are being developed in the context of Aldo Leopold's famous, often-quoted metaphor: "If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering" (Leopold 1953). In this context, knowledge about non-pest forest invertebrate species becomes a necessary component of forest management.

FOREST MANAGEMENT AND INVERTEBRATE POPULATIONS

Is there any evidence that invertebrates are being lost as a result of forestry activity? Such losses are generally accepted as being huge in the tropics (Erwin 1991, Wilson 1992), but undesirable side effects of forest management also have been revealed by research on invertebrate communities in northern forests (Mikkola 1991, Nilsson and others 1995, Niemela 1997). For example, carabid beetle species abundant in primeval montane pine forests of western Canada have not re-established populations in the oldest available regenerated sites *(i.e.,* up to c. 30 years after harvesting) (Niemela and others 1993, Spence and others 1996), suggesting that old-growth specialists will be disadvantaged in harvested landscapes. In a landmark paper, Siitonen and Martikainen (1994) compared the saproxylic beetles of areas in eastern Finland that have been subjected to intensive logging with those of similar areas of Russian Karelia exposed to minimal human disturbance for the past 40-50 years. With comparable effort, they collected 186 individuals of 15 red-listed species from aspen snags in Russia but found only one individual representing this same set of species in Finland.

The important point of the recent work on northern forest invertebrates is that large-scale changes in empirical patterns of species diversity and composition have apparently resulted from the way that humans have repeatedly altered the land through intensive forest management. Most current forestry practices homogenize the landscape, leaving regenerated stands ill-suited for maintenance of the full complement of species that once inhabited them (Angelstam 1997, Niemela 1997). Large scale patterns of unplanned forest fragmentation and the resulting isolation of species with particular habitat requirements may also prevent recolonization of regenerating forests, even when suitable microhabitats develop over time. The recolonization process depends on spatial and temporal scales characterizing the metapopulation dynamics of particular taxa, and thus landscape level planning based primarily on requirements of vertebrates may be at the wrong scale to accomodate arthropods species with different dispersal ability. However, even for arthropods with excellent ability to seek out and colonize appropriate microhabitats, it remains critical to understand and optimize direct, stand-level habitat effects. If appropriate microhabitats are missing, the creatures that depend on them and the ecostystem services that these creatures provide are surely at risk.

Unfortunately, with respect to development of forest management prescriptions in western Canada, we are woefully ignorant of much of the biodiversity that we have agreed to protect as signatories of the Rio

Convention. Thus, we are caught on the two horns of a dilemma: we must conserve this biodiversity, while forests are being cut at an ever increasing rate. The rosy ideal of 'sustainable forest management' represents what we want, but do we have a rational strategy for attaining this state? Furthermore, we urgently need to define how such a strategy connects appropriately to operational measures of biodiversity. In the balance of this paper we discuss how knowledge about invertebrates can contribute to adoption of modern forest management models, and give examples of research about soil and litter-dwelling arthropods that can be applied toward this end.

NATURAL DISTURBANCE AS A MANAGEMENT PARADIGM?

The currently advocated approach to sustainable management of the boreal forest promotes linkage between management regimes and natural disturbance. The boreal forest, like many ecosystems, is reset in fractal mosaics to earlier successional stages and has its successional courses altered and diversified by various natural disturbances (Haila and others 1994). In the forestry arena, a number of approaches to management, including "new forestry" (Franklin 1989) and "ecosystem management" (Kaufmann and others 1994), are converging on the same sort of rationale. Hunter (1993), for example, characterizes the approach as follows: "timber harvesting regimes should be designated to imitate the natural disturbance regimes, such as fire and windfall, which shape the structure of forest ecosystems".

In western Canada the forested landscape reflects a conspicuous influence of wildfire (Rowe 1972, Stelfox 1995). Analogues to fire are already being applied in management regimes for the mixedwood zone of western Canada (Stelfox 1995). From the premise that the boreal biota is well adapted to deal with the natural disturbance of periodic wildfire, it is inferred that imposing similar patterns of forest regeneration on the landscape through harvesting should only minimally disrupt natural processes and patterns of biodiversity. Proponents reason further, and probably correctly, that we cannot know enough to micro-manage our forestry activities for the benefit of every forest species and, even if we did, complete knowledge would doubtlessly paralyze us. The pragmatic approach to resource development in the light of uncertainty is to apply a coarse, general filter in forest management. Thus, we seek to develop and adopt policies for harvest that ensure existence of an appropriate mosaic of habitats on the landscape, as defined by natural disturbance patterns, to maintain our biota as a whole. Fine-filter management geared to the needs of particular biotic elements may be established under this approach, but only for charismatic or exploitable species that are negatively influenced under the coarse filter approach. We tend to ignore small, unengaging or poorly known species, especially those that appear to be unimportant in socio-economic reasoning.

The above arguments ignore practical constraints and make significant leaps of faith. Although the approach seems rational and represents a stage in the process of improving forest management, it is critical that the approach not be canonized as a 'magic bullet', and thus, simply be defined as sustainable forestry. Magic bullets are simple but powerful presciptions that seem to give exactly the results we want (Van Den Bosch 1978). Unfortunately, magic bullets, used to solve environmental problems, frequently fail when the temporal or spatial frame is expanded and unpleasant side effects are noticed. Scientists and research managers may stall recognition of side effects and development of alternative approaches. This comes from insisting on the sort of local focus guaranteed to deliver research dollars from magic bullet makers and those who want fixed truths on which to maximize efficiency of profit-oriented operations. A strictly fire-based natural disturbance model seems like a magic bullet to us. It has been most touted by those familiar with creatures that range widely over a landscape. For many birds and most larger mammals such as bears and ungulates, about which we already have considerable biological knowledge, such an approach has real appeal. Although our comparative ignorance of invertebrates may be blissful for a time, there is no guarantee that little known invertebrates, including those involved in the biotic engine that renews soil fertility and other ecosystem functions, will not be negatively affected by forest management directed at and monitored using the more charismatic fauna. Such negative effects could compromise sustainability of forestry operations in the long term. For this reason, it is imperative that we continue to study all aspects of forest systems brought into harvest rotation.

The strong focus on large-scale spatial patterns, ignores significant concerns from which probable side-effects may spring. Let us consider four rational counter arguments to a strict landscape approach. This is not to dismiss landscape level work but rather to amplify why it remains essential to study processes operating at both smaller and larger scales if we are going to manage them effectively. Afterall, it is the interaction of these processes that produces natural forests.

1) In current discussions about pre-eminence of landscape processes, generation of stand-level variation across successional scales meaningful for forestry is frequently ignored. The within-stand diversity of such harlequin environments is critical to ensure the persistence of species that might be favoured as

background conditions change. Within-stand homogenization resulting from forestry activities could move environmental conditions out of the range of today's levels of natural variation, causing extreme reductions or extirpations of some species dependent on rare microhabitats. If so, we would constrain the system's ability to respond and there would be little basis for assessing the long-term success of adopting a natural disturbance model. For example, the boreal biota is probably not in meaningful equilibrium (Boktin 1990), but is still recovering from the last glaciation (Prentice and others 1991) and probably responding to anthropogenic climate change (Lenihan and Neilson 1995). Biodiversity, including small, rare and/or cryptic species, is a key element in ecosystem response to change (Wilson 1992, Naeem and others 1994). We ignore these changes and the ecosystem features required to buffer them at our peril. Tomorrow need not be like yesterday.

2) Innovative managers are encouraged to emulate natural patterns of stand origin. Under a wildfire-driven natural disturbance model, these are those seen on fire maps. However, natural but erratic spatial-temporal patterns are unlikely to be either socially or economically acceptable for industrial forestry. Even if some vague approach to pattern matching is acceptable, what time-frame should be used to establish the base pattern? Fire frequency and patterns have clearly varied, even recently, both as an effect of active fire suppression and as a result of natural processes (Bergeron and Dansereau 1 993, Gauthier and others 1995). Should we, for example, force landscapes to develop in the form defined by processes that operated in some limited past time window?

3) On occassion, practical implications are reduced to a worrisome short-cut stated as follows: if we don't cut more land annually than was scorched in former times, estimated to be in the range of 2-3% for the boreal mixed wood, the biota will be conserved. However, there is little hard scientific evidence to show that any wildfire-based model, applied strictly at the landscape scale, will be any better for biodiversity than the old "cut it and pray" model. Adopting an untested model does not automatically confer the mantra of sustainability on boreal forestry (Fanklin 1993). Models are tested most stringently by experiment and there are excellent but largely untapped opportunities to develop appropriate experiments in the context of adaptive managment (Hilborn and others 1995). It is unlikely that we have inferred the optimal answer based on incomplete information.

4) The scenario depicted in figure 2 is generally accepted as a description of what happens to forested uplands in the western boreal region (Rowe 1972, Bonan and Shugart 1989; Stelfox 1995). Upland stands are initiated by wildfire and, after a very poorly understood early successional period, come to be initially dominated by trembling aspen. These may have a white spruce understory right away, or may be slowly colonized by spruce, depending on the distance to seed source (Lieffers and others 1996). As a stand becomes more dominated by spruce, the probability of stand replacing fire goes up and eventually the stand burns again to reinitiate the cycle. Two main harvest points will be imposed as we come to a stable rotation in the boreal mixedwood forest. The earlier one, representing a major part of today's harvest in Alberta, is directed at an ecosystem that is rarely re-initialized by wildfire. It is not clear that we will allow natural processes to guide the intervening period to spruce harvest, but even if we do, the age distribution and variation of these spruce stands will surely be truncated. Thus, with respect to the ecological processes inherrent in natural stand development, it is fair to ask whether a natural disturbance model is being followed at all. Should the wildfire analogue be used more deeply than as a weak justification for removal of fiber?

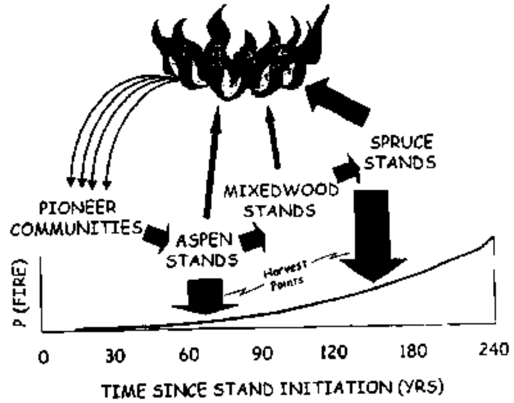


Figure 2-Schematic diagram indicating the general course of succession in the boreal mixedwood forest. The two major harvest points presently envisioned are indicated by the two dark vertical arrows.

The natural disturbance approach is perpetrated mainly as an idea about risk management. As in a game of bingo, it is argued that "chance" will determine the winners and losers as in natural situations. If each species has a fair or "natural" chance to win *(i.e.,* to stay in the game) we might legitimately dodge responsiblity for extinctions. However, we need to know if the rules of the game, under anthropogenic forest managment, are really natural for all players. Thus, we prefer an approach that manages for the results we want to achieve over the long run, rather than rushing blindly to emulate selected aspects of natural process that fit into our socio-economic constraints. We will be responsible for the outcome either way because clearly we will not allow nature to take her own course, even under a natural disturbance model. This is not to claim that we will ever be able to employ perfect knowledge, but we argue that testing and applying the limits of what we know is preferable to 'biodiversity bingo' when we can be sure that the probabilities of extinction will be affected however we manage the system.

A superficial, landscape-oriented approach to basing management on natural disturbance may encourage false security with respect to biodiversity. In the words of song-writer Joni Mitchell, it is common for humans to "pave paradise" as a result of focus on specific objectives. If our forestry practices homogenize forest stands, we might not even know what biodiversity "we've got 'til it's gone". Organizing the size, age and distribution of "parking lots" carefully according to some natural rhythm of land disturbance won't help much if the parking lots themselves are part of the problem.

BEETLES AND SPIDERS OF BURNS AND HARVESTS

Recently burned and recently harvested stands are quite dissimilar to most observers. The question for those interested in managing in the context of sustainability criteria is whether such differences throw biotic succession onto different courses that might threaten some of the biota. As part of a team of forest ecologists, we set out to determine how close succession from burns and havests might be in the aspen-dominated mixed wood. We asked whether harvest was a reasonable subsitute for fire with respect to development of the litter-dwelling invertebrate fauna. If so, we reasoned that fire- and harvest-origin stands would develop increasingly similar faunas as they aged. If the fauna diverged significantly, however, the logic of using harvest as an analogue for fire may be flawed with respect to protection of biodiversity.

Finding suitable harvested and burned stands was a challenging matter, undertaken by P. Lee and his colleagues at the Alberta Research Council. Using forest inventories, aerial photography and ground truthing, they found aspen stands either harvested or burned in 1968, 1982 and 1995. These sites are spread out over a wide geographical area in northeastern Alberta, and thus interpretations of resulting data may be confounded by geographical variation. However, this is the best that can be done with a chronosequence study of aspen forest, given that harvest of aspen was rare in Alberta before the late 1980s.

We have focused our studies on two families of litter-dwelling beetles (Carabidae, Staphylinidae), and spiders (Araneae), using pitfall trapping (Spence and Niemela 1994, Digweed and others 1995). The specific sampling designs will be detailed in future papers. Here, it suffices to say that we ran trap lines of 6 traps, each separted by c. 50 m, in two stands of each origin-age combination during 1996 and 1997. More than 17,000 specimens were collected during the two year sampling period and the definitive taxonomic analysis is still in progress. However, our preliminary findings can be used to illustrate the general level of similarity between fire- and harvest-origin stands.

There were no great differences in overall abundance of these litter-dwelling taxa between harvest and wildfire-origin stands (fig. 3). There is a marginally significant trend for staphylinids to be less abundant in fire-origin stands, but the other taxa show no significant differences in overall abundance. Furthermore, the differences in the first year after fire appear to be much greater than in year 2. We used rarefaction (Simberloff 1978) as a measure of diversity, and the results show that overall diversity of litter dwelling arthropods did not differ dramatically between fire and harvest origin stands at any age (fig. 4). Although there were prominent differences in spider diversity between wildfire and harvest in the first year of the study, these had largely disappeared in the second year. However, analyses of diversity and abundance, however, do not provide much comfort about the fit of harvest effects to natural disturbance, if the species differ between harvested and pyrogenic stands.

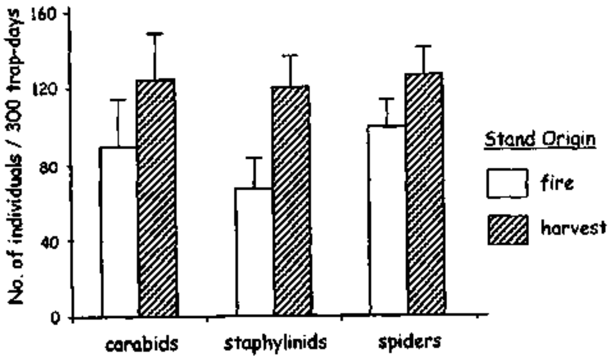
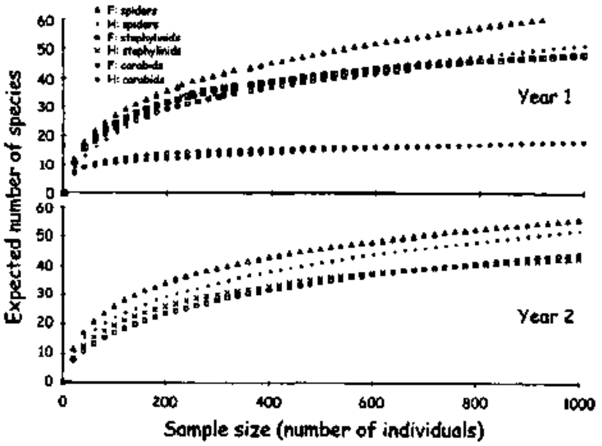


Figure 3-Least square mean abundance (± standard errors) by stand origin for beetles and spiders collected by pitfall traps during 1996.

We have just begun to tackle the problem of distribution of particular species on the chronosequence. As a start, we've used cluster analysis to ask questions about patterns of relative abundance of species. Results using all litter-dwelling taxa collected in year one, suggests that pyrogenic and harvested stands tend to converge on similar species associations. It appears that litter dwelling invertebrates recover faster from disturbance by harvesting than by wildfire as the stands harvested in

1982 are most similar to the 1968 fire-origin stands (fig. 5).



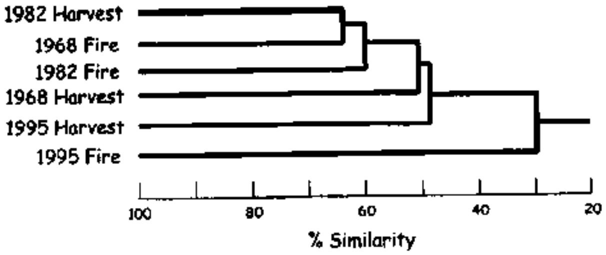


Figure 5-Cluster analysis of Bray-Curtis measures of percent similarity for carabids, staphylinids and spiders collected by pitfall trapping during 1996. Data were standardized to 800 trap-days.

We've used detrended correspondence analysis (DCA) (ter Braak 1987a,b) to further describe these assemblages. An example of this approach is provided by figure 6, in which individual trap data about three taxa are plotted in ordination space defined by the first two DCA axes. The first axis, which has a high eigenvalue, separates the stands quite clearly and consistently with respect to age. As would be expected from the results of the cluster analysis, the harvest-82 and harvest-68 stands are closer together in the ordination than are the comparable fire-origin stands. Although fire- and harvest-origin assemblages start off from quite different points in this ordination-space, they appear to converge in 30-year old stands. Thus, both cluster analysis and ordination support the claim that litter invertebrates converge with respect to general community structure of litter invertebrates by 28 years post-disturbance. However, given that the two chronosequences followed quite different trajectories to reach the present positions in ordination space, it may be risky to predict that community development will be parallel in fire- and harvest-origin stands in the future.

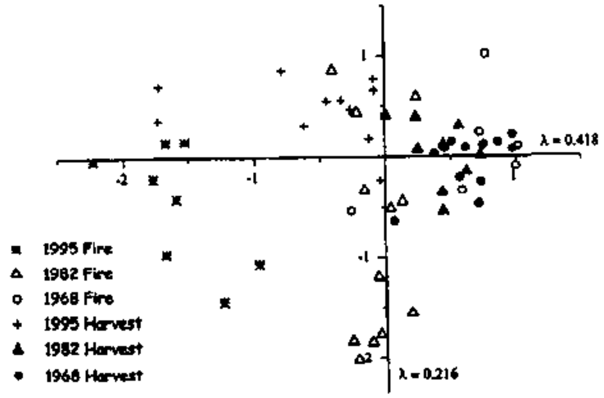


Figure 6-Detrended corespondence analysis (DCA) of sample scores (pitfall traps) derived from 1 53 species of carabids, staphylinids and spiders collected in 1996.

From a biodiversity perspective we still must get down to the level of species. Some species of each taxon are collected only in stands of one age or origin (table 1). Many of these are records of only one or a few individuals and may thus be somewhat discounted. However, some records refer to more abundant species and the data about them are thus less comforting. As we replace fire with harvest, for example, is it possible that early successional species characteristic of pyrogenic stands could drop out of the system? The aspen-dominated mixedwood seems to have relatively few litter-dwelling species that specialize in old stands, but especially among saproxylic species, some may be at risk (Spence and others 1996, 1997).

BEETLES OF FIRE SKIPS

We are studying the ecological significance of old-growth patches of residual forest nested within large burns by looking in detail at the actions of wildfire, and at what sorts of habitats it creates. Fire brings about profound changes in community structure, but it also creates patchiness and spatial heterogeneity on several scales. Today's foresters attempt to re-create some of this local structure by leaving patches of standing green trees in patch-retention logging systems. However there has been little research to characterize invertebrate assemblages of 'fire skips' and to assess whether they are significant for recolonization of the surrounding burned sites. We have set out to describe what happens in both unburned patches and the burned matrix of large burns by comparing the fauna

Table 1-Number of species unique to one type of stand origin (fire or harvest) or age (origin in 1995, 1 982 or 1 968) for two orders of beetles and for ground dwelling spiders. Data from pitfall traps run during 1996.

	Disturbance Type		Year of Stand Origin		
Taxon	Fire	Harvest	1995	1982	1968
Carabidae	4	12	5	1	3
Staphylinidae	4	12	5	3	4
Araneae	19	17	15	10	8

between two large sub-alpine burns, one 15 and another 30 yrs-old, in conifer-dominated forests on the east slope of the Rockies.

We studied the 15 yr-old burn intensively in 1997 and will do the same for the older burn in 1 998. As above, pitfall traps have been used to sample and describe the carabid fauna of unburned patches of various sizes, of the burned matrix and of the surrounding old-growth forest, consisting mainly of Englemann spruce, lodgepole pine and sub-alpine fir. Transects of traps have been laid out to run across the boundaries of fire-skips and burned areas and of burned forest and the undisturbed forests at the edges of the burn. The details of the sampling design will be presented elsewhere.

Although definitive analyses must await completion of the second year of field work, some points of interest emerge from the first year's work. Several numerically dominant old-growth carabid species, including *Calathus advena* and *Nebria crassicornis,* were found in 15-year old fire-skips and the surrounding unburned forest, but were not taken in the burned areas except near skip edges. One interesting parthenogentic species, *Pterostichus empetricola,* which is a predominantly northern species existing in relict populations southward along the Rockies, was collected exclusively from skips. We suggest that this species requires a narrow range of cool, wet habitat that is relatively rare in the forest at large, but which may be disproportionately represented in skips because of their resistance to burning.

The data suggest that beetles move more readily into the burns from the fire skips (fig. 7), perhaps because of population pressures in the smaller skip habitats. Clearly beetle activity-abundances are higher in fire-skips than in either burned or surrounding old-growth forest. Also, it appears that skips of different sizes may retain different mixes of beetles species, perhaps as a result of interspecific interactions intensified in these small areas. For example, *Nebria crassicornis* was found only in larger skips, where it sometimes overlapped with small populations of *C. advena.* However, in smaller skips, *C. advena* was abundant (fig. 8).

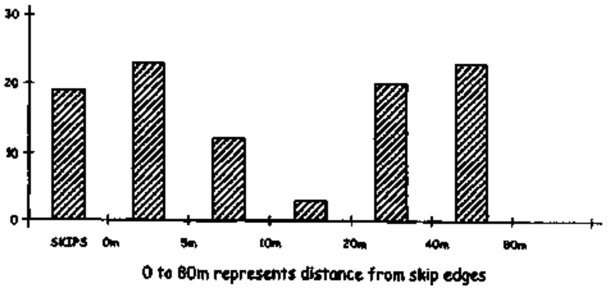


Figure 7-Evidence for recolonization of burned areas from fire skips by the carabid beetle, *Calathus advena.*

Already this study provides several results with implications for the patch retention approach to harvesting. Fire skips do provide refuges for old-growth invertebrate assemblages and these species do re-colonize burned patches from the skips. Patches of different sizes vary in respect to carabid assemblage retained. Thus, distribution of patch size will be an important aspect of emulating natural process. Furthermore, it appears that the location of these skips is not random with respect to microtopographic features, and that especially the largest skips, which occupy wetter microsites, may have remained unburned through at least two fires. This is not the random pattern that proponents of the Natural Disturbance Paradigm have suggested. Thus, the spatial distribution of patches in a logged stand should be adjusted to aspects of intrastand variation that remain to be studied and defined.

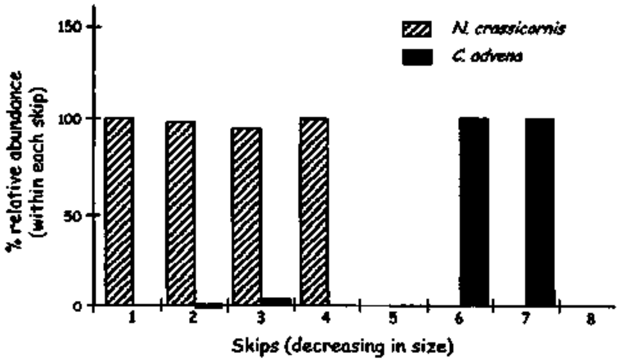


Figure 8-Segregation of two carabid species in fire-skips of differring size.

THE EMEND PROJECT: STAND STRUCTURE AND INVERTEBRATES

Unmanaged stands differ in structure from stands managed for fiber production, by generally having more coarse woody material (CWM) lying about in various stages of decay. This probably has little to do with differences in stand origin, but instead stand developing exclusively under natural processes vary conspicuously in size, age and spacing of trees and CWM as result of ongoing GAP dynamics (Botkin 1972; Shugart and West 1977; Solomon 1986). These smaller scale, within stand disturbances, which diversify stands as habitats for other organisms, kick into high gear as canopy trees begin to senesce, and thus, aspects of these processes are generally eliminated or truncated by harvest rotations. Although surely important components of insect habitats, the effects of complex and variable stand structure are not well studied.

We have recently launched a cooperative project that seeks to determine the significance of stand structure and to put it to work in management of the northern mixedwood forest system. The project goes by the acronym EMEND (Ecosystem Management by Emulating Natural Disturbance) and occupies >1000 ha of mixed wood forest, c. 120 km northwest of Peace River Alberta. The project was developed through nearly 2 years of detailed consultation among research scientists, practicing industrial foresters and public land managers. EMEND has been designed both to meet the needs of industry and to satisfy the requirements for a rigorous scientific experiment. It has been linked to the operating plans of Canadian Forest Products LTD. (CANFOR) and Daishowa-Marubeni International LTD. (DMI) and has been envisioned from the start as a significant research component for adaptive management. The work involves a large, multi-disciplinary team, including biologists, foresters and social scientists.

Our general objectives are as follows: 1) to investigate how retention of forest structure on cut blocks affects forest renewal, including regeneration of biodiversity; 2) to compare a number of alternative harvest options to the effects of wildfire; and 3) to investigate the cost-benefit ratios of alternative prescriptions. The two main driving variables are the extent and type of disturbance and the original forest cover type (aspen dominated [>70% of canopy], aspen dominated with strong spruce understory, mixed forest [white spruce and aspen both <60% of canopy], and conifer dominated [>70% of canopy]). Experimental burns are planned at several intensities and the impacts of these will be compared with those of several practical harvesting regimes. Integrated study of a wide range of response variables, including comprehensive work on invertebrate biodiversity, is planned. A central component of this project is an effort to connect studies of nutrient cycling and long-term site productivity to invertebrate assemblages characteristic of living trees, dead and dying wood, leaf litter and soil organic matter.

During 1997, we collected the ground-level baseline data required to lay out an effective experiment. Our main goal was to select blocks of relatively homogeneous stands for the experiment from a pool of candidate stands identified initially from the enhanced Alberta Vegetative Inventory. Data about the stands selected suggest that we are indeed dealing with rather distinct points along the successional pathway (fig. 9). Spruce volume increases over the sequence and that of aspen falls. There are clear differences in age among the oldest trees found on site. These are somewhat less different than might be expected from the standard successional model, adding support to recent ideas that the process is more complex than frequently envsioned. The various treatments have been laid out over three replicate stands representing each of the four cover types. During summer 1998, we will make pre-treatment measurements on all these stands, with burning and harvest scheduled to begin in the following fall and winter. Further information about the EMEND project, including experimental design, specific biodiversity projects and contacts for questions, can be found at

http://www.biology.ualberta.ca/emend/emend.html. Proposals for additional work to take advantage of the unusual opportunities provided by the EMEND site are welcome.

CONCLUSIONS

It is appropriate that reason and scientific study structures the way in which biodiversity is applied in forest management. However, at present we have too little sound information about the biota of northern

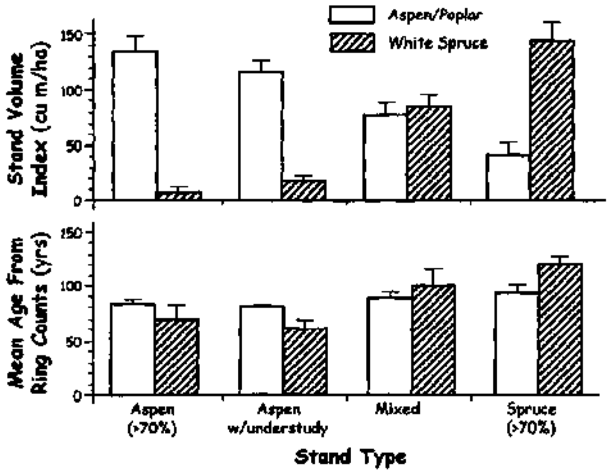


Figure 9-Characteristics of overstory vegetation in stands selected for the EMEND experiment.

forests to corroborate the hypothesized value of new management models based on natural disturbance. Perhaps more than ever before in northern forestry, adaptive management that weds research and operations is in order. Society is clear in the message that biodiversity is to be valued in the context of management of public lands (Kuusipalo and Kangas, 1994; Abramovitz, 1998). Thus, invertebrate biologists must clearly connect their studies of biodiversity to studies of consequences of particular land-use patterns, if concerns about invertebrates are to influence those making the management decisions. It is time for those involved in forest management to leave the value judgments about biodiversity alone and ask rigorous questions about the consequences of adopting any particular concept as a model for forestry development.

At this point we offer the following tentative answers to the questions posed at the end of our first paragraph about the possible influences of extensive forestry activity in the western boreal forest.

- Will it matter? Leopold's dictum about intelligent tinkering cautions us against throwing away things that we don't understand. Even if many forest species contribute little to the sustainability of the forest resource in human terms, many are concerned about the ethical aspects of human-caused extinction.

- How will we know? Forest health monitoring should incorporate some assessment of poorly understood taxa like invertebrates, otherwise we may understand what we have lost only when it is too late to reverse the process. Experiments that compare effects of real management prescriptions and follow these for significant periods of time will also increase our understanding.

Should we do anything about it? In addition to monitoring, the fire-skip study suggests that refugia are important and that their locations could be critical. Thus, we should characterize the patterns of sub-landscape level structure that contribute to the function of these refuges and incorporate such information into cutting plans.

Can we do something about it? This depends both on forestry policies, market pressures and land owners. Balancing study of and attention to biodiversity concerns against the need to generate revenues from a fully allocated forest resource will be tangible proof of commitment.

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QUESTIONS FROM THE FLOOR

Q: I'm wondering if the "magic bullet" isn't stand dynamics and the focus on these scale processes. What about the relationship between biodiversity and landscape dynamics, the "neighborhood" effect on disturbance processes landscape structure?

A: Let me begin by saying that I have no faith in any sort of magic bullets. What we've tried to illuminate is how the present preoccupation with landscape-level processes leaves out concerns important to conservation of species with dynamics on smaller spatial, but perhaps longer temporal scales. I do not argue that work at the landscape scale is not important or that is should not be done, only that it isn't the be-all and end-all for sustainable forestry. We need to be concerned that our forestry practices, as applied at the stand-level, do not homogenize whole regions with respect to microhabitats critical for invertebrate species, like for example, in the case of the saproxylic beetles studied by Sittonen and Martikainen (1994).

Assuming that by "landscape dynamics" you mean changes in the the size and distribution of forest stands of various ages over time, then I think this is possibly important and we've commented on it to some degree in Spence and others (1996, 1997). Indeed colonists available to any isolated habitat unit come from the surrounding matrix. However, the surrounding matrix in forest land is composed of stands as well, and stands are the focus of how harvest technology affects the land, repeatedly across a landscape. The important point that I want to re-emphasize is that we don't know enough about how stand level processes like gap dynamics create habitat complexity that may be crucial for biodiversity. It is clear that short rotation forestry limits the action of these processes. Will there be undesirable consequences? The available evidence does not rule them out.

I cannot address the last part of the question because I just don't understand it.

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MANAGEMENT EFFECTS ON SOIL ORGANISMS AND PROCESSES

SOIL ORGANISMS AND RANGELAND SOIL HYDROLOGICAL FUNCTIONS

Jeffrey E. Herrick[1]

ABSTRACT

Soil organisms control water distribution in rangelands by creating macropores which rapidly conduct water into the soil, by generating stable soil aggregates which prevent crusting and increase water holding capacity, and by controlling litter decomposition. Ants, termites and earthworms have all been shown to increase infiltration capacity; anecdotal evidence suggests that macropore formation by a variety of other macroinvertebrates may have equally dramatic effects. Macroinvertebrates generate aggregates in the form of fecal pellets. Lichens, mycorrhizal fungi, cyanobacteria and other microorganisms also contribute to aggregate formation and soil surface stabilization. The direct effects of rapid litter decomposition on infiltration and soil water storage in arid and semi-arid rangelands is generally negative: litter removal exposes the surface to raindrop impact, which leads to the formation of physical crusts, and increases evaporation from the soil surface. These negative impacts are balanced by the creation of surface-connected macropores and the incorporation of soil organic matter, resulting in the formation of stable aggregates.

Keywords: hydrology, infiltration, soil water, available water holding capacity, invertebrate, ant, termite, earthworm, fungi, rangeland, soil structure, aggregate, soil organic matter

INTRODUCTION

Biomass production in most North American rangelands is limited by soil moisture availability during at least part of the year. Annual precipitation is low, variable often arrives during periods which are unsuitable for plant growth. As a result, monthly potential evapotranspiration (the amount of water which could be lost to the atmosphere from a free water surface) may exceed precipitation by a factor of 100 or more during periods when temperatures are high enough to support plant production (Hargreaves and Samani 1991).

These limitations are compounded on some parts of the landscape by high runoff rates. In closed-basin systems, this water is conserved in lower parts of the landscape, while in open systems it is effectively lost. These losses are not necessarily negative from a regional perspective, as the runoff supports riparian systems and is frequently collected in reservoirs for urban and agricultural uses. Losses from the rooting zone may also contribute to groundwater recharge. High rates of runoff, however, are rarely supported as a management objective.

Water redistribution also occurs at much smaller scales. Redistribution at the scale of tens of meters has been cited to explain patterns of banded vegetation in many arid ecosystems (Tongway and Ludwig 1994). Schlesinger and others (1990) suggested that water and nutrient redistribution at the level of the individual plant are associated with the transition of grasslands to shrublands.

In addition to redistribution, the capacity of the soil to store water also varies across the landscape. The volume of plant-available water which can be stored at any particular point and depth in the profile depends on complex plant-soil interactions. In general, however, more highly structured soils have a higher capacity to store water at tensions at which it is accessible to plants, and provide conditions which favor root exploration of a larger soil volume.

Soil organisms can affect water redistribution, soil water holding capacity and the accessibility of water to plants through a variety of mechanisms. They modify soil structure, alter the form and spatial distribution of above- and below-ground detritus and, ultimately, change the relative growth rates of different plants and therefore plant cover and community composition. The objective of this paper is to review the role of soil organisms in altering rangeland soil hydrology through aggregate and macropore formation. Microbiotic crusts are only briefly considered here. For a more extensive discussion of their role please see recent reviews by Warren (1995), Ladyman and Muldavin (1996), the NRCS (1997), Belnap (this volume) as well as a forthcoming book in the Advances in Ecology series. Recent papers by Eldridge and Greene (1994) and

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[1] Jeffrey E. Herrick is a soil scientist with the USDA-ARS Jornada Experimental Range, P.O. Box 30003, MSC 3JER, Las Cruces, NM 88003-8003 (jherrick@nmsu.edu).

Eldridge and others (1997) have explored the effects of these crusts on soil surface hydrology in Australia.

SOIL WATER INFILTRATION

The volume of water which enters the soil profile at a particular point on the landscape is a function of (1) supply or the depth of water which is available for infiltration, (2) residence time, or the amount of time which water is resident on the soil surface, and (3) infiltration characteristics. Hydrologists often describe soil water infiltration in terms of *sorptivity,* which is related to the initial rate of water movement into a dry soil, and the *saturated hydraulic conductivity,* or the rate of water movement into the soil after it has become saturated. Soil organisms affect both residence time and infiltration characteristics. They can also affect the water supply at one location by modifying the soil surface in adjacent patches, or at other locations higher in the landscape.

Supply

Water available for infiltration is a function of both total precipitation and run-on. The unique plant communities associated with riparian zones and playa lakes owe their existence to supplemental water from higher parts of the landscape. Most studies focus on the effects of soil organisms at a single point and down-slope effects of changes in the populations and activity of soil organisms are rarely considered.

Residence Time

Soil biota affect residence time by modifying surface roughness and the distribution of litter on the soil surface. Both soil surface roughness and the presence of litter slow the movement of water across the landscape. In some cases, small "ponds" may be formed by litter dams (Ludwig and Tongway 1995) or by micro-depressions formed by surface features stabilized by microbiotic crusts (West 1990). Increases in residence time by litter can be important in rangelands which depend on brief, high-intensity storms. Ponds, even if only 10-25 millimeters deep, can be locally significant: 25 millimeters is equivalent to over 10 percent of the average annual precipitation in much of the western United States and northern Mexico.

Soil organisms affect litter distribution and residence time through at least four processes: stabilization, shredding, burial, and consumption. Fungi can temporarily stabilize litter and limit redistribution by wind and water by binding it to the soil surface. Shredders, including both vertebrates and invertebrates, modify the susceptibility of litter to both redistribution and further degradation by reducing fragment size. Litter is removed from the surface through both burial and consumption. Ants tend to bury material in their nests, where it may later be consumed directly or used to culture fungi. Anecic species of earthworms, such as *Lumbricus terrestris,* drag litter into burrows, while epigeic species consume material at the surface (Edwards and Bohlen 1996). A third group (the endogeic species) function solely in the mineral soil and do not contribute to removal of litter from the surface. Dung beetles exhibit an even wider variety of behaviors. Some species bury dung in the soil directly below dung patches (paracoprids), others roll dung balls to another location where it is buried (telecoprids), while a third group lays eggs directly inside the dung patch, leaving the larvae to consume at the soil surface (Bornemissza 1969). Most other important species consume material at the surface and may deposit fecal material both above- and below-ground.

While high levels of soil biotic activity are normally viewed as an indicator of a healthy system, the direct effects on infiltration of litter removal from the soil surface are generally negative. In addition to slowing runoff, litter protects the soil surface from raindrop impacts. This limits the formation of soil physical crusts. This is particularly important in arid and semi-arid rangelands where vegetative canopy cover is generally much lower than 100 percent.

The net impact of direct and indirect effects of litter decomposition on infiltration depend on complex interactions with a number of other processes including the formation of soil structure by the decomposers and changes in soil microtopography. For example, Trojan and Linden (1992) reported that infiltration was deepest where earthworm burrows were located at the bottom of depressions in the soil surface.

Infiltration Characteristics

Infiltration depends on the density, size distribution, and continuity of soil pores. It also depends on the degree of repulsion between soil and water (hydrophobicity), particularly in the early stages of precipitation events. Soil organisms form pores through two basic processes: excavation and aggregation. A third process, root decomposition, also results in the development of new voids.

Pore formation by excavation-Excavation generally results in the formation of transmission pores, or those pores which transmit water during infiltration. These pores are > 30μ in diameter (Marshal and others 1996) and are commonly classified as mesopores (30 - 75μ) and macropores (> 75μ) (Soil Science Society of America 1997). Earthworms, ants and termites are arguably the three groups of invertebrates responsible for the majority of biopore formation in rangeland soils. Direct observations during rainstorms indicate that a number of other species including burrow-forming vertebrates such as pocket gophers (Family Geomyidae), prairie dogs (*Cynomys spp.*) and kangaroo rats (*Spectabilis spp.*) are probably locally important.

Lee and Smettem (1995) state that, "[Earthworm] burrows are the most numerous and most important macropores of animal origin in nearly all soils." Earthworms form burrows by forcing their bodies through the soil, and by swallowing soil to be later excreted as casts either elsewhere in the soil, or at the soil surface. These burrows may range from one to over ten millimeters in diameter. Anecic worms, or those which move between the surface and the subsoil, have been shown to be particularly effective at improving infiltration capacity. Up to 2,000 burrow entrances per square meter have been reported (Lee and Foster 1991). Even much lower densities can dramatically increase infiltration due to the fact that the burrows frequently connect the surface to much deeper layers of soil.

The relative importance of earthworms in rangelands has not been evaluated, however. A recently revised book by Edwards and Bohlen (1996) provides a comprehensive review of the role of earthworms in soils, but contains few references to non-arable systems. The key anecic species are virtually absent from many arid and semi-arid rangelands, including the Chihuahuan (Whitford 1996) and Namib Deserts (Crawford and others 1993). They do occur in moister parts of the Chilean Arid Zone where coastal fogs appear to maintain higher levels of soil moisture in spite of annual rainfall of less than 200mm (Crawford and others 1993). The lack of earthworms in many rangeland ecosystems suggests that other species, including ants and termites, dominate biological macropore formation.

Rangeland termites can be divided into two groups based on whether or not they build mounds. Only soil-dwelling termites (non-mound builders) are found in North America, occurring throughout the southwestern United States and Mexico. They form extensive near-surface galleries and tunnels which extend deep into the soil. Most are detritivores, feeding on dead material below the soil surface. Those which have the highest direct impact on infiltration feed on litter and standing dead vegetation at the surface. Some, like *Gnathamitermes tubiformans* form protective sheaths around vegetation, while others, including *Amitermes wheeleri* feed directly at the surface during periods when evaporation rates are minimal. Soil-dwelling termites can generate very high densities of surface-connected macropores, particularly under concentrated sources of organic matter such as cattle dung. Infiltration rates in a Costa Rican pasture were over twice as high (71 mm/h) under dung patches which had been decomposed primarily by termites than they were in adjacent control plots (34 mm/h) (Herrick and Lal, 1995).

The positive impact of termites on infiltration through macropore development may be balanced by the negative effects of high rates of litter decomposition. This is illustrated by a comparison of two studies in which termites were eliminated with the use of the insecticide, Chlordane. Rainfall simulation was used in both cases to measure infiltration capacity. Four years after termite removal from a Chihuahuan Desert creosote shrubland, infiltration rates had declined by over 40 percent relative to control in areas with less than 5 percent perennial cover. In plots centered on creosote bushes *(Larrea tridentata),* there was no change (table 1; Elkins and others 1986). In a shortgrass prairie in Texas, cumulative infiltration actually increased relative to control plots two to three years after termites were removed (table 2; Spears and others 1975). This increase was associated with a 50 percent increase in organic carbon in the top 1 centimeter of soil and an 80 percent increase in litter mass.

Table 1 —Final measured infiltration rates (mean ± S.E.) based on rainfall simulation on 1m^2 plots on a Chihuahuan Desert bajada four years after termite exclusion (data from Elkins and others 1986).

	Termites excluded	Termites present
	mm/hour	
No shrub; < 5 percent *Erioneuron pulchellum*	51.3±6.8	88.4 ± 5.6
Larrea tridentata canopy	106.4±9.7	100.6±6.1

In Australia, subterranean termites (*Drepanotermes spp.)* increase the density of surface-connected macropores and reduce it in others, leading to redistribution of water at the patch (1 meter) scale. These termites form a cap of up to 2 meters in diameter directly above their nests, and macropores lead to the surface in the area surrounding the nest. Eldridge (1994) reported that ponded infiltration rates into the nest margins were over 16 times higher than in the caps. Rates in control areas were similar to slightly lower than those recorded in the nest margins. In one of the few studies in which soil-dwelling termite activity has been evaluated as a potential management tool, Mando (1997) found that infiltration into a bare, crusted soil was increased by termite activity, and that there was a strong positive interactive effect of mulch and termite treatments on both infiltration and soil water storage. Subsequent microscopic and computerized image analysis confirmed that 60 percent of the macroporosity in the top 10 centimeters could be attributed to termite tunnels and chambers (Mando and Miedema 1997). Enhanced termite activity has also been shown to increase macropore flow in two degraded soils in the Chihuahuan Desert (unpublished data).

Table 2—Characteristics of plots two to three years after initiation of termite exclusion from a shortgrass prairie (data from Spears and others 1975).

	Termites excluded	Termites present
	- mm/40 minutes --	
Cumulative infiltration	18.5	15
	- percent --	
Organic carbon: top 0 - 1 cm	1.8	1.2
	- gm^2 -	
Litter	63	35

Ants create extensive networks of voids and macropores in many rangeland ecosystems. Whitford and DiMarco (1995) calculated that they move one centimeter of soil to the surface per 100 years in a Chihuahuan Desert grassland. Assuming that most of the soil was derived from the top meter, this represents a porosity increase of 1 percent, or a 2 percent addition to the typical pore volume for a sandy loam soil. At nature reserve in New South Wales, Australia, funnel ants *(Aphaenogaster barbigula)* alone cover 2.5 percent of the soil surface per year with their mounds, which they move approximately every 9 months (Eldridge and Pickard 1994). The authors calculate that up to 92.5 percent of the soil surface would be affected after 100 years, resulting in a net transport to the surface of 2.8 centimeters of soil.

Infiltration around entrances has been measured for only a few species. Several Australian studies suggest that ant activity has a generally positive impact on infiltration, at least when the entrance is included. Ponded rates were four (sandy loam) and eight (loam) times higher over funnel ant (A *barbigula)* nests (Eldridge 1993, 1994). Infiltration was positively correlated with nest entrance diameter on both soils. A study by Lobry de Bruyn and Conacher (1994) indicates that these effects probably depend on ant species, soil type and land use. Water infiltration under ponded or near-ponded (5 millimeter tension) conditions was higher under *Pheidole sp.* nests located on a sandy loam in a woodland and on farmland (fig. 1a, b), while nests of a *Camponotus* species apparently had no effect in the woodland (fig. 1c). Two species of *Rhytidoponera* also had no effect on infiltration into a shrub-dominated sand (fig. 1d) (Lobry de Bruyn and Conacher 1994).

The high variability in nest morphology of different species and even within species suggests that effects on infiltration should also vary. Some authors have speculated that while infiltration is increased at nest entrances, it may be reduced in the surrounding area due to vegetation removal (Lobry de Bruyn and Conacher 1990) or by the generation of impermeable caps by species such as *Trachymyrmex smithii* and *Pogonomyrmex maricopa* (Whitford 1993) or *Pogonomyrmex maricopa* (W.G. Whitford pers. commun.).

Where ant nests do increase infiltration, their importance is magnified by the fact that they are able to conduct water deep into the profile (Eldridge 1 993) where it is protected from rapid evaporative loss. This is a function of both the diameter and the continuity of the macropores in the nests. Soil moisture content under harvester ant nests *(Pogonomyrmex wheeleri,* Cole) in a southeastern Idaho sagebrush-grassland was less than or equal to that in control areas to a depth of 40 cm. From 60 to 100 cm, however, soil moisture content was higher under nests (Laundré 1990).

Pore formation by aggregation-Pores are formed each time three or more soil particles are linked together as aggregates. These intra-aggregate pores tend to be much smaller than those formed by excavation, and are more likely to be involved in water storage (Hindell and others 1994), while pores formed between individual aggregates are more likely to contribute to water transmission. Stable aggregates at the soil surface also help maintain infiltration capacity by limiting physical crusting and blockage of surface-connected macropores during storms.

A general hierarchical model of aggregate structure and formation has been proposed by Tisdall and Oades (1982) and refined by Oades and Waters (1991). This model is based on the assumption that soil macroaggregates (> 250μ in diameter) are formed from more stable microaggregates (50 - 250μ) and that different binding mechanisms are dominant at each scale (table 3). Elliott (1986) found that the model could be applied to a Nebraska soil which had been under sod for the previous 14 years. More recent studies have confirmed that the form of soil organic matter is at least as important as total content in the formation of stable aggregates (reviewed in Herrick and Wander 1998).

Soil organisms contribute to soil aggregation directly by forming fecal pellets, by re-arranging particles during

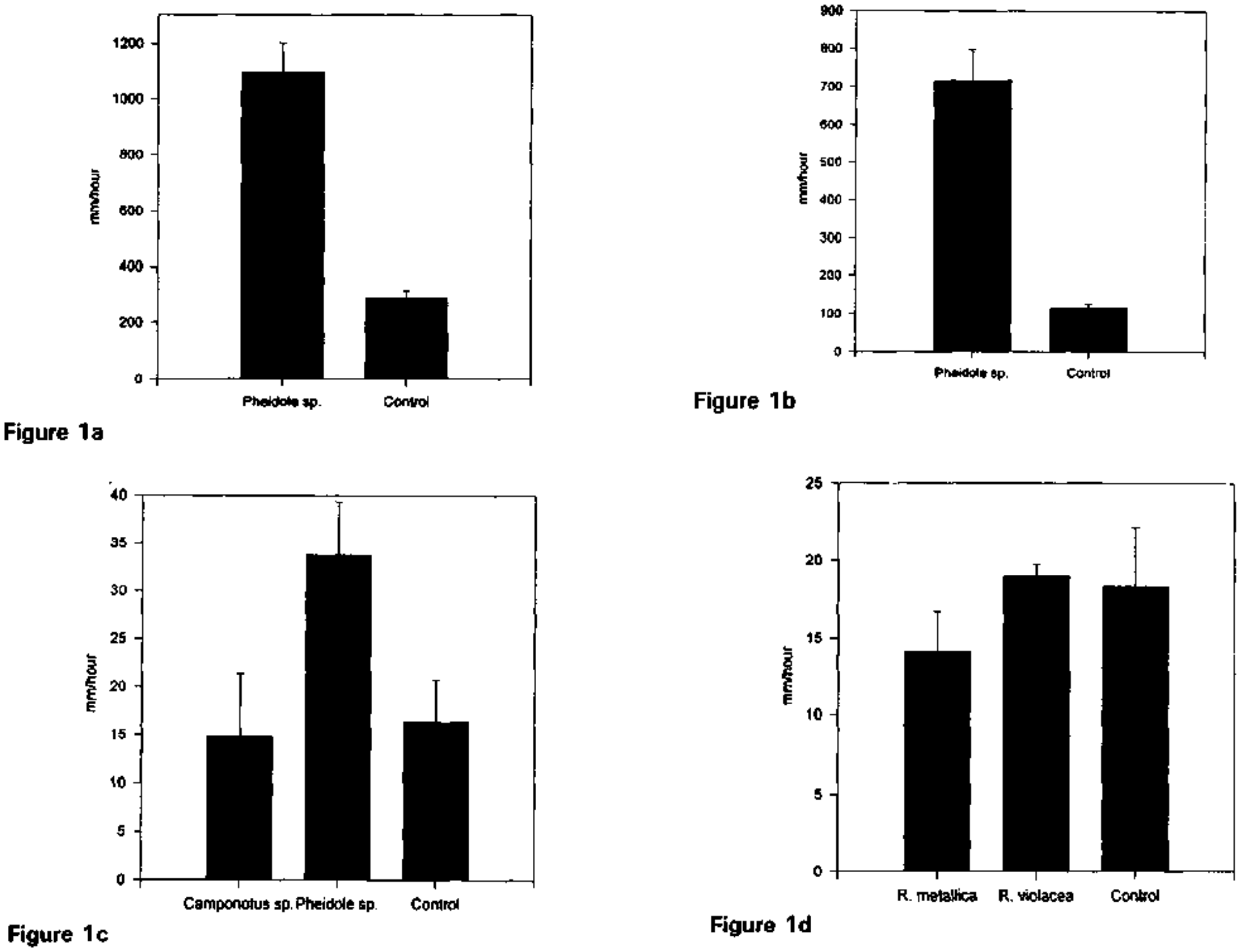
Figure 1a

Figure 1b

Figure 1c

Figure 1d

Figure 1 —Effects of *Pheidole sp.* nests on ponded steady state infiltration into a yellow sand (a) and grey sandy loam (b) in farmland, of *Camponotus sp.* and *Pheidole sp.* into a grey sandy loam in a woodland (c), and of two *Rhytidoponera* species into a yellow sand under heath (d) in Western Australia.

movement through the soil, by cross-linking particles with their bodies (fungal hyphae, for example) and by generating products such as mucilages which act as binding agents. Fecal pellets are formed in a wide variety of shapes and sizes. Microarthropods produce pellets which are generally less than 1 millimeter in diameter (Lee and Foster 1991), while earthworm casts can be well over one hundred times that size (Edwards and Bohlen 1996). As fecal pellets tend to be relatively concentrated sources of energy and nutrients, they are rapidly colonized or consumed by other organisms in the detrital food web. In cattle dung patches colonized by both dung beetles and termites, fecal pellets produced by dung beetle larvae are rapidly attacked by termites (Herrick and Lai 1995). Some pellets, however, persist to form the nucleus for long-term stable aggregates. Earthworm casts, which are predominantly inorganic and therefore less susceptible to attack, may account for over 50 percent of the soil mass in some grassland soils (Lee and Foster 1991).

Table 3 —Primary binding agents for aggregates of different diameters. Note that larger aggregates may be formed from smaller aggregates and/or from primary particles such as sand grains.

Aggregate Diameter (μ)	Primary binding agents
200 - 2000	Roots
	Hyphae
	Fecal pellets
20 - 200	Hyphae
	Bacteria
	Decomposition products
2 - 20	Persistent organic materials
<2	Primarily inorganic

The presence of fungal hyphae has been shown to promote stable aggregate formation in many grassland soils (Tisdall 1991; Degens and others 1996; Chantigny and others 1997). Organic amendments including manure lead to rapid increases in hyphal length density (Roldan and others 1996; Degens and others 1996). The impact of these amendments on aggregate formation appears to depend on environmental factors controlling extension of the hyphae away from the organic substrate into the surrounding soil (Degens and others 1996).

SOIL WATER HOLDING CAPACITY

Soil organisms affect soil water holding capacity through effects on pore volume and size distribution and on the content and form of soil organic matter. Increases in soil organic matter generally increase soil water holding capacity (Hudson 1994) both because of its high absorptive potential and because of its role in the formation and maintenance of soil structure. The water holding capacity of organic matter varies widely depending on its form. Carbon in the form of plant lignin holds relatively little water, but microorganisms can convert this to polysaccharides, which can retain many times their weight in water.

The most important pores for water retention are those located within soil aggregates. Water is held more tightly in small pores than in large pores and water in the smallest pores is unavailable to plants. Clay soils hold much more water than loamy soils, but much of this water is never extracted because it is tightly bound in microscopic pores. Information on soil water content is difficult to interpret without information on the tension of the water. The smallest pores inhabited by bacteria are on the order of 0.2 μ in diameter (Hassink and others 1993). This is the minimum pore diameter from which it is assumed that most plants can extract water (Marshall and others 1996), although there are reports of rangeland plants continuing to transpire at much lower (more negative) tensions.

RELATIONSHIPS TO VEGETATION

Soil hydrology, soil biota and vegetation are intimately linked in rangelands. While the discussion here emphasizes direct impacts of soil biota on infiltration, it is essential to consider the positive and negative feedbacks between soil biota, changes in the soil water regime and vegetative cover, composition and spatial distribution (fig. 2). Increases in plant production generally follow an improvement in the soil water regime in water-limited environments. Higher primary production means more material to support the soil food web, leading to a positive feedback loop. Other papers in this volume describe interactions between soil biota and vegetation. Plant canopy cover is frequently cited as the single most important factor controlling infiltration on rangelands (Spaeth and others 1996). Much of the strength of this relationship is probably due to the association of soil biotic activity with plants, as described above. However, plant canopies also directly enhance infiltration by protecting the soil surface from destructive raindrop impacts. Plant bases increase residence time by increasing tortuosity, slowing the movement of water across the landscape.

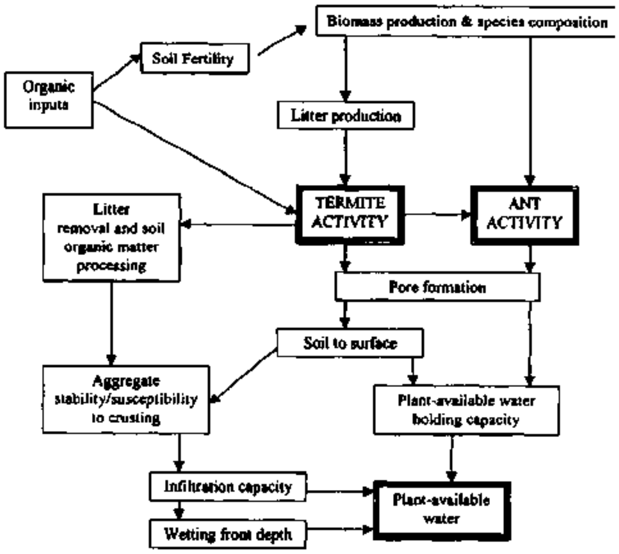

Figure 2 —Simplified illustration of relationships between ant and termite activity, and changes in plant-available water.

Different types of soil organisms alter the hydrologic regime in different ways, affecting both the amount and vertical distribution of water in the profile. For example, anecic earthworms and deep-burrowing harvester ants may favor shrubs by rapidly conducting water to deeper soil layers, while epigeic worms and the smaller Dolichoderine ants would tend to concentrate water in the upper layers of the profile. Similarly, colonization of litter by different species of fungi will change the relative hydrophobicity of the soil surface, altering water redistribution patterns at the surface. Few of these soil organism-vegetation feedbacks have been explored and even fewer tested.

RESILIENCE

The contribution of soil organisms to the resilience of hydrologic functions following disturbance has received relatively little attention. Rangeland soils are constantly subjected to structural degradation caused by raindrop impact, overland flow, wind and the activities of both native and domesticated animals. These processes ultimately lead to physical crusting and compaction. Physical crusts limit infiltration at the surface. This type of crust is distinguished from biologically-stabilized crusts which can enhance infiltration in many cases (Belnap in this volume). Compaction reduces movement of water to deeper layers and can limit surface infiltration during prolonged storms.

The balance between structural degradation and recovery is a function of both biological and physical processes. The importance of biological processes increases in coarse-textured soils. In fine-textured soils charged clay particles bind to each other and to other particles when they are brought into contact by wet-dry and freeze-thaw cycles. In some cases, information on the contribution of soil organisms may be used to promote recovery of degraded systems (DePuit and Redente 1988; Whisenant 1996; Herrick and others 1997). There is a high potential to change the quantity and distribution of plant water availability in rangelands by manipulating soil organism populations through changes in disturbance regimes and organic matter inputs (Lee and Smettem 1995). However, with the exception of studies on earthworms in croplands, the inclusion of *Rhizobium* with seed, the addition of mycorrhizal fungi to extremely degraded mineland (Allen 1988), and the work on termites by Mando (1997), there have been few attempts to develop management tools which directly incorporate soil organisms.

The studies cited in this review, along with preliminary results from recently established studies in southern New Mexico (unpublished data) indicate that recovery of soil structure in a variety of rangeland ecosystems following both small and large disturbances depends on soil organism activity. Resilience is believed to increase with the number of species per functional group (Naeem 1998). Species redundancy appears to be extremely low for hydrologic functions in at least some rangeland ecosystems. For example only two species of termites *{Gnathamitermes tubiformans* and *Amitermes wheeleri)* contribute significantly to macropore formation in the northern Chihuahuan desert. The impacts of removing or limiting the activity of just these two species can be quite dramatic, as illustrated by the termite removal study described above (Elkins and others 1986).

SUMMARY AND CONCLUSIONS

Soil organisms have significant impacts on hydrologic processes and may play a key role in controlling water redistribution on the landscape across a broad range of rangeland ecosystems. These impacts vary across functional groups, microsites, plant communities and regions. Larger macroinvertebrates are responsible for macropore formation and for the breakdown and incorporation of litter, controlling the residence time on the soil surface. Smaller invertebrates, bacteria and fungi contribute to aggregate formation and thereby soil water storage capacity. An understanding of soil biology and the direct and indirect (through vegetation) effects on hydrology can already be used in some areas to direct or guide management practices involving soil surface disturbance and the removal or incorporation of organic matter.

ACKNOWLEDGMENTS

M. Walton provided an early review of this manuscript.

QUESTIONS FROM THE FLOOR

Q: What is the relative importance of hydrophobicity for water infiltration in more xeric rangeland environs?

A: Hydrophobicity varies widely across both space and time in rangeland environments. It is commonly associated with the accumulation of decomposing litter under shrubs, but can also occur in interspaces between plants. In some rangeland environments it can be extremely important during at least part of the year, while in others it is scarcely evident.

Q: Do bacteria & fungi play a bigger role in infiltration rates with black grama (Bouteloua eriopoda) grasslands that are not degraded when compared to ants and termites?

A: I am not aware of any studies which have directly compared the relative contribution of these soil organisms to soil structure in black grama grasslands. All appear to be important. Shrub invasion of black grama grasslands is generally associated with a decline in soil lichen cover. The lichens are frequently replaced by cyanobacteria, which are less apparent, but more resilient. Fungal density is correlated with both live roots and with organic matter inputs. As the system moves from grass- to shrub-domination, these distribution of these resources become more patchy at the decimeter to meter scale. Ants and termites are ubiquitous throughout both degraded and non-degraded systems.

Q: You described binding agents for various size aggregates. Are these representative binding agents, in all ecosystems and if not, what agents occur in different ecosystems or soil types?

A: The binding agents which I described for various size classes of aggregates have been found to occur in all ecosystems. Elliott (1986) found that the basic model described here applies at least in general to a Nebraska prairie soil. However, the relative importance of each type of binding agent does vary across both ecosystems and soil types. Very little information is currently available, particularly for low-organic matter perennial-dominated rangeland soils. A USDA-University of Illinois study was initiated in 1998 to address this issue for the Chihuahuan Desert at the Jornada Experimental Range.

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EFFECTS OF DISTURBANCE ON MICROBIAL ACTIVITY AND N-CYCLING IN FOREST AND SHRUBLAND ECOSYSTEMS

John M. Stark[1] and Stephen C. Hart[2]

ABSTRACT

Disturbances involving removal or destruction of plant biomass or mixing of soil typically increase nitrogen (N) availability. Increased N availability above plant requirements can have detrimental effects by increasing soil nitrate concentrations, which can lead to increased N losses or increased abundance of undesireable weedy plant species. The increase in nitrate concentrations following disturbance can be attributed in part to increases in populations and activity of nitrifying bacteria, but an even more important cause appears to be a reduction in rates of assimilation of nitrate by soil microorganisms. This decline in microbial assimilation rates appears to be direct result of smaller amounts of belowground plant carbon-inputs following disturbance. Maintaining C-inputs to the soil following disturbance will allow continued microbial assimilation of N, which will minimize the adverse affects associated with excess N availability.

Keywords: disturbance, nitrification, microbial assimilation of nitrogen, nitrate, isotope dilution, nitrogen loss

INTRODUCTION

The term "disturbance" is used frequently in ecological discussions, however, the term is quite ambiguous and may describe events that have very different effects on ecosystem processes. In addition, the degree of disturbance that a particular event creates in an ecosystem may be quite specific to that ecosystem. For example, a period of two or three months of drought may represent a disturbance to plants adapted to mesic environments, while that same drought might have little or no impact on plants adapted to semi-arid and arid systems. Likewise, a moderate amount of herbivory might have minimal effects on a plant species that has evolved in the presence of grazing, but could be devastating to a plant that has not. In this paper, we will limit our discussion to two types of disturbances that have direct effects on ecosystem function, soil microbial communities, and nitrogen (N) cycling. These disturbances are: a) destruction or removal of plant biomass (during processes such as fire, grazing, harvesting, etc); and b) physical mixing of soil (during processes such as cultivation, and forest harvesting and site preparation).

These two types of disturbances may have a number of different effects on N cycling. Removal of plant biomass reduces water extraction, uptake of N, and most importantly, reduces the input of carbon (C) to the soil system. All of these factors will tend to promote increased N availability: higher soil moisture contents will lead to greater microbial activity, but with reduced C-inputs soil microorganisms will produce less biomass, and thus, immobilize less N. In addition, since the plants themselves are taking up less N, there will be more left in the available pool.

Soil mixing can increase substrate availability to soil microorganisms by exposing organic materials that were previously trapped in inaccessible locations. Soil mixing may also increase microbial activity by changing soil aeration and water relations. In addition, soil mixing may disrupt fungal hyphae that link soil microsites. Disruption of these fungal linkages reduces the ability of the microbial community to exploit microsites of high N availability, which is likely to increase N availability to plants. Therefore, one of the important outcomes of many disturbances is that there is a temporary increase in availability of N, as well as a variety of other nutrients.

CHANGES IN NITROGEN AVAILABILITY

Increased N availability is in many respects a double edged sword. It may be something to strive for if you are interested in growing highly productive agricultural crops, but where sustained production of more slow-growing native perennial vegetation is the goal, N availability in excess of plant needs may have adverse

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[1] John M. Stark is an associate professor of microbial ecology in the Department of Biology, Utah State University, Logan, UT 84322-5305.

[2] Stephen C. Hart is an associate professor of forest ecosystem ecology at the School of Forestry, College of Ecosystem Science and Management, Northern Arizona University, Flagstaff, AZ 8601 1-5018.

effects. Increased availability of N generally results in greater accumulation of nitrate, the primary anion form of soil inorganic N. This may cause problems for two reasons: nitrate is the form of N that is most readily lost from soils, and high nitrate concentrations may stimulate growth of annual weeds.

Increases in the availability of either form of inorganic N, ammonium (NH_4^+) or nitrate (NO_3^-) may cause increased N loss from soil, but the most important pathways for N-loss from most soils are associated with the NO_3^- pool (fig.1). Denitrification occurs under anaerobic conditions, as bacteria rely on NO_3^- instead of O_2 to carry out respiration processes. During denitrification, NO_3^- is converted to gaseous forms of N which are lost to the atmosphere. High soil NO_3^- concentrations can also lead to increased losses from leaching. Because $N0_3^-$ is an anion, it is not adsorbed to soil colloids as readily as NH_4^+, and thus it is easily washed out as water percolates through the soil.

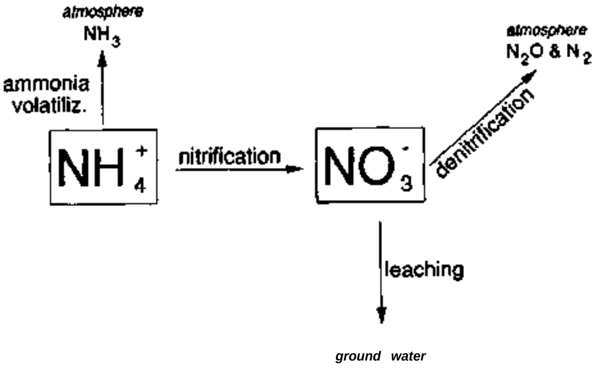


Figure 1 —Pathways for nitrogen loss from soils.

High N availability may also promote growth of fast growing weedy plant species at the expense of the native perennials. Annual weeds frequently show a greater growth response to high N-availability than many slow-growing native perennials (Kay and Evans 1965, Trent and others 1994, McLendon and Redente 1994). In addition, certain annual weeds show a preference for NO_3^- as an N-source, whereas many native perennials show a preference for NH_4^+ (Young and others 1995). Therefore the shift away from NH_4^+-dominated soils and toward NO_3^--dominated soils that usually accompanies soil disturbance, may favor establishment of annuals rather than the more desirable perennial species. It has been suggested, for example, that changes in N-availability and in the abundance of NO_3^- relative to NH_4^+, play important roles in allowing cheatgrass stands to persist in much of the western US.

Because many types of disturbance result in accumulations of NO_3^- in soil, much of the research related to disturbance effects have focused on the process of NO_3^- formation (Robertson and Vitousek 1981). Nitrate is formed from NH_4^+ by a process called nitrification (fig. 2). This process is carried out by two groups of soil bacteria: the first group oxidizes NH_4^+ to nitrite (NO_2^-), and consists primarily of members of the genera *Nitrosomonas, Nitrosospira,* and *Nitrosolobus.* These bacteria get 100% of their energy from the oxidation of NH_4^+, and to create biomass they fix CO_2. Thus, they are quite responsive to changes in the availability of NH_4^+. The second step of nitrification, the oxidation of NO_2^- to NO_3^-, occurs quite rapidly and is carried out by soil bacteria belonging to the genus Nitrobacter.

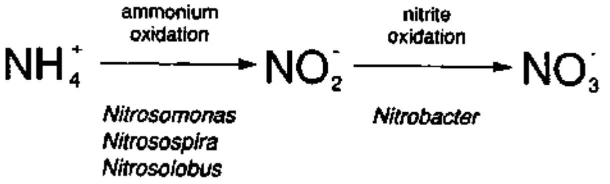


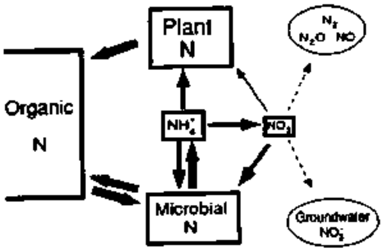
Figure 2 —The two-step process of nitrification and the genera of bacteria that carry out the processes.

N-CYCLING-PAST AND CURRENT VIEWS

Previous research on the process of nitrification has led to the view that in soils of undisturbed late successional ecosystems, very little NO_3^- is produced, and what is produced is taken up by plants (fig. 3a). The vast majority of the N-cycling has been believed to occur between the organic and NH_4^+ pools. With low rates of nitrification, and plant uptake of the small amount of NO_3^- that is produced, N-losses are kept to a minimum.

Another conventional view of the N-cycle has been that soil microorganisms are not important sinks for $N0_3^-$ (Jones and Richards 1977). It has been shown in laboratory studies that the presence of NH_4^+ inhibits microbial uptake of NO_3^- (Broadbent and Tyler 1962). Since NH_4^+ is almost always present in soils, it has been assumed that this will prevent significant amounts of uptake of NO_3^- by soil microorganisms, and thus, plants will be the primary sink for NO_3^-. Upon disturbance, such as removal of plant biomass, plant uptake of ammonium stops (or is greatly reduced), and NH_4^+ pools increase (fig. 3b). Increased NH_4^+ availability allows nitrification to occur, and populations of nitrifying bacteria expand, causing even more NO_3^- to be produced. Because plants are either gone or present in only small amounts, there is no sink for NO_3^-, and NO_3^- accumulates. Under these conditions increased denitrification and leaching cause substantial amounts of N to be lost from the soil. As mentioned

a) in Late Succesion (Revised Model)



b) Following Disturbance

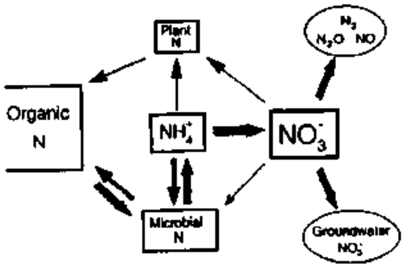
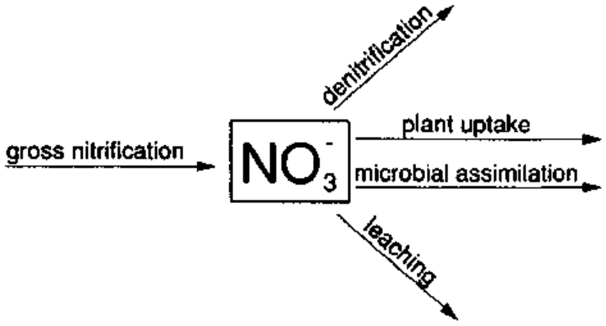


Figure 3-Revised view of the N-cycle in a) late successional ecosystems; and b) early successional ecosystems following disturbance. Even in mature undisturbed ecosystems, a substantial amount of N appears to cycle through the nitrate pool, but microbial assimilation prevents nitrate from accumulating and leading to N-loss.



$$\text{net nitrification} = \text{gross nitrification} - NO_3^- \text{ consumption}$$

Figure 4—Sources and sinks of nitrate in soils. Net nitrification techniques measure the difference between nitrate production and consumption. If consumption processes are significant, then net nitrification rates will underestimate gross nitrification rates. In most undisturbed soils, microbial assimilation of nitrate is a substantial consumptive fate of nitrate.

earlier, higher soil water contents also may follow plant biomass removal due to reduced transpiration, which will increase the likelihood of anaerobic conditions and water percolation, and thus further increase N loss by denitrification and leaching.

Recent studies have provided evidence that this conventional view of N-cycling is not quite correct. The phenomenon of increased N-availability and NO_3^- leaching following disturbance has been well documented, but the mechanisms for the phenomenon have not. Almost all of the work showing that nitrification rates are slow or nonexistent in mature undisturbed forests have utilized measures of net nitrification rates, such as the buried bag technique. In this technique, a soil sample is collected and incubated in the field. The net change in the soil NO_3^- pool during the incubation period is used to estimate nitrification rates (fig. 4). If all of the consumption processes are eliminated, then this net change in the NO_3^- pool will equal the gross rate of nitrification. However, if there is consumption occurring, then the net rate will underestimate the actual gross rate of nitrification. Recent studies using ^{15}N have shown that microbial assimilation of NO_3^- may be much more prevalent than previously thought, and thus net nitrification rates may frequently underestimate gross nitrification rates (Schimel and others 1989, Davidson and others 1990, Davidson and others 1992).

We decided to use a relatively new isotope dilution technique (Hart and others 1994) to evaluate whether or not nitrification rates are low in mature undisturbed forests and shrublands. We used this technique to measure nitrification and NO_3^- consumption in soils of a wide variety of undisturbed forests (Stark and Hart 1997). These sites ranged from the highly productive western hemlock-sitka spruce forests on the central coast of Oregon to a juniper woodland in central Oregon. We also measured rates at a big sagebrush steppe in northern Utah and at sites along an elevational gradient in northern New Mexico, ranging from a subalpine spruce-fir site at 3,400 m to a pinyon-juniper woodland at 2,400 m.

Consistent with previous observations, net nitrification rates were low at virtually all of the sites (Stark and Hart 1997). In fact, in 13 of 19 cases, rates were actually less than zero. In contrast, gross nitrification rates, measured by isotope dilution, were quite high. These rates ranged from about one to two orders of magnitude faster than estimates of plant uptake, indicating that cycling of NO_3^- through the soil microbial population is extremely rapid, even in soils of mature undisturbed forests. Because of the high nitrification rates and relatively small NO_3^- pool sizes, soil NO_3^- pools turned over about once each day.

Another interesting observation was that when measurements were made in intact soil cores, NO_3^- consumption was very tightly coupled to nitrification.

The correlation between NO_3^- consumption and nitrification followed a nearly 1:1 relationship and had an r^2 of 0.89 (Stark and Hart 1997). In other words, virtually all of the NO_3^- that was produced in undisturbed soil samples was rapidly consumed by soil microorganisms. This result contradicts the previously held view and shows that nitrification rates can be quite high in soils of undisturbed forests. In addition, it shows that it is not plants, but soil microorganisms that are primarily responsible for promoting NO_3^- retention in undisturbed ecosystems.

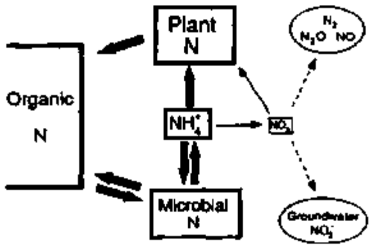
The tight coupling between NO_3^- consumption and production that was seen in intact cores was destroyed when the soil samples were physically disturbed. Following disturbance, the r^2 for the correlation between NO_3^- consumption and nitrification dropped from 0.89 to 0.38. One explanation for this change may be that in undisturbed soils, microsites with high rates of microbial immobilization are linked to microsites with high rates of mineralization and nitrification by fungal hyphae. Through these fungal linkages, N released in high-mineralization microsites is transported back to the high immobilization microsites where it is consumed. Physical disturbance of the soil would break these hyphal connections, and uncouple NO_3^- consumption from production. Therefore, immobilization would stop due to N-limitations, but N-mineralization and nitrification would continue.

This work suggests that we need to revise our view of the N-cycle in undisturbed systems, and our view of how disturbance affects changes in N-availability (fig. 5a,b). Nitrification appears to be a significant part of the N cycle even in undisturbed forest soils; however, nitrification does not necessarily result in high rates of N loss because microbial assimilation of NO_3^- prevents NO_3^- accumulation. Following disturbances that result in removal of plant biomass, belowground inputs of plant C will slow or stop all together, which causes microbial assimilation of N to stop. Without microbial assimilation or plant uptake, NO_3^- accumulates, and increased denitrification and leaching result in substantial N loss.

MANAGEMENT IMPLICATIONS

The management implications of this work are relatively simple: because rates of microbial uptake of N are regulated by carbon availability, maintaining the carbon supply belowground will minimize the adverse effects of disturbance on the N-cycle. Therefore, management practices that maximize the amount of organic debris left on-site and minimize the period of time between vegetation removal and reestablishment will minimize N-losses and limit invasion by weedy plant species.

a) In Late Succession (Classic Model)



b) Following Disturbance

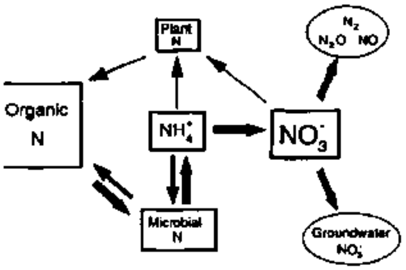


Figure 5 —The conventional view of the N-cycle in a) late successional ecosystems; and b) early successional ecosystems following disturbance.

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NITROGEN TRANSFORMATIONS AND MANAGEMENT INTERACTIONS IN FORESTS

David D. Myrold[1]

ABSTRACT

Nitrogen is often the most limiting nutrient, and often the most limiting of all environmental constraints, to the productivity of forests. The N cycle is also one of the most complicated of all elemental cycles in terrestrial ecosystems. Consequently, it is important to understand its regulation in order to understand the effect that forest management practices have on N cycling and sustainable productivity of forests. Harvesting and site preparation result in an immediate removal of N from the site and can result in elevated losses of N for a period of time as a result of increased N turnover. The long-term impact of these management practices depends upon the size of the remaining soil N pool, how quickly it takes for N consumptive processes to come back into balance with the enhanced production of NH_4^+ and NO_3^-, and an ameliorative efforts to add N to the site through fertilization or use of N_2-fixing plant symbioses. This recovery of the N cycle is site dependent, of course, but can likely be achieved on many sites by carefully balancing N inputs with N removals and using the principles that regulate N cycling to design management strategies that minimize N losses and time to recovery.

Keywords: nitrogen cycle, nitrogen fixation, mineralization, immobilization, nitrification, denitrification

INTRODUCTION

Of all plant nutrients, N is needed in the largest amount and is the nutrient most often limiting productivity of terrestrial ecosystems. Consequently, management activities that alter the amount or availability of N can greatly alter ecosystem productivity, over both the short- and long-term. Most often, forest management practices have the potential for decreasing the N supply, which can result in lower growth and potentially alter forest composition; however, some activities can lead to an excess of N, which may have detrimental environmental consequences.

In this paper I will review the basic principles of N cycling in forest soils and demonstrate how these principles can help us understand the impact that forest management practices are likely to have. In doing so, I will draw primarily on examples of research done in the Pacific Northwest.

OVERVIEW OF N CYCLE PROCESSES

To help understand the cycling of N, it is useful to think in terms of pools and processes. A forest ecosystem has several distinguishable pools of N, for example, N stored in living plants, soil organic N, NH_4 and NO_3^- in soil solution. It is interesting to note that the pools of N that can be readily used by plants are the smallest and those that are least available are the largest (fig. 1). Because the pools of available N are small, the balance between productive and consumptive processes that affect these pools-the inputs and outputs-are extremely important. To aid in conceptualizing the N cycle, it is useful to separate N processes into inputs and outputs to the system from those transformations that are internal to the plant-soil system (fig. 2).

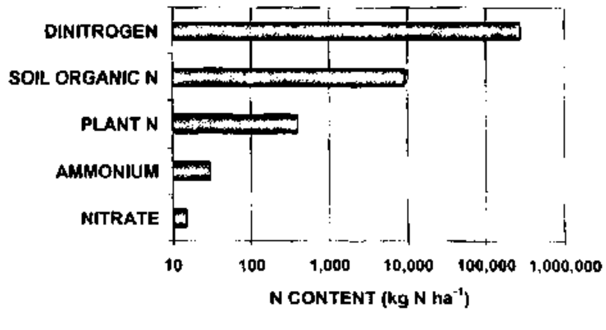

Figure 1 —Sizes of N pools typical for a 30-m Douglas-fir stand in the Pacific Northwest. The N_2 pool is based on the N_2 contained in the top 1 m of soil plus that in the atmosphere within the canopy of the 30-m trees. Soil organic N and plant N are based on Biggar and Cole (1983) and Cole and Johnson (1981). Soil inorganic N pools are typical for conifer forests of the Pacific Northwest (for example, Binkley and others 1992, Vermes and Myrold 1992).

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[1] David D. Myrold is a professor of forest soils and soil microbiology, Oregon State University, Corvallis, OR 97331-7306.

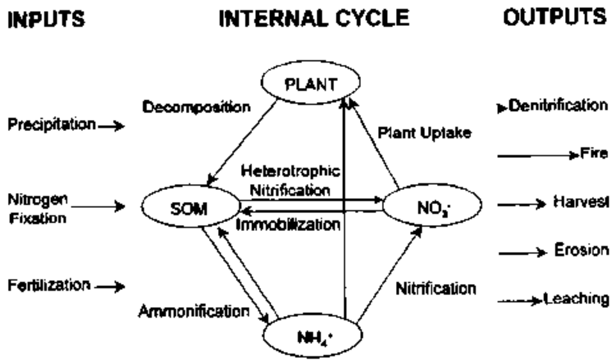

Figure 2—Major pools and processes involved in N cycling in forest ecosystems.

Inputs

Inputs of N into forested ecosystems can be natural or anthropogenic in origin. Natural inputs include precipitation and biological N_2 fixation. Both of these can, of course, be altered or manipulated by human activity. Fertilization is the primary management practice that directly manipulates the input of N to forests.

Precipitation-The most prevalent natural input is inorganic N from precipitation and dry deposition. In pristine forests far from sources of atmospheric pollution, atmospheric inputs of N are low; no more than a few kg N ha^{-1} annually in the Pacific Northwest (Cole and Johnson 1981). Forests located downwind from heavily industrialized regions, high traffic areas, or animal stockyards can have inputs in excess of 10 kg ha^{-1} yr^{-1} (Myrold and Nason 1992).

Nitrogen fixation-The conversion of atmospheric N_2 into plant available forms by bacteria is the second major natural input of N. In most instances, the amount of N accrued by N_2 fixation in forest ecosystems is small, a few kg ha^{-1} yr^{-1} (Dawson 1983). More substantial inputs can occur when plants with root-nodulating, N_2-fixing symbioses are present. In the Pacific Northwest, N_2 fixation rates can exceed 10 kg ha^{-1} yr^{-1} on sites with *Ceanothus* and 50 kg ha^{-1} yr^{-1} on sites with alder (Hibbs and Cromack 1990). It is possible to manage these N_2-fixing plant symbioses to manipulate N inputs at some sites.

Internal Cycling

Within a forest stand, the conversion of N from one form to another is highly dynamic and the major pools of N are interconnected by several biological processes (fig. 2). The relative rates of these concurrent processes determine **the** availability of N, are generally tightly regulated, and can be influenced by management.

Ammonification-Heterotrophic soil organisms can produce NH_4^+ as they decompose plant material and mineralize soil organic matter. This conversion of organic N to NH_4^+ is known as ammonification. Whether ammonification results in the net accumulation of NH_4^+ depends upon the N requirements of the heterotrophic organism relative to the concentration of N in the organic substrate. The general rule of thumb is that NH_4^+ will be produced from an organic substrate with a C:N ratio of about 25 or less; higher C:N ratios will result in inorganic N being immobilized by heterotrophic organisms.

Immobilization-When heterotrophic organisms are limited by available N, they assimilate, or immobilize, inorganic forms of N. Assimilation of NH_4^+ is generally considered to be the dominate route of immobilization, however, recent work in forest soils suggest that sizeable amounts of NO_3^- can also be immobilized (Hart and others 1994). This finding may alter the commonly held conception that NO_3^- production is insignificant in many forest soils.

Nitrification-The production of NO_3^- is key factor in determining N losses from forest ecosystems. Nitrate can be produced by the oxidation of NH_4^+ by specialized genera of nitrifying bacteria, a process known as autotrophic nitrification, or from organic N by a range of heterotrophic microorganisms, a process known as heterotrophic nitrification. Although the autotrophic process is generally considered to be the most important in soils, recent work has shown that heterotrophic nitrification can be dominant in at least some forest soils (Hart and others 1997).

Plant uptake-Plants take up both NH_4^+ and NO_3^- to meet their N requirements. In a forest stand, both ground vegetation and trees take up inorganic N, however, after crown closure, trees are responsible for most plant N uptake. The amount of N taken up by forest trees varies with site productivity (the growth rate of trees, and hence N uptake rates are often dependent upon soil N availability), but typical values for Douglas-fir in the Pacific Northwest are about 20-40 kg ha^{-1} yr^{-1} (Cole and Gessel 1992).

Outputs

Nitrogen leaves forest ecosystems in various forms and by several natural and anthropogenic mechanisms. Management activities can directly remove N through harvest and the use of prescribed fire as well as more indirectly by altering other, more continual outputs, such as erosion, leaching, and denitrification. Although wildfire is a natural component of many forest ecosystems and can result in catastrophic losses of N, most natural outputs of N are continual and generally small.

Leaching-Because it is an anion, NO_3^- is often the dominant form of N lost by leaching, although losses of dissolved organic N can be of a similar magnitude. In general, undisturbed forest ecosystems retain N very tightly and little is lost below the rooting zone. Coniferous forests of the Pacific Northwest loose only a few kg ha^{-1} yr^{-1} through leaching (Sollins and others 1980), although rates can be higher in high productivity coastal forests (Binkley and others 1992). Leaching losses >20 kg ha^{-1} yr^{-1} are not uncommon in stands dominated by red alder (Binkley and others 1992).

Denitrification-Undisturbed forest ecosystems lose small amounts (<1 kg ha^{-1} yr^{-1}) of N by denitrification (Davidson and others 1990). Denitrification losses are somewhat higher in the presence of N_2-fixing plants or following disturbance (Binkley and others 1992, Vermes and Myrold 1992).

Regulation of Nitrogen Cycling

To better understand N cycling and predict the influence of management practices on N cycling it is important to consider the factors that control N cycling in soils. This task is simplified if we divide the internal N cycle into three subcycles: the organic N, NH_4^+, and NO_3^- subcycles (fig. 3).

Organic N subcycle-The major input into the soil organic N pool is the physical incorporation and biological decomposition of plant detritus (fig. 3a). Except when N_2-fixing plant symbioses are present, the N in plant debris represents N that is recycling through the plant-soil system. The bulk of N in plant debris is present in organic forms, largely proteinaceous compounds, which are metabolized by heterotrophic soil organisms. Some of this N may be incorporated into microbial biomass, a relatively small pool of organic N that turns over several times per year; some may be transformed into more recalcitrant compounds or interact with soil minerals and thereby be stored in a more stable soil organic N pool. Small, water soluble organic N compounds, such as amino acids, that are by-products of mineralization may leach out of the soil. The mineralization process can also produce NH_4^+ by ammonification when the C:N ratio of the decomposing plant debris is low enough to provide the decomposers with all the N they require for growth.

Ammonium subcycle-Ammonium produced by biological ammonification, or entering the system as an outside input (for example, precipitation, fertilization), has a variety of fates (fig. 3b). At high pH (above

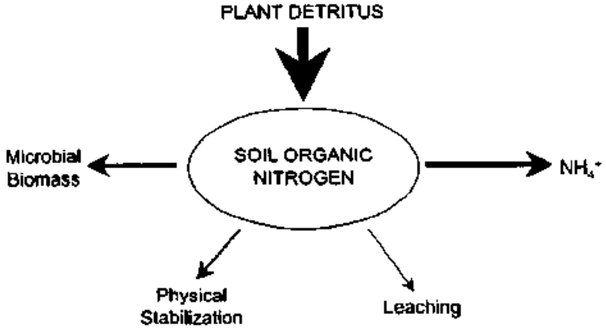

Figure3a

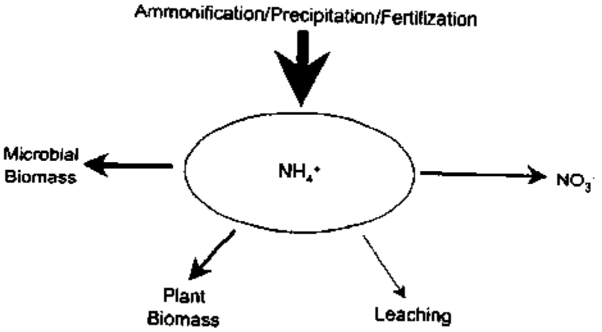

Figure 3b

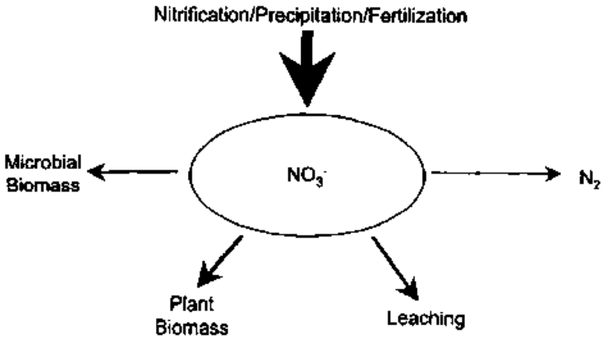

Figure 3c

Figure 3 —The three subcycles of the N cycle: a. soil organic matter subcycle, b. NH_4^+ subcycle, c. NO_3^- subcycle.

8), NH_4^+ can be lost by volatilization to NH_3 gas, but this is highly localized to microsites immediately surrounding animal excreta or urea fertilizer granuales. Because it is positively charged, NH_4^+ is held on cation exchange sites and is not readily leachable. There can also be some chemical fixation of NH_4^+ by illitic clays or soil organic matter, but this is generally a minor fate in most forest soils. Assimilation of NH_4^+ by heterotrophic microorganisms and plants is a more important fate. These organisms compete with nitrifying bacteria for NH_4^+. In many forest soils, C availability is high, consequently heterotrophic microorganisms out-compete plants and nitrifiers, making NH_4^+ immobilization the dominant fate and resulting in plant growth being N limited and relatively low rates of NO_3^- production.

Nitrate subcycle-Nitrate is often the smallest pool of N in the internal N cycle. It is produced biologically by nitrification and can enter the system in precipitation or through fertilization (fig. 3c). Because it is negatively charged, NO_3^- does not interact strongly with soil organic matter or soil minerals and is subject to leaching. In vegetated soils much of the NO_3^- is taken up by plants, however. Heterotrophic microorganisms can also assimilate NO_3^-, and recent research has shown that this can be a major fate of NO_3^- in C-rich forest soils. Some reduction of NO_3^- to N_2 by denitrification can occur in anaerobic microsites of forest soils, but this is usually a minor fate of NO_3^-.

Guiding Principles

Although the exact impacts of forest management activities will always be site specific, there are a few principles that allow us to generalize about the outcome of these activities. First, it is important to remember that N cycling is dominantly biological. Thus the effect of management activities will be determined by how these activities alter the major regulators of biological activity: substrate supply (both quantity and quality), water availability, temperature, etc. Second, with the exception of autotrophic processes (plant growth and nitrification), the cycling of N is intimately linked with C cycling (most of the N in an ecosystem is in organic compounds). This close linkage between C and N means that it is the heterotrophic need for C that often drives the cycling of N and that storage of N is mainly linked to C storage. Third, plant, and even microbial, pools of available N are often in short supply, thus competition between plants, heterotrophic microorganisms, and nitrifying bacteria is the norm. Another way of stating this principle is that competition for available N keeps the sizes of the available N pools small. Four, the turnover rates of N pool are inversely related to their size; small pools, such as NH_4^+ and NO_3^-, turn over very rapidly. Thus, pool size is not necessarily an indicator of biological activity.

MANAGEMENT IMPACTS

Forest management can affect inputs and removals of N as well as influencing the processes of the internal N cycle. In each of these cases, the effect of management can be direct, an immediate response, or indirect, a delayed response. Furthermore, the degree of the effect can vary widely from imperceptible to catastrophic. More subtle effects come about by alterations in soil physical and chemical properties or changes in the microenvironment.

Nitrogen Removals

Nitrogen in forest ecosystems is removed by, or lost as a result of, various management practices. Direct removal of N occurs during timber harvest and the use of prescribed fire. Forest operations can also have less immediate but longer lasting effects through altering rates of erosion, leaching, or denitrification.

Harvesting-The immediate impact of logging is to remove boles, and potentially other portions, of trees. Although significant, the removal of boles represents only about 5-20% of the N stored on forested sites (fig. 4). About an equal amount of N is stored in branches and foliage, therefore complete removal of aboveground tree biomass is a loss of 10-35% of the total system N (Biggar and Cole 1983). The fraction of system N removed in boles is fairly constant for a given species regardless of site productivity, however, relatively more N is removed from low compared to high productivity sites when branches and foliage are harvested. By itself, the amount of N removed by harvesting is not usually large enough to adversely affect the long-term productivity of a site, except possibly on sites with very small reserves of N in the soil.

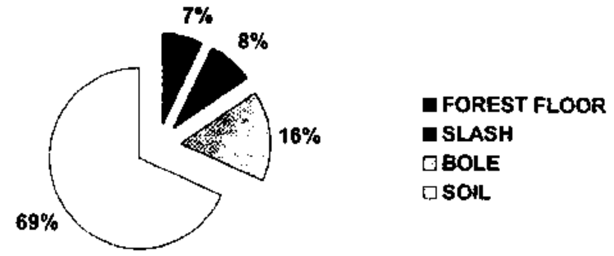

Figure 4—Distribution of N in a Douglas-fir stand (Biggar and Cole, 1983).

As mentioned previously, the major indirect effect of removing trees is to reduce the competition for available N, at least until vegetation regrows. Thus, it is common to find greater rates of net N mineralization and enhanced NO_3^- production during the first few years after harvesting (table 1). This is partly from reduced competition for N but may also be fostered by an improved microclimate (moister and warmer soils) as a result of removing the forest canopy.

Harvesting operations not only remove trees but usually result in exposure of mineral soil, soil displacement, and

Table 1-Indirect effects of harvesting on N lost by denitrification and on internal cycling of N by mineralization and nitrification. The Douglas-fir site is on the east side of the central Coast Range in Oregon; the western hemlock site is on the west side of the Coast Range in southwestern Washington.

Site	Treatment	Net N mineralization	Net nitrification	Denitrification
		- kg N ha^{-1} y^{-1} --	– % -	– kg N ha^{-1} y^{-1} –
Douglas-fir	Old-growth	<10	0	<0.1
	Harvested only	70	60	2
	Harvested/compacted	40	70	4
Western hemlock	Old-growth	<10	0	0
	Harvested only	120	65	0.3
	Harvested/compacted	200	50	0.4

compaction. These changes can also alter N cycling in less direct, but in some instances, longer lasting ways. Decreased vegetative cover and soil exposure can accelerate losses of N through erosion, leaching, and denitrification, at least until there is sufficient regrowth to restore pre-harvest N uptake rates.

A review of studies in several western Oregon watersheds showed that the effect of logging on suspended sediment load in streams is highly variable (Fredriksen and Harr 1981): about half of these studies showed no significant change; the remainder showed 2- to 25-fold increases in sediment load following harvest operations and continued elevated levels of sediment for five or more years. Greater rates of sedimentation were associated with steeper slopes.

Disturbance caused by harvesting operations often causes an increase in NO_3^- leaching (Vitousek and others 1979), although the intensity and duration of this response is highly variable. For example, a study on the H. J. Andrews Experimental Forest in the Oregon Cascades showed that the effect of clearcutting and burning lasted at least six years, although streamwater NO_3^- concentrations were only greatly elevated in the year following slash burning and annual losses at this site were small (Fredriksen and others 1975).

The soil disturbance and compaction that often accompanies harvesting operations can also influence the internal N cycle. Soil mixing may cause a temporary increase in net N mineralization, analogous to the effect of plowing in agriculture. Compaction, on the other hand, by decreasing macropore space and thereby inhibiting aeration, can sometimes slow aerobic microbial activity (table 1). This change in aeration may also enhance denitrification losses on some sites (table 1) but are relatively small in forests of the Pacific Northwest (Vermes and Myrold 1992).

Fire-Prescribed fire has often been used in the past following harvesting for hazard reduction or to prepare the soil for regeneration. The amount of site N lost from burning depends upon the intensity of the fire. Light burns may remove only the small fuel portion of the slash and only the litter (L or O_i) layer of the forest floor; more severe burns may remove all of the slash and forest floor and even volatilize some N from the mineral soil. As illustrated in fig. 4, even a hot burn removes only about the same amount of N as is removed in bole wood.

Because fire is often used in conjunction with timber harvesting practices, it is often difficult to separate its influence from those of tree removal and physical disturbance on N losses by erosion, leaching, and denitrification. Elevated concentrations of NH_4^+ and NO_3^- are often found during the first few years after burning (Weetman and others 1990), which corresponds to the period of enhanced leaching losses.

Nitrogen Inputs

Forest management can also affect the input of N to the system. This is done most directly through fertilization. Nitrogen capital of forest sites can also be managed by including native or introduced N_2-fixing symbiotic plants in mixtures or as part of a rotation.

Fertilization-Forest productivity, particularly on poorer sites, can often be enhanced by N fertilization. This practice has been quite extensive in the Pacific Northwest (Cole and Gessel 1992). In this region, a typical fertilization regime is the addition of about 200 kg N ha^{-1}, which has a growth response of up to about 10 years. The immediate, and most beneficial, result of N fertilization is enhanced tree growth because of plant uptake. In general, the greatest relative response is found on the poorest (most N limited) sites, although greater absolute increases in growth may occur on better sites. Greater response is often seen when fertilization is done in conjunction with thinning.

A review of forest N fertilization studies shows that about 20-30% of the added N is taken up by trees and ground vegetation (Nason and Myrold 1992). Most of the fertilizer N (50-60%) is immobilized into soil organic matter. The remaining 10-30% is lost from the system. When urea is used, much of the N can be lost through NH_3 volatilization. The pulse of available N coming from fertilization usually results in a short-term enhancement of nitrification (Heilman, 1974). This NO_3^- can potentially be lost by leaching and denitrification. The fertilizer N that is incorporated into soil organic matter represents only a small increase (<5%) in the total soil N pool and therefore probably has relatively little long-term impact on N cycling, although there is some evidence that litter decomposition and C mineralization may be depressed for a period of time.

Nitrogen-fixing symbioses-The *Frankia* that form root nodules on actinorhizal plants are the major N_2-fixing symbiosis in temperate forests. In the Pacific Northwest, these actinorhizal plants include *Alnus* spp., *Ceanothus* spp., *Shepherdia* spp., *Cercocarpus* spp., and *Purshia tridentata.* Rates of N_2 fixation range from 20-150 kg N ha^{-1} yr^{-1} for alders, 5-100 kg N ha^{-1} yr^{-1} for *Ceanothus,* and <20 kg N ha^{-1} yr^{-1} for *Purshia tridentata* (Hibbs and Cromack 1990). Whether part of natural succession, grown in rotation, or in mixed stands, these levels of N input can have a significant impact on the growth of associated trees (for example, Hibbs and others 1994) and building of soil organic N reserves (table 2). The continual input of N through the leaf litter and fine root turnover of actinorhizal plants increases the availability of N, which can alter the internal N cycling processes in the soil. Hart and others (1997) showed that the presence of red alder increased rates of N cycling, enhancing rates of NH_4^+ and NO_3^- production relatively more than those of consumptive processes. This often leads to an accumulation of NO_3^- in soils of red alder stands, which can lead to greater leaching losses and sometimes greater denitrification (table 2).

IMPLICATIONS FOR SUSTAINABILITY

There are several points we can draw from the information on N cycling in forests that has been presented:

1. Human activities can decrease or increase N pool sizes depending upon the type of activity.

2. Human activities generally speed up N turnover; N cycles faster as the result of management activities.

3. The combined affect of these two generalizations is that human activities usually result in greater losses of N from forest systems compared to unmanaged forests.

It is always important, however, to keep these generalizations within the context of the degree, or magnitude, of management activities and the inherent characteristics of the site. Some sites are better buffered to changes in N inputs and outputs (resistant) and some recover more rapidly (resilience). Resistance and resilience to management activities, and hence long-term sustainability, will require us to:

1. Balance inputs of N with removals of N.

2. Understand the many factors that control N storage and turnover in forest soils.

ACKNOWLEDGMENTS

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QUESTIONS FROM THE FLOOR

Q: How important is lichen-nitrogen input to forest ecosystems?

A: It is known that lichens that form symbioses with cyanobacteria, such as the *Lobaria oregana,* which grows on the branches of old-growth Douglas-fir trees, can fix N_2. The annual input from these sources is a few kg N ha^{-1} y^{-1} which is similar to inputs from precipitation, and probably balances N outputs. The importance of these lichens in younger forests is probably less and not sufficient to compensate for harvest removals.

Q: How effective are riparian reserves in mitigating loss of NO_3^- through leaching? What characteristics of riparian reserves make them more effective?

A: Vegetated riparian zones have the capacity to take up N and store it in plant biomass and, ultimately, as soil organic matter. Nutrients, such as NO_3^-, in the soil water that moves through the rooting zone of a riparian buffer strip, can be taken up by plants, immobilized in the soil, and, in the case of NO_3^-, volatilized by denitrification. This has been most clearly shown using riparian buffer strips adjacent to agricultural lands. Their exact capacity to mitigate NO_3^- movement to

Table 2-Influence of red alder on N cycling in Pacific Northwest forests (Binkley and others 1992).

Site	Treatment	Soil N	N Leached	Denitrification
		- kg N ha^{-1} -	- kg N ha^{-1} y^{-1} -	- kg N ha^{-1} y^{-1} -
Wind River, WA	Conifer	2100	5	0.1
	Conifer-alder mix	4700	25	0.2
Cascade Head, OR	Conifer	10,000	20	0.1
	Conifer-alder mix	14,000	50	0.1

streams will certainly vary depending upon the size of the buffer strip, soil type, plant community, net primary productivity, and other factors. Obviously bigger buffers have greater capacity and riparian vegetation with greater growth rates can take up more NO_3^-.

Q: Explain what happens to added N fertilizer after 10 years. Does the ecosystem revert back to the Nitrogen cycle balance before added fertilizer? Does the tree growth slow down to what it was before?

A: Empirical studies in the Pacific Northwest have shown that the growth response to the standard 200 kg N ha^{-1} urea fertilization lasts up to ten years, eventually returning to control (non-fertilized) growth rates. There is very little process-level work examining the long-term (>10 y) effect of N fertilization on N transformations in soils. The few ^{15}N studies have shown that 50-60% of the N is immobilized into soil organic matter and 20-30% is taken up by trees and understory vegetation; the remaining N is presumably lost by NH_3 volatilization, leaching, and denitrification. Urea fertilization often results in enhanced nitrification for the first few years following application but this usually returns to pre-fertilization rates after 10 years. Some studies have shown N fertilization to depress decomposition and C mineralization (presumably by inhibiting lignin degrading fungi) during the first few years following fertilization, but longer lasting effects have not be researched.

Q: Yesterday, it was mentioned that if there is less of something within soils-it becomes more critical if some is removed from the system, versus if there is an abundance of something and some is removed there is less of an impact. Question: Much talk about elements C, N, and P. Do forest activities affect micronutrients? Do we know to what degree? What role do these micronutrients play for soil organisms and soil health/resiliency?

A: There are certainly examples when micronutrients, such as Cu and B, are limiting to tree growth, although they are not as widespread as macronutrient growth limitations and have not been studied very intensively. Because micronutrients are required in very small amounts, management practices that selectively remove them (e.g., harvesting, burning of litter layer, etc.) would be expected to be most detrimental. There is not much hard data, however. Soil organisms, like trees, also require micronutrients but there is even less information that they may actually be limited by them in forest soils, except for a study that suggested that N_2-fixing bacteria may be Mo-limited on some sites.

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WILDFIRE VS. CLEARCUTTING: IMPACTS ON ECTOMYCORRHIZAL AND DECOMPOSER FUNGI

S. Visser[1] and D. Parkinson[2]

ABSTRACT

Intense wildfire is more destructive to the forest floor than timber harvesting with potentially more impact on fungal communities as loss of forest floor structure, microhabitat and resource diversity is more extreme after wildfire. After intense wildfire, decomposer and EM fungi associated with the forest floor are virtually eliminated since the organic matter may be almost completely combusted exposing the underlying mineral soil. Clearcutting and site scarification may compress and redistribute forest floor organic matter, but losses are low relative to those from intense wildfire. Studies in lodgepole and jack pine forests in Alberta indicate that wildfire destabilizes the EM community to a greater extent than clearcutting and recovery to pre-disturbance conditions is more rapid following clearcutting. Decomposer fungi in the forest floor are significantly reduced by intense wildfire while the fungal community in the underlying mineral soil remains relatively unaltered. Composition of the decomposer fungal community in the forest floor recovers rapidly after burning while community structure requires a longer timeframe to stabilize. However, changes in the decomposer fungal community following intense wildfire has negligible repercussions on litter decomposition. Clearcutting, either with or without site preparation appears to have minimal effects on the composition and structure of decomposer fungal communities. Management of harvested sites for the protection of EM and decomposer fungi should concentrate on minimizing soil disturbance during site preparation, eliminating prescribed burning, and ensuring rotation times are sufficiently long to allow slow-growing fungi to complete their lifecycles.

Keywords: wildfire, clearcutting, site preparation, ectomycorrhizal fungi, decomposer fungi, recovery, community composition, community structure, decomposition

INTRODUCTION

As parasites, symbionts and decomposers, fungi contribute significantly to the regeneration, growth and maintenance of forests. Forest fertility, resilience and sustainability are determined by the ability of the fungi to acquire, translocate, immobilize and recycle nutrients essential to ecosystem function. Diversity of substrates and microhabitats in forest soils as a result of annual inputs of a wide range of dead plant residues (wood, leaves, roots) creates ideal conditions for the development of species-rich fungal communities with wide enzymatic potentials. Resiliency of forest soils to disturbance has been attributed to the presence of highly diverse microbial communities with inherent functional redundancy although the degree of resiliency as related to the extent and intensity of disturbance are not well understood.

Two of the main types of disturbance in northern temperate forests are wildfire and clearcutting. Recently, there has been much interest in basing silviculture on natural ecosystem dynamics such as those following wildfire, with the goal of preserving biodiversity and ecosystem productivity (Bergeron and Harvey 1997). However, in order to develop silvicultural regimes patterned after natural (wildfire) disturbance it is essential that the abiotic and biotic processes associated with forest recovery be well understood. Plant community dynamics following wildfire or clearcutting have been well-researched (Keenan and Kimmins 1993; Johnson 1981; Shafi and Yarranton 1973) while the dynamics of fungal communities and associated nutrient cycling processes have received much less attention. This aspect of forest recovery is considered in the present paper which reviews the relative impacts of wildfire versus clearcutting disturbance on ectomycorrhizal and decomposer fungal communities in lodgepole *(Pinus contorta),* jack pine *(Pinus banks/ana)* or mixedwood *(Populus tremuloides; Picea glauca)* forests in the boreal zone of Alberta and Ontario.

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[1] Suzanne Visser is a research associate and adjunct assistant professor, Dept. of Biological Sciences, The University of Calgary, Calgary, AB T2N 1N4.

[2] Dennis Parkinson is a faculty professor, Dept. of Biological Sciences, The University of Calgary, Calgary, AB T2N 1N4.

COMPARISON OF WILDFIRE AND CLEARCUTTING ON ECOSYSTEM ATTRIBUTES

Wildfires in the boreal forest tend to be large-scale with fires over 10,000 ha in area accounting for 90% of the area burned (wildfires 100,000 ha in area are not uncommon) (Johnson 1992). Fire return intervals (recovery time) average 100 years (Johnson 1992). Disturbance intensity is often high in that there is high mortality of the canopy, understory and groundcover and extensive combustion of the forest floor organic matter.

In contrast, clearcutting is conducted on a smaller scale with allowable cuts in Alberta ranging from 60 to 100 ha (Alberta Environmental Protection, Lands and Forest, personal communication). Rotation times are unknown but have been estimated to be 80 to 100 years, a timescale similar to the average fire return interval. Harvesting eliminates the canopy while understory and groundcover species may increase in abundance and productivity (Keenan and Kimmins 1993). Forest regeneration practices generally involve some form of site preparation such as scarification where the forest floor is disrupted by mechanical means to expose the mineral soil so regenerating conifers will have a competitive advantage over more rapidly growing species. Scarification results in redistribution and mixing of soil organic matter.

Abiotic and biotic parameters important in the composition and structure of both mycorrhizal and decomposer fungal communities and which may be altered by either wildfire or clearcutting disturbance include soil temperature, pH, organic matter content, total and available nutrients and plant community composition and structure. Removal of the canopy following wildfire or timber harvesting causes an increase in soil temperature (Keenan and Kimmins 1993; Kozlowski and Ahlgren 1974). The production of ash during a wildfire increases the pH of the surface soil more so than disturbance of the surface soil horizons caused by harvesting and site preparation where the pH may increase slightly or remain unaltered (Kozlowski and Ahlgren 1974; Pietikainen and Fritze 1995). Combustion of the forest floor during an intense wildfire significantly reduces soil organic matter (fig. 1) thereby reducing pools of total nutrients. However, available phosphorus and nitrogen increase following wildfire disturbance as nitrogen mineralization is enhanced and ashing renders phosphorus more available (Raison 1979; Raison and McGarity 1980). Indeed in a study by Visser (unpublished), there was little difference in extractable nitrogen in the upper 20 cm of soil in 6, 41 and 65 year old jack pine stands. Recovery of the forest floor in jack pine stands following wildfire in northern Alberta is relatively rapid as no differences in organic matter accumulation were detectable amongst 41, 65 and 122 year old stands which had originated from wildfire (fig. 1).

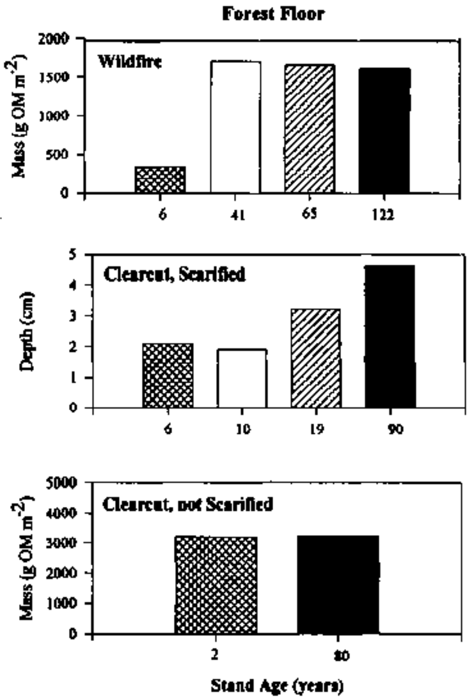

Figure 1 —Forest floor mass or depth in a chronosequence of pine or mixedwood stands following wildfire or clearcutting.

Harvesting alone appears to have little impact on mass of organic matter in aspen/spruce mixedwood stands over the short term (fig. 1). Although harvesting followed by scarification may cause compaction and redistribution of soil organic matter in the surface horizons, thereby reducing the depth of the forest floor (fig. 1), it may not have a significant impact on mass of organic matter in the surface soil horizon (fig. 1). These data indicate that intense wildfire is more destructive to the forest floor than timber harvesting with potentially more impact on fungal communities as loss of forest floor structure, microhabitat and resource diversity is more extreme in the case of intense wildfire. As observed for wildfire, available nitrogen and phosphorus often increase following clearcutting and scarification (Keenan and Kimmins 1993).

Alterations in soil organic matter quality and quantity in conjunction with changes in plant community composition and structure following either wildfire or harvesting/scarification disturbance would be expected to have significant impacts on the soil fungi since these factors drive symbiont and decomposer fungal communities. Removal of the canopy and increased dominance of forbs and grasses after both types of disturbance would lead not only to major shifts in the composition, availability, distribution and physiology of regenerating mycorrhizal hosts, but would also shift the quality and quantity of plant residues feeding the decomposer fungi. How these fungi respond to these changes and their patterns of recovery in regenerating forests and their forest floors is unknown.

WILDFIRE VS CLEARCUTTING/SITE PREPARATION EFFECTS ON ECTOMYCORRHIZAL FUNGAL COMMUNITIES

Fruitbody-producing Ectomycorrhizal (EM) Fungi - Occurrence and Abundance

It is recognized that fruitbody presence does not provide a complete picture of the symbionts colonizing the roots (Jansen and De Nie 1988) since some ectomycorrhizal fungi do not form conspicuous fruitbodies and fruiting occurs at various stages of the life-cycle depending on species, host and environmental conditions. Nevertheless, when combined with observations of ectomycorrhizal fungi colonizing the roots, fruitbodies confirm the presence of a particular species and can provide valuable information on the dynamics and life-history strategies of mycorrhizal fungi involved in forest recovery.

Based on fruitbody observations, recovery patterns of ectomycorrhizal fungi in pine stands disturbed by either wildfire or clearcutting/scarification appear to be very similar (Bradbury and others 1998; Visser 1995) (tables 1, 2). The initial impact of both clearcutting and wildfire disturbance is a reduction in the number of fruiting mycorrhizal fungi, but with time the number of fruiting species increases and the complement of fungi becomes more similar to that observed in mature 90 to 122 year old stands. However, the greater similarity between fungi in young and old stands following clearcutting than following wildfire suggests that the ectomycorrhizal community may recover more rapidly or may not be as impacted by harvesting as it is by wildfire. Species which are typical of younger stands, for example *Suillus* spp., persist throughout the lifetime of the stand although their abundance may change with forest maturation, thus there is no evidence of complete replacement of species (succession) with time (Bradbury and others 1998; Dahlberg and Stenstrom 1989; Visser 1995). The increase in number of fruiting species with stand age may reflect the growth rates of the various species and the time it takes each species to amass enough energy to fruit. For example, species such as *Hygrophorus purpurascens* and *Hydnellum peckii* fruit only in older stands presumably because they are very slow growing and require decades to produce a mycelium capable of fruiting. As a result, these are species which may be most susceptible to clearcutting disturbance if rotation times are shorter than the time required for them to recover and complete their lifecycles.

Root-colonizing Ectomycorrhizal (EM) Fungi — Occurrence and Abundance

A more accurate evaluation of the EM fungi associated with a particular host is obtained by conducting a microscopic examination of the fungi colonizing the feeder roots and identifying them using criteria outlined in identification manuals published by Agerer (1987-1994) and Ingleby and others (1990). This approach has been applied to assess the recovery of the EM fungi in lodgepole and jack pine stands in Alberta (Bradbury and others 1998; Visser 1995).

In these pine stands, both wildfire and clearcutting/scarification disturbance reduced the number of EM species colonizing pine roots, but the reduction was greater following wildfire (56%) than following clearcutting/scarification (32%) (Bradbury and others 1998; Visser 1995) (tables 3, 4). Although EM community similarity to that in the mature stand increased with stand age, pre-disturbance conditions were attained much more rapidly following clearcutting than following intense wildfire. Six years after clearcutting and scarification, EM community composition and structure were very similar to that in mature, uncut stands; this was not observed in stands regenerating after wildfire where community composition and structure in the young stand were distinctly different from that in the older stands (tables 3, 4; fig 2). Thus wildfire appears to destabilize the EM community to a greater extent than clearcutting and recovery to a large, multispecies community is more rapid following clearcutting than after wildfire.

Fungi colonizing the roots of regenerating trees in both clearcut and wildfire-disturbed stands were also found on roots in mature, undisturbed stands suggesting no distinct EM succession with stand maturation which supports the fruitbody observations (Bradbury and others 1998; Visser 1995). However, the abundances of the fungi comprising the communities appeared to change with time as was evident also in the fruitbody observations. The functional significance of changes in abundance of various EM species with time is unclear but an increase in the size and density of perennial mycelia of particular species over time may result in more efficient acquisition of water and nutrients and closer linkages with the decomposer microflora. Also, it has been proposed that EM fungi which dominate roots of mature stands have greater enzymatic capabilities providing access to organic carbon, nitrogen and phosphorus in forests which become more nutrient-limited with age (Dighton and Mason 1985).

Table 1 —Most frequent ectomycorrhizal fungi observed fruiting over three growing seasons in a chronosequence of lodgepole pine stands following clear-cutting disturbance. (+ = 1-9, + + = 10-99, + + + = 100-999, + + + + > 1000 fruitbodies). Data modified from Bradbury and others (1998).

Species	Stand age (years)			
	6	10	19	90
Cortinarius spp.	+ +	+ + +	+ + +	+ + +
Laccaria laccata	+ +	+ +	+ +	+ + +
Lactarius rufus	+	+	+ + +	+ + + +
Leccinum ponderosum	+	+ +	+ + +	+ + +
Suillus tomentosus	+	+ +	+ +	+ + +
Suillus umbonatus	+ +	+ + +	+ + + +	+ + +
Hygrophorus hypothejus		+	+	+ + +
Hygrophorus eburneus			+	+ + +
Hydnellum peckii				+ + +
TOTAL (all species)	19	25	30	35
SIMILARITY (with time)[a]	0.6	0.7	0.8	1

[a] Based on Sorenson's qualitative index of similarity.

Table 2 —Most frequent ectomycorrhizal fungi observed fruiting over two growing seasons in a chronosequence of jack pine stands following wildfire disturbance. (+ = < 10, ++ = 10-20, + + + = > 20 fruitbodies per growing season). Data based on Visser (1995).

Species	Stand age (years)			
	6	41	65	122
Suillus brevipes	+ + +	+	+ +	+ +
Inocybe spp.	+ + +	+ + +	+ +	+
Lactarius deliciosus	+	+ + +	+ +	+ +
Tricholoma zelleri		+ + +	+	
Suillus tomentosus		+ + +	+ + +	+ + +
Cortinarius spp.		+ + +	+ + + +	+ + +
Bankera fuligineo-alba		+ + +	+ +	+
Russula spp.		+ +	+ + +	+ + +
Hydnellum peckii			+ + +	+ +
TOTAL (all species)	14	33	40	33
SIMILARITY (with time)[a]	0.3	0.6	0.7	1

[a] Based on Sorenson's qualitative index of similarity.

Table 3—Most frequent ectomycorrhizal fungi colonizing lodgepole pine roots in a chronosequence after clear-cutting. Data modified from Bradbury and others (1998) and expressed as % relative abundance.

Species	Stand age (years)			
	6	10	19	90
Lactarius deliciosus	21	1	0	2
Suillus brevipes/tomentosus	28	35	17	2
Mycelium radicis atrovirens	27	21	21	22
Piloderma fallax/byssinum	4	24	20	30
Cenococcum geophilum	7	13	14	6
Tomentella	8	1	9	1
Russula	2	4	9	9
Cortinarius/Dermocybe	2	2	9	7
Hygrophorus	0	0	0	2
TOTAL (all species)	13	15	15	19
SIMILARITY (with time)[a]	0.8	0.9	0.9	1

Based on Sorenson's qualitative index of similarity.

Table 4—Most frequent ectomycorrhizal fungi colonizing jack pine roots in a chronosequence after wildfire. Data from Visser (1995) and expressed as % relative abundance.

Species	Stand age (years)			
	6	41	65	122
Cenococcum geophilum	7	2	2	3
Mycelium radicis atrovirens	12	1	1	14
Suillus brevipes	77	23	14	5
Russula spp.	1	19	23	19
Tricholoma spp.	1	13	12	10
Suillus tomentosus	0	19	1	5
Lactarius deliciosus	0	1	9	0
Cortinarius spp.	0	2	13	5
Hydnellum peckii	0	6	6	3
Piloderma byssinum	0	1	10	10
Hygrophorus spp.	0	0	0	6
TOTAL (all species)	12	20	25	27
SIMILARITY (with time)[a]	0.2	0.3	0.5	1

Based on Renkonen similarity coefficients.

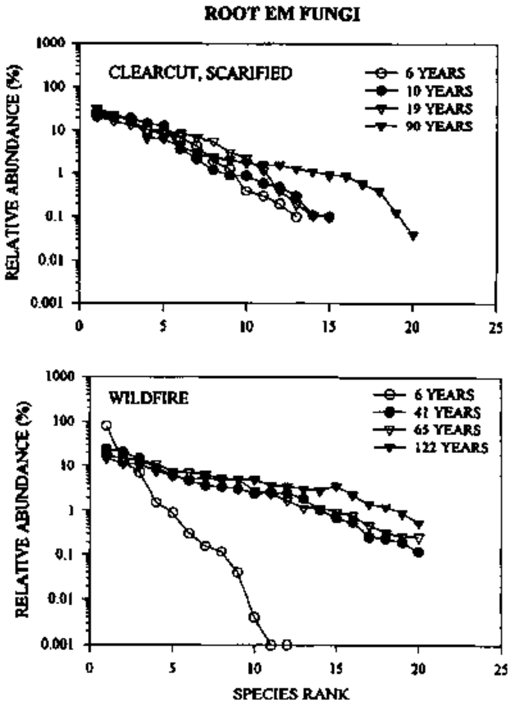

Figure 2—Recovery of EM fungal community structure following clearcutting/scarification or intense wildfire based on rank abundance curves of fungi colonizing pine roots in an age sequence of stands.

The few studies conducted to date indicate that in inland boreal forests intense wildfire alters EM communities more extensively than clearcutting and scarification do, possibly because the extent and degree of host/soil disturbance is greater after wildfire than clearcutting. Harvesting accompanied by burning of logging slash reduces EM fungal inoculum (Harvey and others 1980; Parke and others 1984) more than clearcutting and scarification suggesting EM fungi are more sensitive to burning than other types of silvicultural disturbances. Although patterns of EM recovery are similar after either wildfire or clearcutting, rates of recovery appear to be more rapid following clearcutting than following wildfire.

Both jack pine and lodgepole pine forests are adapted to frequent wildfires and can recover rapidly following this type of disturbance. Adaptation of life histories to fire cycles by both the hosts and their EM symbionts would explain the resilience exhibited by these communities. This resilience allows EM communites to recover rapidly from other types of disturbance as well, such as clearcutting and scarification. Management of harvested sites for the protection of EM fungi should concentrate on minimizing soil disturbance during site preparation, avoiding burning of slash and ensuring rotation times are long enough to allow slow-growing EM fungi to complete their lifecycles.

WILDFIRE VS. CLEARCUTTING/SITE PREPARATION EFFECTS ON DECOMPOSER MICROFUNGI

Wildfire Effects—Fungal Occurrence and Abundance

Through their extensive enzymatic capabilities, the decomposer fungi are essential in the decomposition and mineralization of nutrients from dead plant residues, nutrients which are subsequently taken up by the EM fungi and translocated to the host. Therefore, recovery of this component of the soil flora following clearcutting versus wildfire disturbance should also be considered in the development of forest management plans. Few studies address decomposer fungal community dynamics following disturbance; the following discussion is based on research conducted in a chronosequence of jack pine stands originating from wildfire and boreal mixedwood stands in Alberta (Visser unpublished) and Ontario (Houston and others in press) after harvesting with and without site preparation.

In jack pine stands in northern Alberta, intense wildfire almost totally eliminated the forest floor (fig. 1) including the decomposer fungal community associated with it (Visser 1995). However, as the forest floor redeveloped in the regenerating stands, the fungal community recovered so that 41 years after wildfire disturbance (possibly sooner, stands between 6 and 41 years were not studied), species richness and the composition of the decomposer fungal community were very similar to that in a mature stand (table 5). Although the composition of the community appeared to recover within 41 years of wildfire disturbance, species abundance curves revealed that community structure required 65 years to stabilize. At 41 years, the decomposer fungal community tended to be dominated by three species which is typical of an early successional community (fig. 3). By 65 years, an increase in complexity of the plant community and forest floor microhabitats probably resulted in a more stable fungal community composed of more species whose abundances were more equally distributed (fig. 3). The structural difference between the fungal communities in the 41 and 65 year old stands is interesting and may reflect differences in the state of forest floor decomposition between the two stands. With age, humification of forest floor organic matter and microhabitat and resource complexity would be expected to increase leading to a more diverse and stable decomposer community.

Table 5—Dominant decomposer fungi in the forest floor and mineral soil of a chronosequence of jack pine stands originating from wildfire. Data expressed as % relative abundance.

Species	Stand age (years)			
	6	41	65	122
FOREST FLOOR:				
Oidiodendron griseum	NA	2	21	56
Mycelium radicis atrovirens		1	11	15
Trichoderma viride		87	39	17
Mortierella ramanniana		21	23	28
Penicillium spp.		10	34	38
Mucor sp.		11	5	14
TOTAL SPECIES.		34	42	40
MINERAL SOIL (0-10 cm):				
Fusarium spp.	25	0	0	0
Trichoderma viride	13	26	6	1
Oidiodendron griseum	41	17	48	55
Penicillium spp.	64	35	31	41
Thysanophora penicillioides	25	10	19	33
Mucor circinelloides	13	6	31	24
Mycelium radicis atrovirens	6	4	12	19
TOTAL SPECIES	38	30	38	35

NA = not applicable; forest floor absent.

Regardless of stand age the fungal communities in jack pine forest floors were dominated by *Oidiodendron griseum, Mycelium radicis atrovirens* complex, *Trichoderma viride, Mortierella ramanniana, Penicillium* spp. and *Mucor* spp. while the communities in the underlying 0-10 cm deep mineral soil were dominated by *Fusarium* spp. (6 year old stand only), *Trichoderma viride, Oidiodendron griseum, Penicillium spp., Thysanophora penicillioides, Mucor circinelloides* and *Mycelium radicis atrovirens.* Although the fungi in the forest floor were significantly affected by wildfire, the fungal community in the mineral soil appeared to be unaltered relative to that in a 122 year old stand. Similar observations have been made in burned and unburned subalpine, coniferous forests in the Rocky Mountains six years after a moderately severe wildfire (Bissett and Parkinson 1980). The occurrence of *Fusarium* spp. in the 6 year-old regenerating stand and not in the older stands may be explained by the increase in grasses following wildfire. *Fusarium* is commonly associated with grassland soils. The

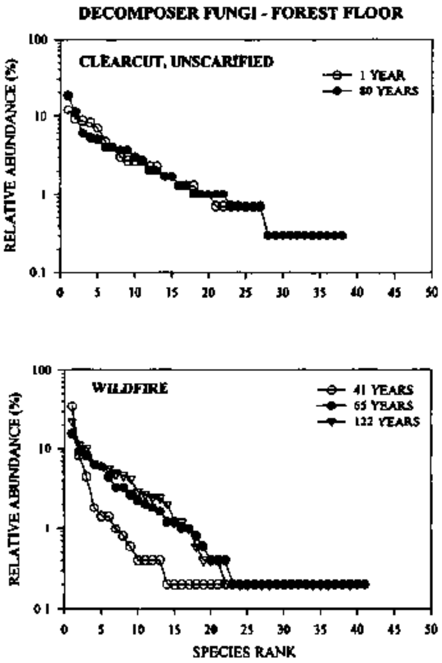

Figure 3 —Recovery of decomposer fungal community structure following clearcutting or intense wildfire based on rank abundance curves of fungi in the forest floor of variously aged jack pine (wildfire) or mixedwood (clearcut) stands.

increase in abundance of *Oidiodendron griseum,* a mycorrhizal symbiont of the Ericaceae, in the forest floor with stand age (table 5), may be indicative of increased colonization of the forest floor by roots of ericaceous plants such as Vaccinium.

Most of the fungi found in the mineral soil also occurred in the forest floor suggesting that colonization of forest floor organic matter as it accumulates in regenerating jack pine stands is to some extent facilitated by fungi in the mineral soil. During wildfire, killing temperatures are restricted to the upper 5 cm of mineral soil (Sims 1976) and it is assumed that fungi surviving below this depth would rapidly recolonize any microhabitats vacated as a result of high temperatures. Aerial and insect/animal dispersal of fungal propagules would be another mechanism for reintroducing decomposer fungi eliminated by fire.

Clearcutting/Site Preparation Effects —Fungal Occurrence and Abundance

In contrast to wildfire disturbance, timber harvesting in the absence of site preparation had no immediate impact on forest floor organic matter (fig. 1) and no detectable effects on either the composition or the structure of the decomposer fungal community (table 6, fig. 3) two years after harvesting a mixedwood *(Populus tremuloides, Picea glauca)* site near Edson, Alberta. The decomposer fungi in both two year old harvested stands and 80 year old unharvested stands were very similar and dominated by the same species - species ubiquitous to well-developed, mature mixedwood forest floors. These results suggest that if the forest floor is not extensively disturbed during timber harvesting, short-term impacts on the decomposer microfungi are negligible.

In a similar study conducted in two mixedwood sites in Ontario, there were few differences in fungal community composition and structure between unharvested sites and adjacent sites seven to nine years after clearcutting and site preparation (Houston and others in press). Although a few species such as *Penicillium canescens* and *Oidiodendron tenuissimum* occurred in either the harvested or unharvested sites, frequencies of the 14 most abundant fungi were similar between disturbed and undisturbed sites (table 7; Houston and others in press). Rank abundance curves (not presented) revealed no differences in community structure in the forest floors of harvested and unharvested sites (Houston and others in press). These observations suggest that harvesting and disturbance of the forest floor by scarification either has no immediate impact on fungi in the forest floor or that recovery of the decomposer microfungi to pre-disturbance levels occurs relatively rapidly, or a combination of both factors. Minimal effects on fungal community structure following clearcutting have been reported also by Bääth (1981) and Baath and others (1995) for pine forests in Sweden.

Based on studies conducted to date, wildfire alters microfungal community composition and structure to a greater extent than clearcutting and site preparation, primarily because high intensity wildfire heats and combusts forest floor organic matter, thereby eliminating microhabitats, reducing fungal biomass and changing the quality and quantity of organic matter available for microbial consumption. Indeed, timber harvesting appears to have few deleterious effects on the microfungal community, particularly if disturbance to the forest floor is minimized. Recovery of the decomposer fungi in the forest floor to pre-disturbance conditions may take many years following intense wildfire whereas recovery following clearcutting/site preparation appears to be rapid. The extent to which wildfires affect fungal communities is probably related to the intensity of the fire and recovery rates probably vary depending on fire intensity and the amount of heat generated. Research is required to confirm this.

Implications of Fungal Community Disruption on Ecosystem Function

Although fungal community composition and structure can be significantly disrupted by severe disturbances such as high intensity wildfire, it is unclear how this disruption translates into effects on ecosystem function. A key ecosystem function is organic matter

Table 6—Decomposer fungi in the forest floors of two unharvested and adjacent harvested mixedwood sites. The forest floor was not scarified following harvesting. Data expressed as % frequency of occurrence.

Species	Stand Age (years)	
	2 (Harvested)	80 (Unharvested)
Trichoderma polysporum	61	40
Mycelium radicis atrovirens	28	23
Penicillium canescens	15	10
Trichoderma oblongisporum	13	22
Cylindrocarpon didymum	10	28
Mucor hiemalis	15	19
TOTAL (all species)	37	38

Table 7—Decomposer fungi in the forest floors of two unharvested and adjacent harvested mixedwood sites in Ontario. The forest floor was scarified following harvesting. Data based on Houston and others (in press) and is expressed as % frequency of occurrence.

Species	Stand Age (years)	
	7 - 9 (Harvested/scarified)	75-101 (Unharvested)
Cladosporium cladosporioides	8	3
Mortierella vinacea	23	17
Penicillium janthinellum	7	3
Trichoderma viride	5	9
Penicillium canescens	0	8
Oidiodendron tenuissimum	6	0
TOTAL SPECIES	42	45

decomposition and measures of this function include microbial respiration and rates of litter decomposition. Six years after wildfire disturbance, microbial respiration and biomass carbon of unburned grey needles and FH material were significantly lower than those measured in the forest floors of 41, 65 and 122 year old jack pine stands, possibly because fire alters the quality of microbially-available carbon in unburned organic matter left after a fire (Pietikäinen and Fritze 1995). However, in a laboratory-controlled decomposition study, mass losses of pine needles placed on soil cores from 6, 41, 65 and 122 year old jack pine stands for three months were almost identical even though the forest floor in the 6 year old stand was almost completely absent (fig. 4). Therefore, losses in the microfungal community as a result of forest floor combustion does not translate into a reduction in decomposition potential over the short-term. This may be explained by colonization of pre-abscission needles by litter decay fungi introduced in the air spora and continued decomposition of the needles by these fungi after deposition. Also, numerous forest floor microfungi which survive in the mineral soil during wildfire have the capability of degrading needles deposited by the regenerating stand thereby recreating the forest floor. These dispersal and survival mechanisms contribute to the maintenance of resiliency within microfungal communities allowing rapid recovery of the decomposition function.

Effects of timber harvesting on soil respiration appear to be negligible either in the presence or absence of scarification (Houston and others in press; Visser unpublished) and this combined with no significant impact on microfungal community composition and structure strongly indicates that the litter decomposition function would remain unaltered also. This was confirmed in a 2 year litter decomposition study in the field where mass loss of fireweed in two-

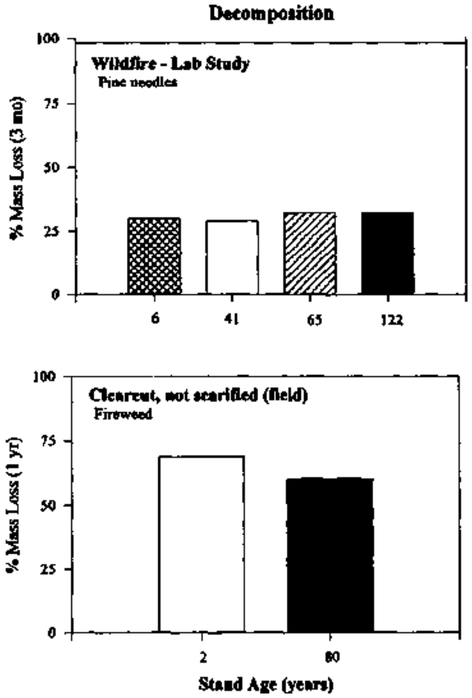

Figure 4—Laboratory decomposition of jack pine needles placed on soil cores from a chronosequence of jack pine stands originating from wildfire and field decomposition of fireweed leaves placed in a two year old mixedwood clearcut and adjacent uncut site.

year old harvested sites and adjacent unharvested sites were not significantly different (fig. 4).

SUMMARY

When comparing the impacts of wildfire versus clearcutting/site preparation on EM and decomposer fungi, intense wildfire has more significant effects on community composition and structure mainly due to high mortality of EM hosts and combustion and chemical alteration of forest floor organic matter. After intense wildfire, decomposer and EM fungi associated with the forest floor are virtually eliminated since the organic matter may be completely combusted exposing the underlying mineral soil. Clearcutting and site scarification may compact and redistribute forest floor organic matter, but losses are low relative to those from intense wildfire. Data from lodgepole and jack pine forests in Alberta indicate that wildfire destabilizes the EM community to a greater extent than clearcutting and recovery to predisturbance conditions is more rapid following clearcutting. Decomposer fungi in the forest floor are significantly reduced or eliminated by intense wildfire while the fungal community in the underlying mineral soil remains relatively unaltered and serves as a source of inoculum in the regenerating forest floor. Composition of the decomposer fungal community in the forest floor recovers rapidly with the accumulation of litter and development of the forest floor, but community structure requires a longer timeframe to stabilize. However, alteration of the decomposer fungal community following intense wildfire does not appear to have negative repercussions on ecosystem function as expressed in litter decay rates. Clearcutting, either with or without site preparation appears to have minimal effects on the composition and structure of decomposer fungal communities. Both EM and decomposer fungi are sensitive to prescribed burning when conducted in conjunction with harversting resulting in significant reductions in EM inoculum and decomposer fungal biomass. Management of harvested sites for the protection of EM and decomposer fungi should concentrate on minimizing soil disturbance during site preparation, eliminating burning of slash and ensuring rotation times are of sufficient length to allow slow-growing fungi to complete their lifecycles. This paper has emphasized the impacts of intense wildfire; response of EM and decomposer fungi to varying degrees of wildfire intensity and variable combustion of the forest floor requires further examination.

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DECOMPOSITION AND NITROGEN MINERALIZATION IN FORESTS OF BRITISH COLUMBIA: EFFECTS OF FOREST MANAGEMENT PRACTICES

Cindy E. Prescott[1] and Lisa M. Zabek[2]

ABSTRACT

The productivity of most forests in the Pacific Northwest is limited by the availability of nitrogen. Nitrogen availability is largely controlled by the rate at which N is recycled from organic matter, through the processes of decomposition and mineralization. These processes are controlled by the factors that limit the activities of the soil organisms involved, particularly temperature, moisture, and the physical and chemical nature of the organic matter. Forest management activities may influence each of these factors and thereby affect rates of decomposition, N mineralization and N availability.

The influences of several common forest management activities on decomposition and N mineralization were examined in a suite of experiments across British Columbia. Rates of decomposition were compared in forests and adjacent clearcuts at 22 sites, and rates were either the same or slower in the clearcuts. Several sites had additional silvicultural treatments that provide a range of either opening size or removal intensity. Decomposition rates were not influenced by opening size, but rates of net N mineralization and nitrification were increased in openings greater than 0.1 ha. Tree species influences N mineralization in the forest floor, with highest rates occuring in Douglas-fir and broadleaf species and lowest rates in cedar and pines. The decomposition rates of foliar litters was best predicted by its lignin concentration. The influence of managing to maintain a component of broadleaf species was examined in decomposition experiments with pure and mixed litter of aspen and spruce, Douglas-fir and alder, and lodgepole pine, Douglas-fir and paper birch. There was no effect of mixing litters on their rates of decomposition. Likewise, N fertilization had no effect on decomposition rates in trials in coastal Douglas-fir and aspen.

Keywords: decomposition, mineralization, nitrogen, fertilization, clear cut, alternative silviculture systems, species, species mixtures

INTRODUCTION

Through the processes of decomposition and mineralization, the nitrogen bound in organic matter is released in inorganic forms (NH_4-N and NO_3-N) which can be taken up by plants. Decomposition is the actual breaking down of material and is measured as rates of weight loss over time. Mineralization is the release of nutrients from organic material as it is broken down. Some portion of the mineralized nutrients are taken up and temporarily immobilized by microorganisms, then remineralized upon death. Rates of mineralization are therefore net rates, *i.e.* the difference between rates of mineralization and immobilization. Nitrification refers to the production of NO_3-N; this can be rapidly reassimilated by microorganisms, so the net rate of this process is measured. Rates of decomposition and mineralization are affected by factors which influence microbial activity, the most important of these are the climate and the nature of the organic material. It is critical to keep in mind that the effects of these environmental factors are mediated through their influence on the soil microbial and faunal communities, whose activities directly affect rates of these processes (fig. 1).

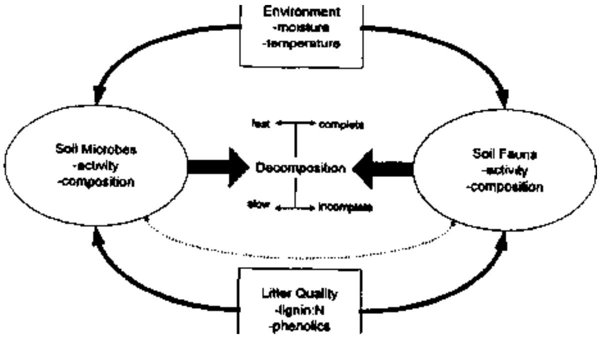

Figure 1 —Factors controlling rates of litter decomposition.

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[1] Cindy E. Prescott is assistant professor in the Faculty of Forestry, University of British Columbia, Vancouver, B.C. V6T 1Z4.
[2] Lisa M. Zabek is a graduate student in the Faculty of Forestry, University of British Columbia, Vancouver, B.C. V6T 1Z4.

The overriding influence of temperature and moisture on rates of decomposition has been demonstrated in laboratory experiments (Bunnell and others 1976), and relationships between decomposition rate and climatic variables such as actual evapotranspiration (AET) across a wide range of climatic conditions have been developed (Meentemeyer 1978). British Columbia has a diversity of climates, due to its size (49°- 60°N), maritime influence, and mountainous topography. The result is a diversity of forest types, from coastal rainforests to ponderosa pine savannas to boreal mixedwoods, which have been used to divide the province into 14 biogoeclimatic zones (Klinka and others 1991). Rates of decompositon of standard litter substrates have been measured at 26 installations in 9 forested biogeoclimatic zones within British Columbia. At each installation, rates of mass loss of pine needle litter, forest floor material and aspen leaf litter are being measured for 5, 4 and 3 years, respectively. Rates of mass loss will be compared with climate measurements at each site or from the nearest climate station, to determine the best relationships for predicting rates of decomposition. Site fertility parameters such as soil texture and C:N ratios of forest floor and soil will also be measured to determine if they have an additional influence on decomposition rates. Average values for the weight of pine needles remaining after decomposing for 3 years at each site were generally fastest in forests on the coast (CWH, CDF and MH zones) and in the interior wet-belt (ICH), and slowest in dry interior forests (PP) (table 1). This suggests that moisture is more influential than temperature on rates of litter decomposition in British Columbia.

The physical and chemical nature (or "quality") of the litter also determines its rate of decomposition. Of particular importance are the relative concentrations of labile and recalcitrant materials, *i.e.* those which are readily metabolized by the microbes and those which are not. Ratios such as C:N, lignin:N, lignin:cellulose:N have proven to be useful predictors of decomposition rates of different substrates (Berg and others 1987, Taylor and others 1989a). Determination of C fractions in litter by nuclear magnetic resonance spectroscopy (^{13}C NMR) has also proven useful in characterizing litters with respect to their potential to decompose and release nutrients. Recent studies (Prescott and Preston 1994, Baldock and Preston 1995) have suggested that the content of alkyl C (waxes and cutin) in particular,

Table 1 —Weight of lodgepole pine needle litter remaining after decomposing for 3 years at sites in each biogeoclimatic zone. Initial litter weight was 2.0 g. Mean (and standard deviation) of 7 samples per site.

Zone[a]	Mean annual temperature	Mean annual precipitation	Site	Weight remaining (g)
BWBS	-1.4	452	Inga Lake	1.07 (.06)
			Bear Mt	0.83 (.17)
			Fairbanks	1.41 (.04)
CDF	9.5	873	Shawnigan S	0.88 (.06)
			Shawnigan N	0.77 (.11)
CWH	9.2	2140	Blaney Lake	0.86 (.21)
			Pt McNeill	0.69 (.12)
ESSF	1.1	1177	Otter Creek	0.77 (.11)
			Spanish Lake	1.05 (.20)
ICH	6.9	1063	Adams Lake	1.01 (.16)
			Malakwa	0.63 (.10)
			Hidden Lake	0.87 (.10)
IDF	4.2	414	Valentine Lake	1.07 (.11)
			Boston Bar	1.06 (.17)
MH	5.0	2954	Strachan	0.89 (.15)
			Garibaldi	0.88 (.15)
PP	8.6	332	Skihist	1.55 (.08)
			Trout Creek	1.24 (.19)
SBS	3.3	628	Beedy Creek	0.66 (.11)
			Topley	0.88 (.14)

[a] BWBS = Boreal Black and White Spruce
CDF = Coastal Douglas Fir
CWH = Coastal Western Hemlock
ESSF = Engelmann Spruce Subalpine Fir
ICH = Interior Cedar Hemlock
IDF = Interior Douglas Fir
MH = Mountain Hemlock
PP = Ponderosa Pine
SBS = Sub-boreal Spruce

may be a useful indicator of litter decomposability. High polyphenol concentrations in litter are generally associated with reduced decomposition, mineralization and nutrient availability (Baldwin *and others* 1983). The reductions are thought to result from the inhibition of microbial activity and the combination of polyphenols with leaf proteins or soluble forms of organic nitrogen to produce humic polymer precipitates that are resistant to microbial attack (Handley 1954; Haynes 1986; Palm and Sanchez 1991). The influence of litter quality on rates of decomposition of 1 2 substrates, including needles, leaves, moss, roots, cones and wood (Taylor and others 1991) are illustrated in figure 2. Decomposition rate was the most closely related to lignin content of the litter.

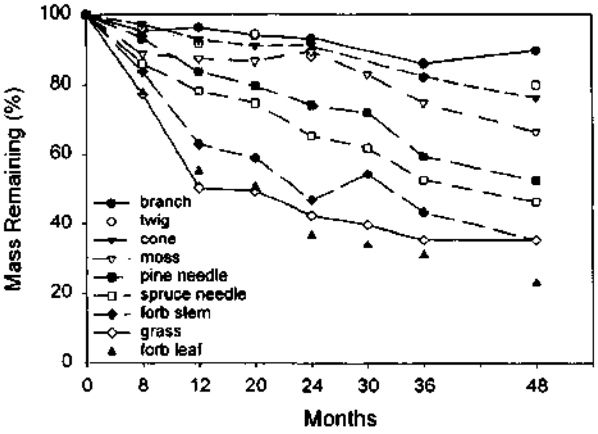

Figure 2—Decomposition of materials of different litter quality in a Rocky Mountain Pine forest (Taylor and others 1991).

Any forest management activity that affects the prevailing moisture and temperature conditions or the nature of the litter produced has the potential to substantially alter rates of decomposition and N mineralization in forest floors. This will influence the amount of organic matter present, the availability of N and other nutrients, and losses of N from the site through leaching. Predicting the effects of a given activity is still difficult due to our imperfect understanding of the controls on these processes and the effects of each management activity on site conditions. Following are results from a series of field trials in British Columbia designed to test the influence of several forest management activities on rates of decomposition and N mineralization.

METHODS

Organic Matter Decomposition

Rates of weight loss of litter were measured using the litterbag technique, in which known-weight samples are enclosed in fiberglass mesh bags and incubated on site. In addition to litter collected at the study site, most experiments employed standard litters: lodgepole pine needles and trembling aspen leaves from the Kananaskis Valley in Alberta (Prescott and others 1989), and forest floor from a coastal forest of western red cedar, western hemlock and Douglas-fir near Vancouver (Prescott and Preston 1995). Bags containing foliar litter were pinned to the surface of the forest floor; bags containing forest floor material were buried in the forest floor. Bags were constructed of fiberglass screening and were 10x10 cm. They were transported to the site in envelopes and spillage into the envelope was weighed and subtracted from the original weight. At annual intervals for 5 years, seven bags of each type were collected from each plot. The contents of each bag was dried at 65°C, and the weight of litter remaining was measured.

Nitrogen Mineralization

Nitrogen mineralization in forest floor material and mineral soil from plots of each treatment were measured during incubation in the field. About ten samples of the forest floor (FH layers) and 10 samples of the upper 20 cm of mineral soil were collected from one plot of each treatment. Roots and live vegetation were removed and the sample was mixed well. A subsample (about 100g) of each sample was put into a polyethylene bag, sealed, and inserted into the forest floor or soil near the place from which it had been removed. After about 6 weeks, the bags were retrieved and final concentrations of NH_4-N and $N0_3$-N were measured using an Alpkem RFA autoanalyzer following extraction in 2M KCl (Page and others 1982). Because initial concentrations of inorganic N were ususally negligible, the final N concentrations were used to estimate net N mineralization during the incubation. For studies of tree species influences, rates of potential N mineralization and nitrification were measured by incubating samples of the forest floors of each species under standard temperature and moisture conditions in the laboratory.

CLEARCUTTING

Increased availability of N is commonly reported after forests are clearcut (Bormann and Likens 1979, Vitousek and others 1979, Smethurst and Nambiar 1990) and has been attributed to faster decomposition and mineralization of the residual organic matter

(Covington 1981, Kimmins 1987). This in turn has been attributed to greater microbial activity resulting from the warmer, moister conditions in clearcuts (Edmonds and McColl 1989, Frazer and others 1990). However, studies have shown that decomposition rates may actually be faster, slower, or the same in clearcuts compared with forests, depending on the regional climate (Yin and others 1989). Further, clearcutting may have different influences on decomposition rates at different depths in the forest floor (Binkley 1984, Yin and others 1989).

Experiments to determine the effects of forest removal on rates of decomposition of litter and forest floors have been established at 22 sites in several forest types in British Columbia. Litterbags containing the same standard substrates were installed in forests and in adjacent clearcuts. After 3 years, rates of decomposition of pine needle litter was slower in clearcuts than in adjacent forests at almost all sites, and significantly so at 7 of the 16 sites (table 2). This may be an effect of drier conditions in clearcuts during the summer, when temperatures are adequate for decomposition.

Table 2—Weight of lodgepole pine needle litter remaining after 3 years decomposition in adjacent forest and clearcut sites. Original weight was 2.0 g.

Zone[a]	Site	Forest	Clearcut
BWBS	Bear Mt	0.83 (.17)	0.93 (.19)
CDF	Shawnigan S	0.88 (.06)	1.00 (.12)[c]
	Shawnigan N	0.77 (.11)	0.85 (.08)
CWH	Pt McNeill	0.69 (.12)	0.98 (.14)[c]
	Blaney Lake	0.86 (.21)	1.22 (.03)[c]
ESSF	Otter Creek	0.77 (.11)	0.79 (.09)
	Spanish Lake	1.05 (.20)	1.06 (.19)
	Lucille Mt[b]	1.04 (.23)	1.00 (.11)
ICH	Adams Lake	1.01 (.16)	1.16 (.14)
	Malakwa	0.63 (.10)	1.12 (.14)[c]
	Hidden Lake	0.87 (.10)	1.23 (.16)[c]
	Date Creek[b]	1.06 (.11)	1.11 (.02)
IDF	Valentine Lake	1.07 (.11)	1.16 (.16)
	Boston Bar	1.06 (.17)	1.09 (.07)
SBS	Topley	0.88 (.14)	1.26 (.06)[c]
	Aleza Lake[b]	1.01 (.13)	1.26 (.07)[c]

abbreviations as in table 1.

2-year data.

clearcut significantly different from forest based on oneway ANOVA.

ALTERNATIVE SILVICULTURAL SYSTEMS

Alternative silvicultural systems such as partial cutting or patch cutting have been proposed as a means of reducing the negative consequences of clearcutting. Little is known about the effects of these alternative systems on organic matter and nutrient dynamics. In an oak forest, Yin and others (1989) found rates of decomposition in a shelterwood (15 years after harvest) to be more similar to those in an uncut forest than in a clearcut (5 years after harvest). Thinning forests has been shown to increase (Piene and Van Cleve 1978), decrease (Weetman 1965) or have no effect (Will and others 1983) on decomposition rates. Greater rates of litter decomposition and net N mineralization were reported in a 0.25 ha patch cut compared to an adjacent lodgepole pine forest (Prescott and others 1992b). Parsons and others (1994) reported increased rates of N mineralization only after removal of at least 15 trees in another lodgepole pine forest. In a beech forest, Bauhus and Barthel (1995) found rates of N mineralization higher in 30-m gaps than in the forest during the first year after cutting, but lower rates during the second year. Rates of net N mineralization and decomposition have been measured in several silvicultural systems trials in British Columbia, in openings of different sizes, or in patch or partial cuts. Following are results from two of the trials.

Montane Alternative Silvicultural Systems Trial

In this trial in a montane forest of western hemlock and amabilis fir on Vancouver Island, treatments were old-growth, shelterwood (200 stems ha^{-1}), greentree retention (25 stems ha^{-1}), 1.5 ha patch cut and a 65 ha clearcut (Prescott 1997). Rates of N mineralization and nitrification in the forest floor were greatest in the clearcut, intermediate in the other silvicultural systems, and least in the old-growth forest (fig. 3). This suggests that the alternative silvicultural treatments have a smaller effect on N mineralization than clearcutting. The lack of a clear gradient in concentrations of mineralized N between clearcut, greentree, shelterwood and old-growth suggests that rates of N mineralization cannot be predicted from basal area removed. The clearcut system appears best for supplying N to regenerating conifers, since it consistently had higher concentrations of extractable N in both forest floor and mineral soil. However, the higher nitrate concentrations in the clearcut indicate that it is more prone to loss of N through leaching, and so the other silvicultural systems may be preferable for maintaining the N capital of the site.

Decomposition rates of foliar litter of hemlock, pine, aspen and forest floors were measured in plots of the five silvicultural treatments (old-growth, shelterwood, patch cut, greetree retention, and clearcut) in a montane coastal forest (Prescott 1997). After decomposing for two years, the weight of hemlock and pine needle litter remaining in the bags was significantly less in the old growth forest than in the other treatments (fig. 4). Forest floor material

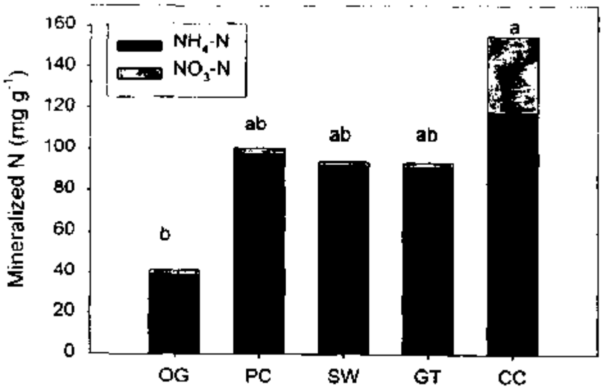

Figure 3—Net N mineralization from forest floors of a coastal montane forest during a 63-day field incubation. OG = old growth, PC = patch cut, SW = shelterwood, GT = greentree, CC = clearcut. Means for treatments with different letters are significantly different ($p < 0.05$) (Prescott 1997).

decomposed slowly in all treatments. The overall tendency was for decomposition to be fastest in the old-growth followed by the clearcut, and slowest in the alternative silvicultural treatments.

The faster decomposition in the old-growth forest in this study suggests that temperature is not the major factor controlling rates of litter decomposition in this ecosystem. Average surface temperatures and growing degree days (>4°C) were substantially lower in the old growth forest than in any of the silvicultural systems (Dunsworth and Arnott 1995). Moisture levels in the forest floor in mid-summer of 1995 were higher in the old growth forest than in the silvicultural systems, suggesting that summer moisture may be more critical for decomposition in this ecosystem. The similarity in decomposition rates in all silvicultural treatments indicates that the alternative treatments are similar to clearcutting in terms of their effect of rates of litter decomposition. This might suggest that surface climatic conditions are more similar among the silvicultural systems than in the old growth; some data supporting this were presented by Dunsworth and Arnott (1995). Alternatively, the higher rates of decomposition in the old growth forest may reflect more intact communities of soil microorganisms and fauna in the undisturbed forests. Reductions in soil microflora and fauna have been reported after clearcutting in other forests (Blair and Crossley 1988, Seastedt and Crossley 1981, Sundman and others 1978), including one on Vancouver Island (Vlug and Borden 1973). Disruption of the forest floor and reduced root activity in the silvicultural treatments may have as great of an effect on the activities of soil microbes and fauna as the microclimatic changes.

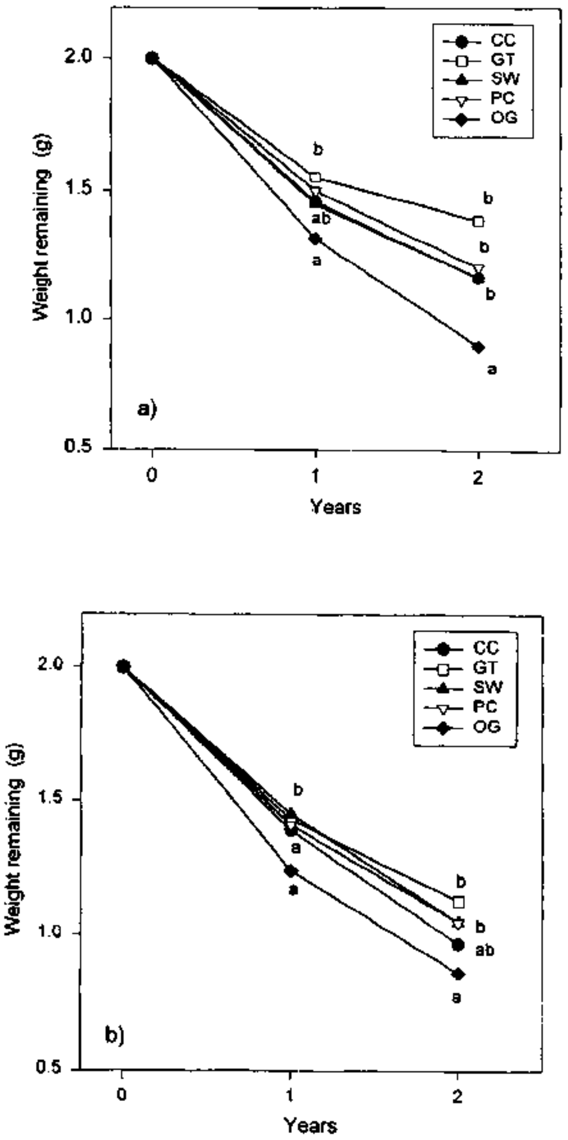

Figure 4—Decomposition of needle litter of western hemlock (a) and lodgepole pine (b) in a coastal montane forest. Treatments as described in figure 3. Means for treatments with different letters are significantly different ($p < 0.05$).

Sicamous Creek Silvicultural Systems Trial

In a high elevation forest of Engelmann spruce and subalpine fir in interior British Columbia, rates of net N mineralization were measured in three plots of each opening size (uncut control, single-tree, 0.1 ha, 1.0 ha and 10 ha) during the first and second growing seasons after harvesting. At each time, 8-12 samples of the forest floor and of the mineral soil were collected from and incubated in the center of each opening for about 6 weeks. Rates of N mineralization in the single-tree removal plots usually did not differ from in the control plots; those in the 0.1, 1.0 and 10 ha openings were consistently greater than in the controls (fig. 5). There was no further increase in mineralization rates in

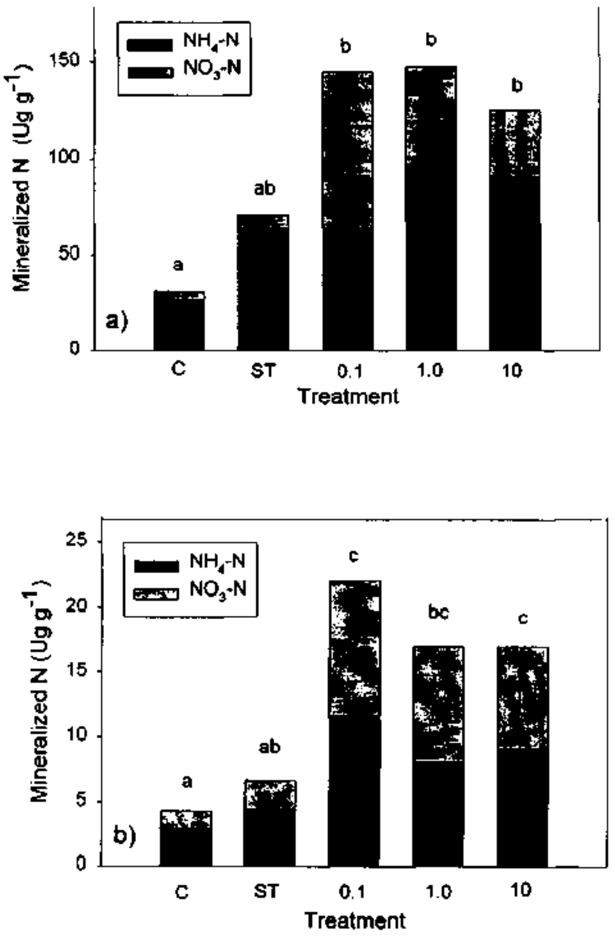

Figure 5—Net N mineralization in forest floor (a) and mineral soil (b) from an Engelmann spruce-subalpine fir forest during a 6-week field incubation. Silvicultural treatments: clearcut (C); single tree (ST); 0.1,1.0, and 10 ha openings. Means for treatments with different letters are significantly different ($p < 0.05$).

openings greater than 0.1 ha. During the first year, nitrate formed a very small proportion (<7%) of the extractable N pool in forest floors, but up to 25% in mineral soil. Nitrate concentrations were much higher during the second year, particularly in openings of at least 0.1 ha, where nitrate accounted for 25-50% of the available N. Decomposition of pine needles, aspen leaves and spruce-fir needles were similar in plots of all opening sizes during the first year (fig. 6). Similar studies at 5 other silvicultural systems trials in British Columbia also showed no opening effect.

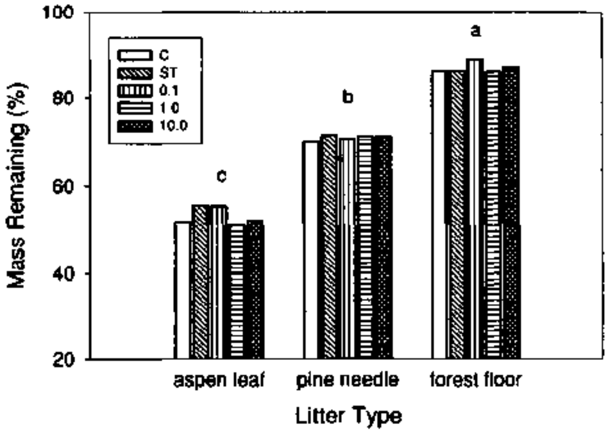

Figure 6—Decomposition of three litter types in an Engelmann spruce-subalpine fir forest. Treatments as described in figure 5. There were no significant differences among treatments.

Greater availability of inorganic N in clearcuts is often attributed to increased rates of decomposition of organic material in openings. In these studies, rates of net N mineralization and nitrification were indeed greater in the clearcuts, but rates of decomposition were not. An alternative explanation is the reduced input of fresh carbon in litter after clearcutting. This would reduce the microbial biomass and its capacity for immobilizing N, thereby increasing the amount of extractable NH_4. Vitousek and Matson (1985) found that immobilization of N in microbial biomass was the major process retaining N in the ecosystem after clearcutting loblolly pine plantations, and that retaining residues as substrates for microorganisms increased N retention. The higher concentrations of NH_4 would also stimulate nitrification, resulting in the higher concentrations of NO_3 after clearcutting. Assimilation of NO_3 would be reduced due to the diminished microbial biomass (Davidson and others 1992), further increasing NO_3 availability in the clearcut. Hart and others (1994) reported increased net nitrification coincident with a decline in microbial biomass during long-term incubations of a coniferous forest soil. The sudden increase in NO_3 concentrations was attributed to a decrease in NO_3 immobilization by the microbial biomass as the quality of C substrates declined during the incubation. A similar situation may exist in forest floors in clearcuts that are deprived of C inputs in fresh litter following the removal of trees. Thus, high rates of N mineralization and leaching in the clearcut may be related more to changes in C supply (litter inputs) than alterations in microclimate.

SPECIES

The influence of tree species on soils has been of interest for decades, but has been difficult to establish because of the difficulty in separating the influences of site and species in natural forests. Recent studies in "common garden experiments" (Binkley 1995), *i.e.* pure plantations of different species on one site, have demonstrated considerable differences in N mineralization rates in forest floors under different tree species (Harmer and Alexander 1 986, Binkley and

Valentine 1991, Harris and Riha 1991, Gower and Son 1992). Each of these studies has been conducted on a single site, which makes it difficult to generalize about individual tree species. However, indications from these and other studies have suggested that N availability is relatively high under broadleaves (Stump and Binkley 1993, Harris and Riha 1991), cedar (Harmer and Alexander 1986, Turner and Franz 1985) and larch (Gower and Son 1992, Harmer and Alexander 1986), and low under pine (Miller and others 1979, Prescott and others 1992a,b) and spruce (Mardulyn and others 1993, Pastor and others 1987). Gower and Son (1992) found that differences in N availablity in the forest floors under 5 tree species were closely correlated with the lignin:N content of the litter, which in turn is closely related to its rate of decomposition. This suggests that the nutritional environment of a tree is largely determined by, and therefore can be predicted from, the resource quality of its litter and the rate at which it decomposes.

The influence of tree species on N availability has been examined by measuring rates of net N mineralization in forest floors from plots of pure species during 30-day laboratory incubations. In the first set of experiments (Prescott and others 1995), three species trials were examined: 35-year-old plantations of western red cedar, western hemlock and Douglas-fir at the UBC Research Forest near Vancouver, 25-year-old plots of lodgepole pine, Douglas-fir and paper birch near Skimikin in interior British Columbia, and 38-year-old plantations of 13 species at Clonsast Bog in Ireland. There were some consistent patterns in relative rates of net N mineralization of tree species in the three trials (table 3). The relative rates of the three species in the University of British Columbia trial (Douglas-fir > western hemlock > western red cedar) were the same in the Clonsast Bog trial. Douglas-fir also had the highest rate of N mineralization of the three species in the Skimikin trial. We might expect, therefore, to find relatively high rates of N mineralization in forest floors under Douglas-fir, and relatively low rates under western red cedar. High rates of net N mineralization and nitrification in Douglas-fir forest floors have been observed in several other trials in British Columbia (Prescott 1996). Other studies have also suggested that N mineralization under cedar is relatively low (Prescott and Preston 1994). The slow mineralization in pine plots is in keeping with low availability of N reported in other pine forests (Fahey and others 1985, Miller and others 1979, Prescott and others 1992a).

The observation of high rates of N mineralization in forest floors under Douglas-fir and low under western red cedar (Prescott and Preston 1994) was tested by measuring rates of N mineralization in forest floors under cedar, hemlock, spruce and Douglas-fir in replicated experiments at four sites in coastal British Columbia. As shown in figure 7, there was very little N mineralized in forest floors from two sites, but large amounts from the other two sites. At UK Main and San Juan, rates were highest in cedar plots, followed by Douglas-fir plots. The large between-site differences in N mineralization were not related to characteristics of the mineral soils. The sites with low rates of N mineralization were located at higher elevations on mid-slopes and the ground vegetation was dominated by salal; the sites with high rates of N mineralization were located at the base of slopes and had vegetation more characteristic of moist sites, such as salmonberry. Due to slow growth of cedar relative to other species on all sites, cedar plots had more open canopies and greater densities of ground vegetation. Rates of N mineralization in the forest floors appear therefore to be influenced by site moisture conditions and related composition of the understory vegetation; these site influences make it difficult to generalize about the influence of tree species.

Foliar litter represents the largest single source of N to be recycled within a forest, and as such its "quality" and resulting rate of decomposition will influence N availability in the forest. Rates of decomposition of foliar litter are often related to their initial C:N, lignin or lignin:N contents. Rates of decompositon of foliar litter of 10 species of trees in British Columbia are being measured at two locations, in the boreal forest and in the coastal forest, and related to initial "quality". Rates of weight loss during the first 3 years are shown in figure 8. Western red cedar, firs and western hemlock decomposed more slowly than other species. The strongest relationship was with % lignin ($r^2 = 0.31$), which ranged from 18% in Engelmann spruce to 38% in cedar (fig. 9).

SPECIES MIXTURES

Recent interest in management of mixedwood forests in British Columbia has highlighted our limited understanding of the interactions among species in mixed forests, particularly as they influence belowground processes. Studies in other forests have demonstrated that having seral stages or interplanting with other species, particularly hardwoods, can significantly improve growth of regenerating conifers, partly through improved nutrition of trees in mixed forests. In the U.K., Sitka spruce in mixtures with larch or pine grow significantly faster than those in single species plantations, and this has been linked to greater availability of N in the forest floor of mixed plantations (Carlyle and Malcolm 1986). Williams and Alexander (1991) suggested that the improved N availability in mixed plantations was at least partly due to more complex fungal-faunal interactions in mixed plantations, which increased rates of decomposition and N release from litter. Development of hardwood

Table 3—Rates of N and C mineralization during laboratory incubations of forest floors from adjacent plantations of different trees species in three trials.

Species and Trial	N Mineralization $\mu g\ N\ g^{-1}\ d^{-1}$	C mineralization $\mu g\ c\ g^{-1} d^{-1}$	PH
UBC Forest			
Douglas-fir	5.5 a	191.4 a	5.2 a
Western hemlock	3.2 ab	202.1 a	4.2 b
Western red cedar	1.6 b	144.5 b	5.1 a
Skimikin			
Douglas-fir	45.9 a	415.2 b	5.8 b
Paper birch	20.5 ab	406.5 b	6.4 a
Lodgepole pine	15.7 b	820.3 a	4.9 c
Clonsast Bog			
Sissile oak	226.3 a	355.2 abc	4.7 bc
Sitka spruce	151.3 b	313.8 bcd	4.8 bc
Grand fir	151.1 bc	234.9 def	5.0 b
Douglas-fir	138.6 bc	282.6 cde	4.4 cde
Norway spruce	127.0 bc	239.0 def	4.9 b
Lodgepole pine	125.7 bcd	195.3 ef	3.9 e
Japanese larch	123.7 cde	279.0 cde	5.7 a
S. spruce + J. larch	98.0 cde	216.1 def	4.3 cde
Western hemlock	89.0 cdef	204.0 ef	3.9 e
Scots pine	73.7 def	385.4 abc	4.7 bc
Monterey pine	52.7 efg	138.1 f	4.1 de
Calluna	41.0 fg	446.5 a	4.6 bcd
Western red cedar	12.3 g	409.4 ab	6.1 a

Note: Each value is the mean of 14 (UBC Forest), 24 (Skimikin), or 10 (Clonsast Bog) samples. Within each trial, values for different species followed by the same letter are not significantly different ($p>0.05$), based on oneway ANOVA and Sheffe's multiple range tests.

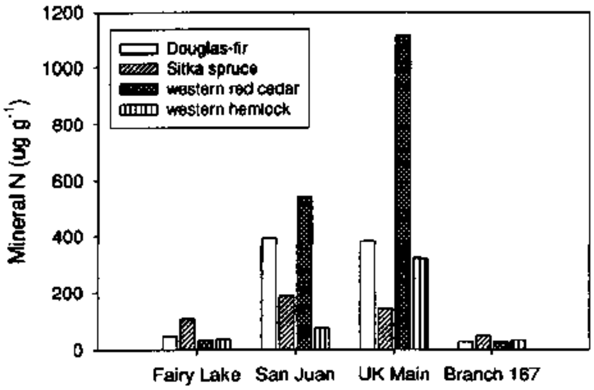

Figure 7—Net N mineralization in forest floors of four tree species at each of four sites in coastal BC during a 4-week laboratory incubation.

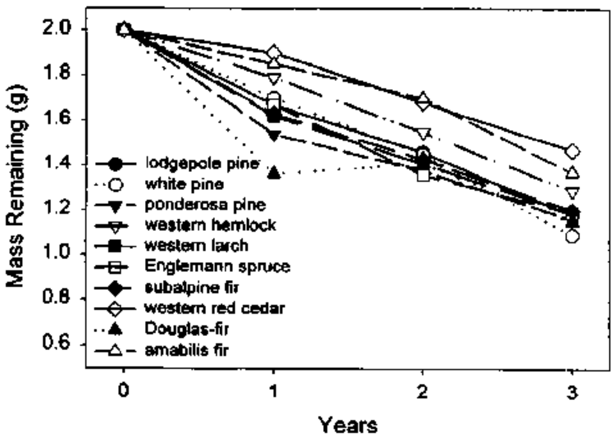

Figure 8—Decomposition of foliar litter of ten conifer species in a boreal spruce forest.

clumps after clear-cutting white spruce in the boreal forest contributes to acceleration of nutrient cycling, due to higher concentrations of N and P in foliar litter of aspen and poplar and subsequent faster decomposition (Pare and Van Cleve 1993). Conifer litter often decomposes more rapidly when mixed with hardwood

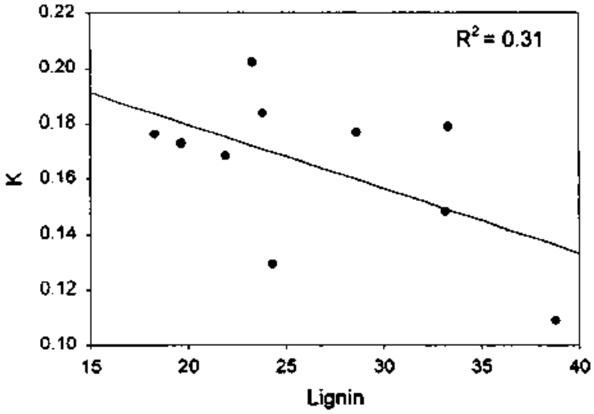

Figure 9 —Relationship between decomposition rate (k value) and % lignin (acid insoluble fraction) of foliar litter of ten coniferous species.

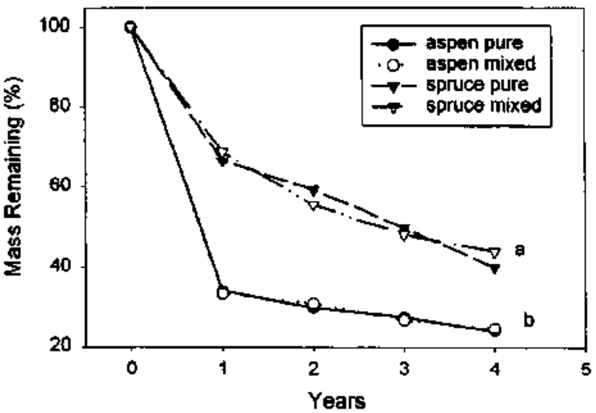

Figure 10—Decomposition of pure and mixed foliar litter of trembling aspen and white spruce in a boreal spruce forest. Means for treatments with different letters are significantly different ($p < 0.05$).

leaf litter (Taylor and others 1989b), suggesting that decomposition of conifer litter may be faster in mixed plots. The influence of mixing litters of either hardwoods or conifers have been less consistent (Blair and others 1990).

Experiments have been established to determine the effects of mixing litter in the three major mixedwood forest types in British Columbia: boreal (white spruce/trembling aspen), interior wet-belt (Douglas-fir/paper birch/lodgepole pine) and coast (Douglas-fir/ red alder). Rates of decay of pure and mixed litter of each species is compared during incubation in pure and mixed forests. After decomposing for four years at four sites in the boreal forest, there were no significant differences between pure and mixed litter of spruce and aspen (fig. 10). After decomposing for 2 years in a coastal forest, there was no difference in rates of decomposition of pure and mixed alder and Douglas-fir. Mixtures of lodgepole pine, birch and Douglas-fir decomposed more slowly than pure litters.

FERTILIZATION

It is generally assumed that increasing N availability through fertilization will increase the rates of litter decomposition. However, direct studies of the effects of N fertilization on decomposition rates have had variable results, and indicate that external N supply has little effect on decay rate (Hunt and others 1988, Prescott 1994). The effect of higher N concentrations in litter of a single species on decay rates is also unclear. Berg and others (1987) found that greater N availability in pine needles stimulated decay in the early stages but inhibited decay during the later lignin decay phase, but Prescott (1994) found no influence. Prescott and others (1992b) suggested that decay of litter with low lignin and high labile C contents may be stimulated by fertilization, whereas litter with high lignin and low labile C contents will not.

Two experiments have been established, one in a trembling aspen stand in northern British Columbia fertilized once with N or NPK, and one in a Douglas-fir stand in coastal Washington fertilized repeatedly with N. At each site, litter from control and fertilized plots is decomposing. In both trials, litter from fertilized plots had higher initial concentrations of N than litter from control plots. After two years, Douglas-fir litter was decomposing more slowly in fertilized plots than in control plots, but by year four there was no difference in rate of decomposition (fig. 11). There was no apparent influence of needle source (*i.e.* endogenous N concentration). There was no effect of either higher N concentrations in the litter or in the surrounding forest floor on rates of decomposition of aspen litter (fig. 12).

CONCLUSIONS

Clearcutting

- increased net N mineralization and nitrification
- decomposition of pine litter same or slower than in uncut forests

Alternative silvicultural systems

- increased net N mineralization and nitrification in openings greater than 0.1 ha
- no effect on decomposition rates

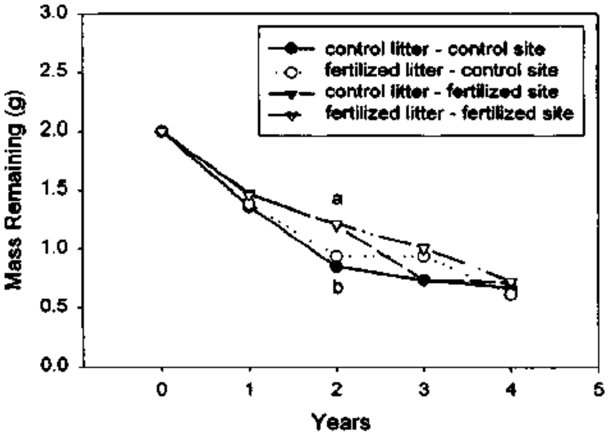

Figure 11 —Decomposition of fertilized and control needle litter of Douglas-fir incubated in fertilized and control plots. Means for treatments with different letters are significantly different ($p < 0.05$).

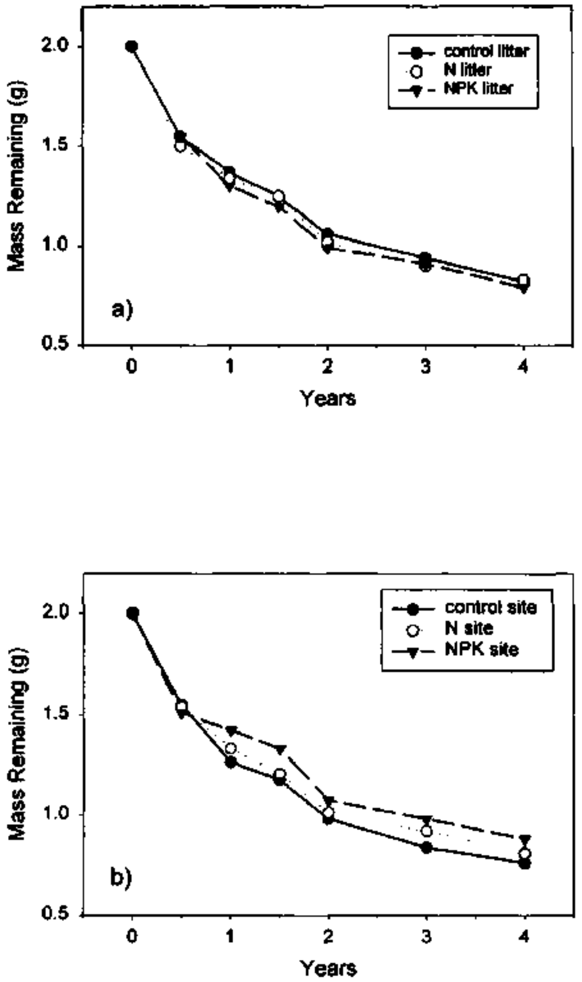

Figure 12—Decomposition of trembling aspen leaf litter from fertilized and control plots (a), or incubated in control and fertilized plots (b) in a boreal aspen forest. There were no significant differences between treatments at any sampling time.

Species

- net N mineralization and nitrification high under Douglas-fir, low under western red cedar
- decomposition fastest in broadleaves, slowest in cedar
- decomposition related to lignin content of litter
- influence of tree species confounded by site factors, understory vegetation

Species mixtures

- no effect of mixing litter on decomposition rates

Fertilization

- no effect on decomposition rates

ACKNOWLEDGMENTS

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TREE SPECIES COMPOSITION CHANGE - SOIL ORGANISM INTERACTION: POTENTIAL EFFECTS ON NUTRIENT CYCLING AND CONSERVATION IN INTERIOR FORESTS

Alan E. Harvey[1], Russell T. Graham[2] and Geral I. McDonald[3]

ABSTRACT

Current conditions in western Interior forests show large-scale changes in species compositions and accompanying above- and below-ground structures and nutrient distribution. Typical forests occupy constantly changing, often resource limited environments. Biological decomposition does not keep pace with production and natural wildfire is critical to recycling. Appropriate protection and recycling of nutrients is key to both short- and long-term productivity and sustainability. Comparisons of physical, physiological and genetic natures of the species dominating historic (pines/larch), current and likely future forests (firs/cedar/hemlock) indicate microbe/fire codependant processes mediating adaptation of forest vegetation, nutrient use rates, soil nutrient storage and recycling processes will all be significantly altered. This is likely to produce forests that are drought, pest, competition and change intolerant with high mortality rates, and high fuel accumulation/loss potentials, when compared to historic norms. Prudent future management would emphasize reintroduction of appropriate pine stocks and western larch at every opportunity! Control of density in dry forests can also make an important contribution.

Keywords: forest soils, forest health, forest fire, decomposition, ectomycorrhizae, nitrogen fixation, soil organic matter, soil wood, long-term productivity, sustainability

INTRODUCTION

Widespread interest in and much reporting on the "forest health crises," or lack thereof, in the Interior West has occurred since the late 1980s. Opinions vary as to the relative threat of changes in inland forests this century, but there is widespread agreement that significant changes have indeed occurred (Baker 1988, Brown 1983).

For the most part, changes are characterized by a general shift from open pine *(Pinus ponderosa* Laws.) to closed pine and/or Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco) stands in dry ecosystems (Gast and others 1991, Mutch and others 1993, Wickman 1992). In moist forests, the change has been from tall, moderately closed pine/larch *(Pinus monticola* Dougl. ex. D. *Don/Larix occidentalis* Nutt.) to relatively short, closed grand fir/hemlock/cedar *(Abies grandis* [Dougl. ex. D. *Don.]/Tsuga heterophlla* [Raf.] *Sarg./Thuja plicata* Donn) stands (Byler and others 1994, Harvey and others 1994b, O'Laughlin and others 1993, Moeur 1992, Monnig and Byler 1992).

Common to these reports is an observed shift toward late successional species in all ecosystems and a view that insect-pathogen activities are generally increasing in many (about half [Quigley and others 1996]) of the resulting stands (Hessburg and others 1994, Lehmkuhl and others 1994, Sampson and others 1994). However, since half still exhibit relatively low pest activities, it has lead to much "active discussion" of the "state of health" and function (positive vs negative effects) of endemic "pests" in these forests (Haak and Byler 1993, Harvey 1994, Martin 1988, Showalter 1994).

Variable fire regimes, successional processes and endemic insect and pathogen activities generally worked in concert to produce the stable and resilient forest structures and species compositions of the past (Harvey 1994, Harvey and others 1992, Martin 1988). However, it is clear that exotics, like white pine blister rust *(Cronartium ribicola* J.C. Fisch.), are producing destabilizing impacts in most interior forests (Byler and others 1994, Harvey and others 1994b, Monnig and Byler 1992, Hoff and Hagle 1990)!

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[1] Alan E. Harvey, Supervisory Plant Pathologist for the Rocky Mountain Research Station, Forestry Sciences Laboratory, 1221 S. Main St. at Moscow, Idaho 83843-4211.

[2] Russell T. Graham, Research Forester, Rocky Mountain Research Station, Forestry Sciences Laboratory, 1221 S. Main St. at Moscow, Idaho 83843-4211.

[3] Geral I. Mcdonald, Research Plant Pathologist, Rocky Mountain Research Station, Forestry Sciences Laboratory, 1221 S. Main St. at Moscow, Idaho 83843-4211.

CURRENT TRENDS

In effect, the changes in vegetation in both dry and moist ecosystems of the Inland West have compressed successional processes. By a factor of at least 10 in some locations! In dry ecosystems, where ponderosa pine may (or may not) give way to Douglas-fir in 300-400 years with historically frequent fire regimes, the change occurred in only 40 years on the Boise Basin Experimental forest in southern Idaho (see Sloan in Harvey and others 1994b). Similarly, In western white pine dominated ecosystems with mixed and variable fire regimes, seral species may (or may not, depending on fire history) give way to climax species in 200-300 years. That conversion took place in just 30 years at Deception Creek Experimental Forest in northern Idaho (Moeur 1992).

This time compression process is usually most evident in dry forests where lack of frequent fires, stand conversions, and high densities are obvious (Covington and others 1994). But lack of fire is also a major force for change in moist forests where effects are more subtle and have been confused to some extent by aggressive harvesting of seral species plus the impacts of the blister rust fungus the last century (Quigley and others 1996, Monnig and Byler 1992).

VEGETATION PARAMETERS

Associated with the rapid change from serai to climax dominated stands are significant alterations of the above-ground, structural geometry of individual trees and, thus, the stands and landscapes that support them. Perhaps the most striking, at least in dry forests, is the increased number of stems relative to historical forests (Covington and others 1994, Gast and others 1991, Baker 1988). However, other changes are no less significant or less important, if visually less striking. Some are even more widespread and are often typical of both dry and moist forest environments. For example, canopy height and shape, foliar dispersion, density (flammability) and nutrient content are all changed in both dry and moist ecosystems.

Ponderosa pine, western white pine and western larch all tend to be tall and self prune well, even in moderately dense stands. They also carry large branches high in their crowns and have good foliar dispersion (Minore 1979). Foliage and small branch wood from western white pine and western larch is of particularly low bulk density (and nutrient content) compared to most climax species (Minore 1979). Consequently, stands of pines (except lodgepole pine *[Pinus contorta* Dougl. ex Laud.) and western larch carry their canopies well above surface fuels, tend not to have ladder fuels, do not carry crown fires well, and generally have low nutrient content. Thus, canopy nutrient stores are relatively well protected from fire.

In comparison, intermediate-age Douglas-fir, true firs, western hemlock and western red cedar are not tall, do not self prune well (especially when young), carry large branches low in their canopies (strong conical shape), do not have good foliar dispersion, and have relatively high bulk densities with resulting high nutrient concentrations in foliage and small branchwood (Minore 1979, Brown 1978, Van Wagner 1977). So, stands dominated by these species often have ladder fuels, carry crown fires well and have a generally high nutrient content in tissues susceptible to loss from fire.

Below-ground there are similar changes. Pines and larch tend to be deep rooted while the firs, hemlock and cedar all tend to be relatively shallow rooted with high levels of feeder root development (and mycorrhizae) in the high nutrient content, shallow soil organic layers (Gale and Grigal 1987, Harvey and others 1986, Minore 1979). Douglas-fir also shows these trends when compared to ponderosa pine but less so than with other climax species (Minore 1979).

Thus, nutrients and nutrient turnover tend to be dispersed vertically in soils dominated by seral species and concentrated in shallow soil horizons with climax species where fire cycles approximate historical conditions. Feeder roots of all plants tend to accumulate in the shallow, high resource organic horizons (Marschner and Marschner 1996, Robinson 1994). So, soil surface nutrient stores and feeder roots in climax species dominated stands (or seral stands if surface organics accumulate from fire exclusion) can be more at risk to wildfire, or other disturbance, than those in historic pine and/or larch dominated stands. This risk can be magnified, especially on infertile sites, because in dense stands climax species may be much more demanding of resources (nutrients and water) than the historically open stands of seral species and, in some species combinations, they may also be less tolerant of short supply (Minore 1979).

Even more subtle, but no less important, are differences in the overall genetic nature of these forests. Western white pine, ponderosa pine, western larch and western red cedar all tend to be broadly adapted to a wide range of sites and environments, the others tend to be more finely tuned within their respective ranges of sites and environments (Rehfeldt 1994). Western white pine is particularly well suited to variation in site and environment.

Sress based on site resource limitations, competition and short- or long-term environmental variation, is therefore much more likely in climax species stands (except for western red cedar) than with seral species stands. Similarly, tolerance to disturbances within the stand, or with climatic variations or trends that affect the stand externally, can be expected to cause rapid responses *{stress)* with climax and low or no responses in stands dominated by seral species.

MICROBIAL INTERACTIONS

It should not be surprising that seral species are far more tolerant of endemic insects and pathogens than climax species (Harvey 1994, Harvey and others 1994a) or that climax stands should tend toward high insect- and pathogen-mediated mortality, i.e., aggressive and continuous removal of highly stressed individual trees by endemic "pests," perhaps most notably by aggressive root pathogens (Harvey 1994, McDonald 1991). Thus, activities of endemic organisms tend to "rogue," climax species and stressed trees, encouraging domination of historical ecosystems by serai species with intermixed "best adapted" individuals representing climax species.

Exotic pests are an exception. Despite a wide latitude for tolerating variation in sites, environments and activities driven by endemic microbes, especially root pathogens, western white pine is heavily damaged by the imported white pine blister rust. In a very real sense, arrival of the blister rust fungus changed the rules in white pine dominated ecosystems (Monnig and Byler 1992). Microbe-mediated selection is now discouraging rather than supporting historical forest compositions on western white pine sites. Also, since insects and pathogens are now operating in ecosystems dominated by susceptible species under stress, they generate momentum and are likely to become much less selective in their actions than in historical forests (Harvey 1994, Lehmkuhl and others 1994).

SOIL MICROBE-MEDIATED NUTRIENT CYCLING

Most striking of the changes in microbial actions in pine vs fir forests are differences in vertical distribution of ectomycorrhizal short roots in dry ponderosa pine compared to dry Douglas-fir or moister ecosystems (Harvey and others 1986). Such differences are not evident with western white pine compared to western hemlock, despite the relatively deeper root system of the pine (fig. 1). Ponderosa pine carries a much greater proportion of its ectomycorrhizal activities in mineral soil vs shallow organic horizons. Douglas-fir, western white pine and western hemlock dominated ecosystems all have most of their ectomycorhizae concentrated in surface organic horizons.

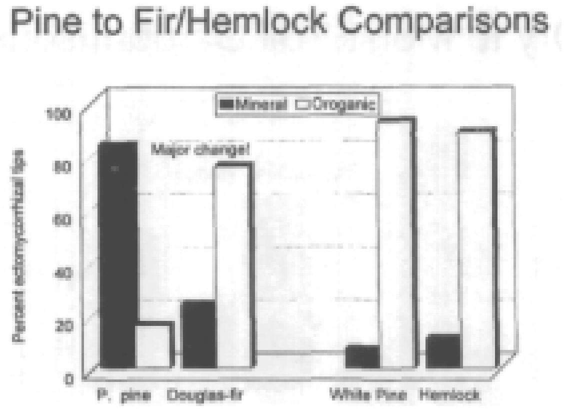

Figure 1 —Comparisons in distribution of ectomycorrhizal activity in mineral versus organic soil horizons of pine and fir/hemlock-dominated ecosystems from dry and moist forests typical of the Inland West (Harvey and others 1986).

Thus, ectomycorrhizal-mediated nutrient acquisition and turnover are relatively well protected from wildfire damage only in relatively natural ponderosa pine dominated systems. This seems quite appropriate considering the participation of frequent fire in the nutrient cycling processes of historical ponderosa pine ecosystems.

However, with the shift to fir-type forests, wildfires can be expected to have a much larger impact on ectomycorrhizal-mediated, post-fire acquisition and cycling of nutrients. It may also increase the likelihood of uncoupling any continuity of current with preceding vegetative communities by altering critical soil microbial legacies, especially ectomycorrhizae (Amaranthus and Perry 1994).

Another soil-based change in pine vs fir ecosystems is the relative distribution of nutrient storage, especially nitrogen. There is a gradual shift in percent of soil nitrogen reserves and organic matter in mineral layers of pine forests to surface organic horizons in fir or hemlock forests (fig. 2). Similarly, the microbe-driven non-symbiotic nitrogen fixation process fueled by carbon from organic horizons reflects these same changes (Jurgensen and others 1997). As with roots and mycorrhizae, vertical distribution of nitrogen storage and fixation are compressed upwards. Again, dry pine forests tend to have critical nutrient-related processes better protected from surface disturbances than fir or hemlock forests.

Accumulation of both above- and below-ground biomass from roots, canopies and boles in dense fir-type forests is greatly accelerating activities of decomposers by increasing and changing basic substrates, both live and dead. An inescapable dictum of interior forests is that biological decomposition

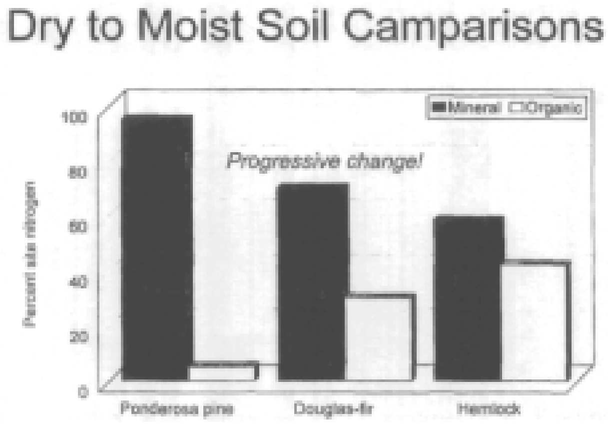

Figure 2—Comparisons of nitrogen distribution in mineral versus organic soil horizons of ponderosa pine, Douglas-fir and hemlock dominated forests typical of the Inland West (Jurgensen and others 1997).

(respiration-driven) is more limited than biological production (photosynthesis-driven). So, rapid accumulations are inevitable (Harvey 1994, Harvey and others 1994a).

The net result can be accumulations of materials that differ substantially from those of historical pine-type forests. Increasing canopy-derived litter and more prolific formation and death of fine roots (and mycorrhizae) will change the type and can greatly increase the quantity of organic matter at the soil surface (Edmonds 1991, Minore 1979).

Associated with changes in litter type and quantity is a likely change in soil surface chemistry, including allelopathic substances with potential to alter a wide variety of microbial activities, including ectomycorrhizae (Rose and others 1983). A change of dominant tree species also provides both live and dead stem wood that is far more vulnerable to internal decay and defect, and the increased mortality that accompanies activities of the causal organisms (Wagener and Davidson 1954).

Will this provide an increased supply of important coarse woody debris which can add to site fertility and wildlife habitat? Likely not, at least in many cases. Most of the wood being added to interior forests (grand fir, white fir *[Abies concolor* Gord.&Glendl. Lindl. Ex Hildebr.], subalpine fir *[Abies lasiocarpa* Hook. Nutt.], western hemlock, western red cedar) is prone to white-rot. Douglas-fir and western white pine are exceptions! White rot end products are dispersed in soil relatively rapidly (Larsen and others 1979). Brown rotted wood on the other hand (i.e., the end products from decomposition of pine, larch and Douglas-fir) is persistent in forest soils for at least several rotations (hundreds of years [Harvey and others 1987]).

High accumulations of woody debris have been measured in north Idaho's most productive western white pine sites, i.e., western hemlock/clintonia habitat type (Jurgensen and others 1997, Graham and others 1994). Although this represents one of the most productive ecosystems in interior forests, seemingly high accumulations may indicate blister rust-driven mortality occurring over the last 50 years or so in these forests (over a 90% loss of the type [Monnig and Byler 1992]) have made an unwelcome, if long-term addition to north Idaho soils and soil-related processes (fig. 3).

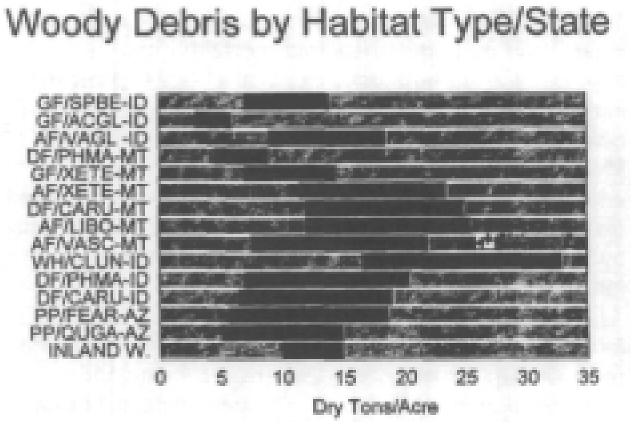

Figure 3—Ranges of coarse woody debris measured on forested sites of the Interior West. Sites identified by state and habitat type. Note the heavy volumes located in the western hemlock/clintonia habitat type of northern Idaho (Graham and others 1994). This habitat type is representative of what were the best western white growing sites in the region.

EFFECTS ON NUTRIENT CONSERVATION AND CYCLING

With lowering of base height and increasing density of canopies, plus increasing canopy-and fine root-derived litter, there are accompanying changes in both the location of nutrients and the microbial-mediated processes that affect them. These changes effectively drive nutrients and nutrient cycling process up from deep in the soil, or down from high in the canopies, to the soil surface (litter and humus). Both are highly vulnerable to disturbance-related effects, especially site preparation-driven physical removal or wildfire-driven volatilization (Jurgensen and others 1997).

With increases in wood from climax species there is also an increase in white rotted woody products that also ultimately contribute primarily to surface litter and humus horizons. With accumulations of Douglas-fir and pine wood there is an increase in nutrients sequestered in a recalcitrant organic horizon. Such an effect can be good or bad, depending on the nature and history of the site. Site nitrogen and potassium stores and cycling are of particular concern (Jurgensen and others 1997, Moore and others 1991, Mika and Moore 1990)

Thus, the roles of microbes can be larger and different than in historical forests. As a result, nutrients are likely to be more concentrated near soil surfaces in virtually all forest ecosystems in the interior west than in the past. Where forests are changing composition from a few large stems of ponderosa pine to many smaller stems of Douglas-fir, this process is likely sequestering substantial nutrient resources into a recalcitrant organic material slow to release them and susceptible to fire or harvesting-related loss (Jurgensen and others 1997, Mann and others 1988). A situation likely to cause problems in both the short- and long-term.

Where woody debris is accumulating in forests once dominated by live western white pine, any gain in soil organic matter is likely to be offset by the general loss of resistance to endemic root pathogens. This is not likely a good tradeoff with already fertile soils! Such changes emphasize the microbe-fire codependency in regulating nutrient cycling processes in interior forest soils and how important it is to understand how they interact when dealing with the productivity and sustainability issues affecting them (Harvey and others 1994a, Olsen 1981).

OVERALL EFFECT ON THE "NATURE" OF INTERIOR FORESTS

The strong interaction between above- and below-ground processes of historical versus most current forests highlights the importance of activities that may not originate in but will affect the soil (fig. 4). White pine blister rust and lack of fire serve as conspicuous examples. However, many soil-based, microbial-driven processes are directly impacted. Among these are both saprophytic and internal or live stem decay processes (and end products), root pathogen mortality, mycorrhizal activities and non-symbiotic nitrogen fixation.

Linked with inevitable fire related (or lack thereof) changes, these *microbial processes are quite capable of participating significantly in creating very different future forests, both above- and below-ground.* In many cases the new forests are not likely to have some of the best features of those being replaced.

Historical "pine type," largely seral forests were likely well matched to soil resources, relatively resistant to detrimental fire effects, well adapted to wide ranges of site and short-term climate variation, subject to modest (largely beneficial) insect and pathogen mortality, generally tolerant of long-term climate change and could be considered long-lived and relatively stable.

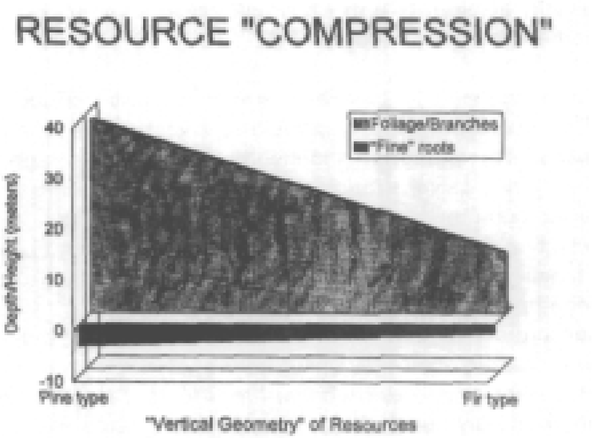

Figure 4 —A graphical schematic representation of resource compression, as represented by above-ground canopy characteristics (height, density, weight, nutrient content) and below-ground root and soil characteristics (root depth, density, ectomycorrhizal activities and soil nitrogen content), resulting from the conversion of "pine type" to "fir-type" forests currently taking place in the Inland West.

In contrast, current "fir type," climax forests are probably not well matched to soil resources. They are also not as resistant to detrimental fire effects or well adapted to the wide range of site and climate variation. They are often subject to very high insect and pathogen mortality, and they can not be considered either long-lived or stable, especially if faced with significant long-term climate change.

Sustainability of historic rates of carbon fixation, soil stability and related amenities (including wildlife, diversity and other features) in many current forests are in doubt and, in general, experiences with such forests are not encouraging.

OBJECTIVE-BASED "SOLUTIONS"

Means to counter some of the undesirable features of current forests with "forest health" problems have been widely cussed and discussed. There are differences of opinion as to whether there are problems and what, if anything, should be done about them. Because there have been no generally accepted concepts of forest health (see discussions in this symposium), there are widely divergent opinions on what effects management, fire or no management might create. In addition, most of the "general" solutions thus far proposed and implemented can either help or hurt, depending on details of history, current condition and future trends in affected forests. Such solutions usually attempt to apply a simple fix to a variety of sometimes complex problems.

For example, if lack of fire is the problem, introduce fire. But current fuel accumulations and distributions place both vegetative and soil resources at very high risk. Then salvage logging can reduce the fuels to levels commensurate with appropriate fire effects. But resulting roads and soil impacts can be detrimental. Thinning, with or perhaps without prescribed fire, must then be the answer. But thinning root disease susceptible species is likely to set off an epidemic of root disease activities, upset natural selection processes or perhaps worsen fire effects if slash is not appropriately dealt with. How about clearcuts with heavy fuel removal and species conversion? Excessive fuel removal could put site nutrient stores in jeopardy. And the list continues!

The fact is, scientifically or politically, we must address site specific problems with customized, site specific and objective oriented solutions. For the most part such *specific solutions need not be extremely difficult, just well considered and carried out.* Appropriate, site specific silviculture! In some cases intervention may seem expensive, but if long-term environmental costs are factored in, it may well be much less costly than doing nothing (Oliver and others 1994a, 1994b, Mutch and others 1993) One thing seems certain, without active intervention many, perhaps most solutions for problems now facing interior forests will get more difficult, more expensive and the current trends more potentially damaging as time goes on (Sampson and others 1994).

QUESTIONS FROM THE FLOOR

Q: You mentioned an interaction between Nitrogen & Potassium. Is that just an issue of which is more limiting in a system or is there a biochemical interaction... if yes can you give a quick sketch of what it is?

A: Nitrogen-potassium interaction. Idaho forest nutrition coop has discovered when they add N it often sets off an Armillaria "explosion" or increased damage by defoliaters but, if they add K to the N, the Armillaria or other pest effects are much reduced. In many inland sites, the 2nd most limiting nutrient is K! Proposed explanation...inducing growth with N under shortage of K limits trees ability to form secondary defense chemicals thus making tree more susceptible to pests. Since K is intimately involved in production of phenolics and precursers the proposed interaction is at least interesting and quite plausible.

Q: Which has a greater adverse effect on soil health? A high severity fire resulting from unnaturally high dense forest stands or repeated commercial thinning entries on an order of 1 entry per 10-15 years with ground - based logging systems (e.g., mechanical harvesters) resulting in widespread and chronic soil disturbance (compaction and displacement)?

A: Excessively hot fires versus repeated entry (compaction/displacement) and forest soil health. Obviously, both have the potential to cause great damage. As described, repeated entries that cause "widespread" compaction and displacement could be worse than fire because restoration will be slow at best and impossible at worst (for example loss of ash cap)! Neither should be acceptable.

Q: Your research on coarse woody debris (CWD) levels being used in "Eastside" effort as targets - we (in Blue Mts) believe these (high tonnage) levels not sustainable or realistic if/or with more natural fire cycles - comments/help!

A: I don't think eastside Oregon and Washington are any more difficult to retain CWD than southwest Montana, southern Idaho or Arizona D-fir or P-pine. Five tons CWD/acre is almost nothing, two or even three times that should be possible, in at least some situations. So what is the problem? Main point to our recommendation is be aware of it's importance and do the best job you can to keep it in the system, without creating a fire hazard. Simply put, do not destroy or discourage formation of such a valuable commodity in the ecosystem. You might even be able to get more in the system safely (with the added productivity) than the natural system normally supports. I think this might be doable in some systems, certain Douglas-fir and subalpine fir forests come to mind as interesting possibilities.

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OUT OF SIGHT, BUT NOT OUT OF MIND: SOIL MICROORGANISMS IN MOISTURE-LIMITED FORESTS

Matt D. Busse[1]

ABSTRACT

Microorganisms play a critical role in the maintenance and productivity of forest ecosystems by their regulation of soil nutrient availability and organic matter decomposition. Regardless, it is uncommon for managers to consider the microbial community and its processes when assessing forest management options. The reasons for this incongruity are of little surprise. Microorganisms lack the charisma attributed to key plant and wildlife species, and thus are "out of sight, out of mind." More detrimental, however, is our incomplete understanding of how microorganisms respond to natural and management-induced disturbances. Whether changes in microbial processes following disturbance are sufficient to alter the sustainability of forest ecosystems is unclear, thus providing limited input for decision making by forest managers. Information from studies of moisture-limited forests on the eastern slopes of the Cascade Mountains indicates that (1) microbial communities are well adapted to the conditions of water stress, (2) long-term decline in microbial biomass can result from continuous silvicultural treatment, and (3) microbial activity is limited by available soil carbon content. Management options which maintain or enhance site organic matter are recommended as the best practice to sustain microbial processes.

Keywords: soil processes, microbial community, ponderosa pine, moisture stress, forest management practices

INTRODUCTION

Should land managers consider the composition or function of soil microorganisms when selecting forest management options? Common sense might argue yes. After all, the microbial community is responsible for a multitude of essential functions, from organic matter decomposition and nutrient cycling dynamics to enhancement of soil structure and degradation of xenobiotic compounds. Partial or complete disruption of these processes would, without question, place irreparable stress on most terrestrial ecosystems. Unfortunately, common sense is not always a practical option.

Forest managers must make operational decisions that impact ecosystem health and stability, yet rarely do they have the time or knowledge to account for every resource component. Further complicating their decision-making process are the seemingly constant demands from diverse social, political, economic, and environmental interest groups. In considering the responsibilities facing forest managers, Kimmins (1994) stated, "it is neither possible, nor is it necessary, to consider all of the processes and components of a forest ecosystem in order to make useful predictions about the long-term consequences of forest management." Although few would argue against this viewpoint, it fails to offer us any direction for the selection of characteristics vital to ecosystem sustainability versus those considered superfluous. For example, are microbial communities sufficiently resilient following natural and human disturbances to warrant their disregard (are they superfluous from a management perspective?), or could such an indifference result in a long-term degradation of site quality? If indeed we accept Kimmins statement as an "operational reality", then the challenge is to identify, without bias, which processes and components are most important to the sustainability of a given ecosystem.

While few would suggest that microorganisms are superfluous to the function of forest ecosystems, some ground work is required before endorsing their consideration in forest management decisions. Specifically, there must be evidence that (1) management practices or natural disturbances alter the function of microbial communities, (2) resulting changes in microbial function following disturbance produce detrimental, long-term changes in forest ecosystems, or (3) key species or functional groups (a set of species that have similar effects on a specific ecosystem-level process) lack resilience and are irrevocably lost following disturbance. Herein lies the problem. While there are numerous site-specific examples of the impact of disturbance on microbial communities (for examples, see Atlas and others 1991, Fritze and others 1993, Staddon and others 1997, Visser and Parkinson 1989), the evi-

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[1] Matt D. Busse is a Research Microbiologist with the U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 2400 Washington Ave., Redding, CA 96001.

dence to support or refute these principles, particularly (2) and (3), is far from complete.

Therefore, in this paper I will argue that attempts to incorporate our knowledge of microbial processes or community composition in management decisions, while good intentioned, are impractical and premature. Scientific and theoretical applications of microbial ecology have yet to catch-up with the disciplines of plant and wildlife ecology; we still lack knowledge of the diversity of organisms present in forest soils, how active they are, how they interact with other organisms, and how resilient they are to management practices (Madsen 1996, Wardle and Giller 1996). I will also argue, however, that ignorance is not bliss, and that soil organisms should not be overlooked by forest managers. To the contrary, sustainable forest management requires explicit understanding of both above- and below-ground processes. Certainly soil microorganisms are difficult to relate to and lack a certain degree of charisma associated with more popular organisms. Nevertheless, awareness by managers of their role in forest ecosystems and protection of their habitat needs (primarily site organic matter) is emphasized.

The forests on the dry, east side of the Cascade Mountains provide a unique backdrop for the discussion of the role of microbial communities. These forests are less biologically complex and maintain slower rates of biogeochemical cycling in comparison with the forests in western Washington, Oregon, and California as a consequence of their stress and disturbance regimes. I will focus on three topics as they pertain to the inland forests, with emphasis given to the ponderosa pine forests of central Oregon:

1. How well do microbial communities adapt to stress and human-caused disturbance? Whether their prevalence (population size and activity) fits within the demands of the system, as suggested by Zak and others (1994), will be questioned. In addition, two case studies will be presented to emphasize the differences in long-term versus short-term responses of microorganisms to common silvicultural disturbances (thinning, harvesting method, prescribed fire, fertilization, and vegetation control).

2. Gaps in our knowledge of forest soil biology: what are the causes and what are the potential solutions?

3. What role can forest management play to insure a functioning microbial community.

MICROBIAL RESPONSES TO STRESS AND DISTURBANCE GRADIENTS

External stress (moisture, temperature, or nutrient limitations for example) and disturbance (flooding, wildfire, or silvicultural treatment for example) are of fundamental importance in defining ecosystem composition, structure, and processes (Grime 1979, Kimmins 1996, Wardle and Giller 1996). This is particularly evident in forests east of the Cascade crest where stress and disturbance gradients strongly regulate ecosystem productivity. Low annual precipitation, cool temperatures, poor nutrient supply, and wildfire all contribute to restrict growth conditions. A key question to ask, therefore, is whether soil processes can function effectively in these harsh conditions, or, conversely, whether the microbial community is unable to adapt and thus becomes a limiting factor to forest health and productivity.

In attempting to deal with a very complex subject, I will limit my discussion to the effects of moisture stress and silvicultural disturbance. Further, microbial processes will be viewed from a synecological perspective (combining bacteria, fungi, algae, and viruses as a whole), ignoring the concern of Ohtonen and others (1997) that stress should be discussed at the species level to address differences in stress tolerance between soil organisms. My aim in this section is to show that soil microorganisms are arguably the most tolerant group of organisms in dealing with stress and disturbance.

Adaptation to Water Stress

There is no immunity to the debilitating effects of moisture stress. Soil microorganisms respond to water stress with a decline in total activity and biomass (Sommers and others 1981), as do most organisms. As an example, monthly measurements of microbial respiration (an index of total activity) decreased linearly with increasing water stress in soil collected from central Oregon ponderosa pine forests (fig. 1). Microbial biomass (not presented) showed a similar, although less dramatic, decline as the soils dried. These responses should come as little surprise. Decreasing soil water content results in reduced motility of microorganisms (with the exception of fungi and actinomycetes that have a hyphal network to span air spaces), as well as reduced nutrient diffusion, and increased energy requirements to maintain cellular integrity.

Most theoretical evidence, however, suggests that microorganisms can adapt or become tolerant of stress more easily than higher organisms (Atlas 1984, Wardle and Giller 1996, Ohtonen and others 1997). This premise is attributed to several inherent characteristics of microorganisms. Most important is the tremendous

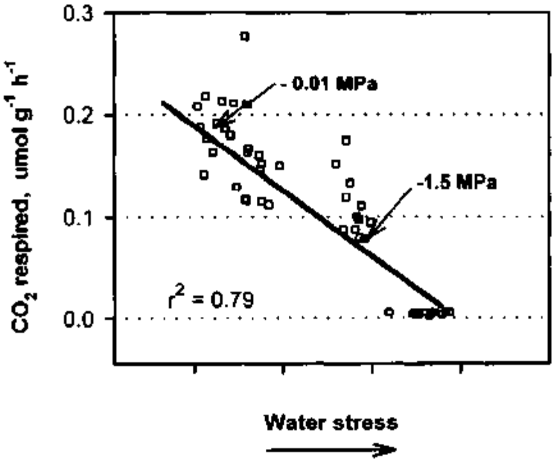

Figure 1—Relationship between microbial activity and water stress in mineral soil from the central Oregon pumice zone. Water potentials of -0.01 and -1.5 MPa represent field capacity and permanent wilting point, respectively, for the pumice zone soil. Samples were collected monthly from May through October 1990 at eight replicate ponderosa pine stands.

genetic diversity and malleability of soil microorganisms. Bacteria alone have as high as 4,000 different genomes per gram of soil (Torsvik and others 1990). Short generation times in comparison to higher organisms also provides a mechanism for rapid genetic transfer, leading to environmentally responsive mutations. In addition, microbial communities are physiologically versatile; no other group is capable of utilizing such a wide range of compounds for their energy and nutrient requirements (virtually no natural or manmade compound can escape their degradative abilities). Finally, microorganisms are ubiquitous in natural environments, possess a large surface area for nutrient and water uptake, and have a high rate of metabolic activity, all characteristics that promote a rapid recovery following the alleviation of stress.

A good example of microbial adaptation to moisture stress is illustrated in figure 2. The optimum soil moisture conditions for microbial biomass in this study depended on the geographical origin of the soil. The microbial community adapted to arid conditions was actually stimulated by the onset of water stress, while the community from a subalpine soil declined rapidly in size. A related strategy was identified by Atlas and others (1991). They found that the addition of chemical pollutants resulted in a reduction in the genetic diversity of soil microorganisms. The remaining population, however, had greater versatility in carbon substrate utilization and tolerance to external conditions (temperature, salt, and pH), indicating that a generalist population had been selected for which was better adapted to the conditions of stress.

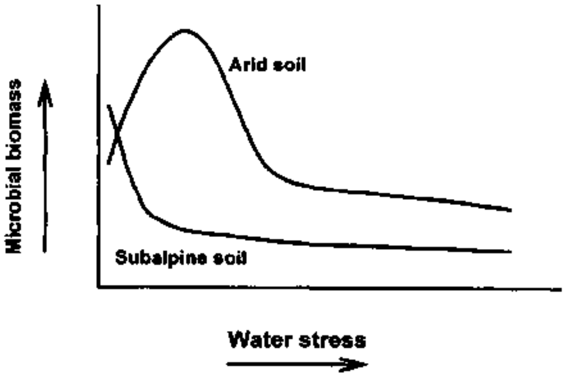

Figure 2—Differential adaptation of microbial communities to water stress. The arid soil is from an *Artemisia* tridentata dominated site and the subalpine soil is from an *Abies lasiocarpa* site, both in northern Utah. Microbial biomass was measured as ATP concentration. Adapted from Knight and Skujins (1981).

The ability of microbial communities in central Oregon soil to tolerate moisture stress can also be inferred by comparing their population size and activity with other terrestrial ecosystems. Zak and others (1994) provide such an opportunity with their reported estimates of microbial biomass for various North America ecosystems. A partial summary of their results is presented in figure 3 (sites 1-7), along with the average microbial biomass that I measured in central Oregon during the 1990 growing season (site 8). I would like to emphasize two points here. First, microbial biomass in the ponderosa pine forests of central Oregon is intermediate to the poorly productive, desert grassland (site 1) and the highly productive forests in the Pacific Northwest (site 6) and North Carolina (site 7), as expected. Second, Zak's group found a strong relationship existed between microbial biomass and annual net primary productivity (ANPP). This synchronicity suggests that microbial and plant communities respond in a similar fashion to meet the carry capacity of a given ecosystem. Using their regression equation that predicts microbial biomass as a function of ANPP, the predicted microbial biomass in central Oregon is 315 kg/ha (based on the ANPP value from Gholz (1982)), well below my measured value of 507 kg/ha. Actual microbial biomass in central Oregon, therefore, exceeds its predicted carrying capacity, and supplies further evidence that microbial populations are not a limiting component in these forests.

A similar conclusion can be drawn by comparing rates of microbial processes in central Oregon with those from the highly productive forests on the westside of the Cascades Mountains. For example, the litter decay rate in central Oregon (Monleon and Cromack 1996) is about three-fold lower than the rate in western Washington (Edmonds 1980). This also approximates the relative differences in symbiotic nitrogen fixation (Busse in press) and ANPP (Gholz 1982) between the two

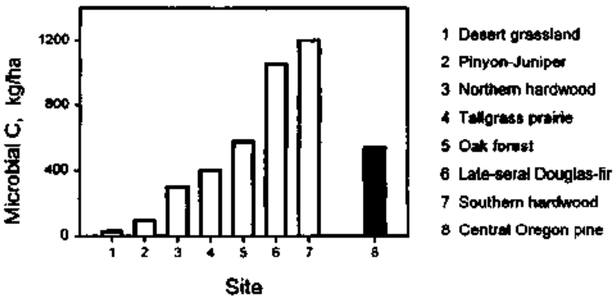

Figure 3—Comparison of microbial biomass from a central Oregon ponderosa pine forest (site 8) with other sites across North America. Microbial biomass values for sites 1-7 were extrapolated from Zak and others (1994).

regions. Therefore, although water stress reduces the absolute rates of processes, the microbial community is able to function within the demands of the system.

Impacts of Silvicultural Treatments

Silvicultural manipulation plays an important role in the design of many temperate and tropical forests (Attiwill 1994, Kimmins 1996). Treatments such as harvesting, site preparation, prescribed fire, vegetation control, and others can alter site biogeochemistry (accumulation, loss, and availability of carbon and nutrients), biodiversity, microclimate, wildfire risk, and long-term productivity. Knowledge of how ecosystems respond to silvicultural treatments, in turn, is required if we are to understand the processes that determine sustainable forests.

Several pitfalls are encountered in discussing the impact of disturbance on forest ecosystems. Topping the list is the unpredictable nature of disturbance. For instance, changes following silvicultural disturbance can range from undetectable to large-scale modifications in forest composition, structure, and function (Kimmins 1994). As a result, attempts to make generalities regarding ecosystem responses to disturbance are often ill-advised. Prescribed fire can serve as a prime example: increases in soil nitrogen availability after fire can either be high (Covington and Sackett 1992), intermediate (Monleon and others 1997), or low (Simon 1990) depending on the burn conditions.

A conceptual diagram of the impact of disturbance on ecosystem integrity is presented in figure 4. Ecosystem integrity declines with increasing disturbance until either mitigation is required or sufficient time is needed to insure natural recovery. Mitigation of soil compaction on federal lands when bulk density increases more than 20 percent above pre-disturbance values is a classic example of this principle. The diagram also points out a troublesome fact: there is a poorly defined transition zone between acceptable and unacceptable levels of disturbance that highlights the unpredictable natural of disturbance ecology. As a result, hard targets for mitigation standards are often the result of educated guessing. What is acceptable or unacceptable will remain a subjective issue until we increase our understanding of the mechanisms responsible for long-term changes in ecosystem sustainability.

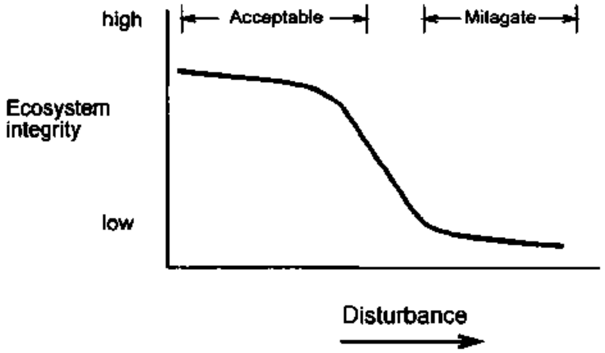

Figure 4—Conceptual diagram of the relationship between disturbance and ecosystem integrity.

The information that follows is derived from two studies of microbial responses to silvicultural practices in moisture-limited forests. Admittedly, these studies do not represent a thorough analysis of the subject. Instead my intentions are to (1) question whether common management practices alter microbial characteristics sufficiently to require mitigation, and (2) emphasize the importance of long-term experiments to avoid misinterpretation of initial findings. The first study, which began in 1959 on the Pringle Falls Experimental Forest in central Oregon, is a long-term comparison of the effects of understory vegetation control on ponderosa pine growth and soil quality. The second study, shorter in duration, compares the effects of common silvicultural practices (thinning, prescribed fire, organic matter removal, and fertilization) on microorganisms and vegetation in central Oregon forests.

Experiment #1: Long-term effects of vegetation control—The initial objective of this study was to determine whether competition from understory vegetation reduces ponderosa pine growth (Barrett 1982). The hypothesis was that continual removal of competing vegetation would result in greater tree growth due to improved water and nutrient status. Two treatments (understory vegetation present, understory vegetation absent) were compared at five levels of initial thinning of a young pine stand. Barrett's hypothesis was confirmed after 20 years; understory vegetation significantly reduced tree growth. Surprisingly however, continued measurements of tree growth have found that the benefits of understory removal were short-lived, and that from 1976 through 1994 there were no differences between treatments in the rate of tree growth (table 1; Busse and others 1996). A similar response was also found for a productive pine plantation on the Challenge Experimental Forest in California (Bill Oliver, personal communication). The take-home message is simple: use caution when interpreting findings from short-term studies out of respect for the complexity of forest ecosystems.

Table 1 —Long-term response of a ponderosa pine forest in central Oregon to continuous vegetation control.

	Understory vegetation		Percent
Component	Absent	Present	Change
Tree growth, m^3/ha/yr			
1959 - 1975	2.36	1.84	- 20
1976 - 1994	4.41	4.52	2
Mineral Soil			
Organic C, g/kg	28.3	35.3	17
Total N, g/kg	1.1	1.6	17
Microbial biomass, ug/g	778	944	21
0 horizon			
C, Mg/ha	11.5	14.2	23
N, kg/ha	146	193	32
Microbial biomass, kg/ha	406	304	34

A summary of selected soil properties from the experiment is also presented in table 1. Presence of understory vegetation produced substantial increases in soil C, N, and microbial biomass. This was likely the result of increased organic matter input from litterfall and root turnover by understory shrubs. Since the total nutrient content of the system was not altered by either treatment (leaching losses were minimal and only a minor nitrogen input from symbiotic nitrogen fixation was evident), my assumption is that the presence of understory vegetation produced a reapportionment of nutrients into a more active biological pool, and resulted in increased microbial biomass. Whether the improvement in soil quality with understory vegetation present might have contributed to the long-term overstory response is an untested, yet intriguing hypothesis.

Experiment #2: Short-term responses to silvicultural treatments—The Deschutes National Forest in central Oregon responded to a mountain pine beetle outbreak in the early- to mid-1980's by targeting about 100,000 acres of second-growth ponderosa pine for thinning. The Bend Long-term Site Productivity Study (LTSP) was developed to monitor the effects of this thinning program and to evaluate the effects of several other silvicultural practices on ecosystem productivity. The main treatments in this study include thinning, prescribed fire, fertilization, and four harvesting methods (whole tree removal, bole only removal, no removal, and no thinning; see Shea (1993) for treatment and site descriptions). The primary hypothesis is that the level of organic matter retention following harvesting or burning is an important determinant of site quality and sustainability.

The short-term response by the microbial community to selected treatments is presented in table 2. Unlike the long-term experiment at Pringle Falls (which has the same soil type and climate), there has been virtually no measurable response from the microbial community to silvicultural treatment in the initial six-year period. Prescribed fire resulted in a slight decline in microbial biomass, however this was offset by an increase in carbon use efficiency (qCO_2) by the remaining population. Differences in microbial characteristics between the four methods of harvesting treatments were also nominal (not shown), suggesting that organic matter (forest floor) retention has minimal impact on short-term microbial responses. Table 3 also points to the relative insensitivity of microorganisms to management practices in the Bend LTSP study. Overstory and understory vegetation responded positively to fertilization, while microbial biomass was unaffected. This supports my contention that microorganisms are the least sensitive group of forest biota to stress or disturbance.

KNOWLEDGE GAPS

Developing practical applications for forestry has been a challenging and often frustrating goal of soil microbiologists for most of this century. There are notable exceptions of course, such as the study of forest pathology, mycorrhizae (for plant nutrition or edible mushroom production), and symbiotic nitrogen fixation. Nevertheless, the struggle to provide 'hands-on' information continues. To understand this dilemma requires an understanding of the limitations to the study of soil microbiology.

The difficulties in studying soil organisms are unique. Bluntly, soil is a lousy medium for conducting ecological studies. It is opaque, heterogeneous, and has a tremendously complex physical and chemical structure. Adding insult to injury, most microorganisms are too damn small to be identified without the use of time consuming methods. As a result, theories of organism succession, population dynamics, and disturbance ecology remain at infancy in comparison with those of plant ecology.

Methodological limitations abound in the study of soil microbiology. In the 1920's for example, Selman Waksman commented that "the lack of proper methods for a microbiological investigation of soils is widely

Table 2 —Short-term response of soil quality indicators to disturbance in central Oregon ponderosa pine forests. Soil C, microbial biomass, and qCO_2 were measured in the fifth growing season after treatment; litter decomposition was measured for a 2-year period beginning the second growing season after treatment. The metabolic quotient (qCO_2) is an index of carbon use efficiency by microorganisms.

Treatment	Soil C	Microbial Biomass	qCO_2	Litter decay rate
	g/kg	ug/g	resp/biomass	yr^1
Control	2.3 a[a]	372 a	048 a	0.181 a
Prescribed burn	2.3 a	316 b	0.55 b	0.183 a
Fertilize	2.4 a	389 a	0.44 a	0.178 a

[a] Means within a column followed by the same letter are not significantly different at the 0.05 level.

Table 3— Growth responses to fertilization (nitrogen, phosphorus, and sulfur) in central Oregon pine forests.

Lifeform	Control	Fertilized	Percent Increase
Ponderosa pine, m^3/ha/yr	3.1 b[a]	4.9 a	61
Shrub biomass, kg/ha	971 b	1420 a	46
Herbaceous biomass, kg/ha	18 b	324 a	1700
Microbial biomass, mg/kg	372 a	389 a	4

[a] Means within a row followed by the same letter are not significantly different at the 0.05 level.

recognized" (Waksman 1925). Unfortunately, a similar quote was also made in 1997: "the practical difficulties encountered in identifying soil organisms. . . . seem to be insurmountable at the moment" (Ohtonen and others 1997). The difficulties in developing useful methods has been partly responsible for our inability to answer the following fundamental questions outlined by Madsen (1996):

1. What microorganisms are present in terrestrial ecosystems?

2. What are the microorganisms actually doing?

3. How can we make accurate measurements of in situ microbial processes that are integrated in time and space?

It is no wonder that practical applications have eluded soil microbiologists. The struggle to understand the basic ecology of soil organisms still faces an uphill battle.

Another limitation in the study of soil microbiology is the relatively large number of microbial species found in nature (table 4). According to Hawksworth (1991) the best estimate is that about 10 percent of bacteria and only 5 percent of fungi on earth have been identified. This fact alone makes it practically impossible to determine whether the taxonomic diversity of soil organisms is important to forest processes, or whether external factors such as stress and disturbance impact soil diversity. It is also responsible for what Kennedy and Smith (1995) criticize as the 'black box' approach to soil microbiology. That is an approach in which only the inputs and outputs of processes are measured, without any understanding of the nature of the organisms directly responsible for the processes.

Is help on the way? Perhaps. Improvements in methods of detection have been dramatic during the past ten years. In particular, microbiologists now have an arsenal of molecular techniques available for taxonomic and ecological studies (Head and others 1998). Bornemann and Triplett (1997), for example, used rDNA sequencing to identify changes in bacterial species following the conversion of a mature tropical forest to pastureland. Changes in microbial functional groups in response to forest management can also be identified now using carbon-substrate utilization patterns (Garland and Mills 1991), fatty acid signatures (Zelles and others 1992), or ribosomal RNA methods (Muyzer and others 1993). Whether these methods will deliver soil microbiology to a level that has direct applications for forest managers remains to be seen.

	Number of species	
	Described	Estimated
Bacteria	3,000	30,000
Fungi	69,000	1,500,000
Algae	40,000	60,000
Viruses	5,000	130,000

A ROLE FOR FOREST MANAGERS?

What can managers do to insure a functioning microbial population in dry inland forests? Education is the first step; it is important to recognize the role of soil organisms in forest ecosystems, and to recognize that moisture limitations do not override the importance of microbial processes such as nutrient cycling and decomposition. Granted, these processes do not function at the impressive rates found in more productive forests; they are still an inherent requirement of any ecosystem however. Recognition of this fact can then become a factor in the critical-thinking process that occurs during the design of forest management options.

The next step is to acknowledge that microbiologists will not be able to provide managers with many practical solutions to important soil biology questions. At least not in the immediate future. For example, concepts such as standards and guidelines for microbial processes, identification of keystone species (or functional groups) for given habitat types, and inexpensive, user-friendly methods are still a source of frustration for the scientific community. This frustration will remain, unfortunately, until the knowledge gap in our understanding of population dynamics and processes are narrowed. Until then, we will continue to use the nefarious 'black box' approach to describe soil processes.

The best approach that managers can take to insure the sustainability of microbial processes, therefore, is to protect key soil resources, *particularly forest floor and mineral soil organic matter,* that serve as habitat for microorganisms (fig. 5). Following either natural or human-caused disturbance, changes in the availability of soil resources dictate microbial population dynamics. Managing for microorganisms thus becomes an indirect process of selecting options which insure the stability of the soil resource. I have singled out organic matter as the key soil resource because of its role in fulfilling the habitat needs of most microorganisms for energy, nutrients, and water.

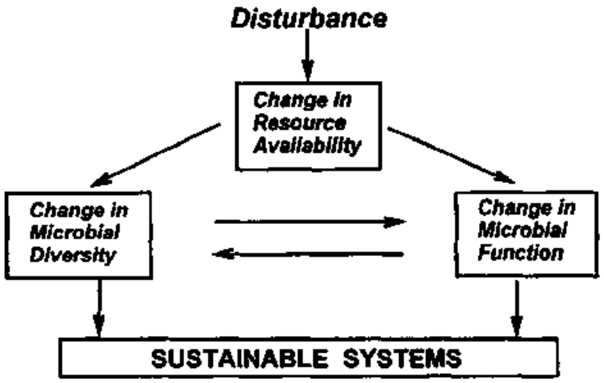

Figure 5—Importance of conserving soil resources. Changes in resource availability, particularly site organic matter, have a direct impact on microbial communities and ecosystem sustainability.

The premise that microorganisms in moisture-limited forest soils are limited by organic matter is verified in figure 6. Only those treatments that received an input of available carbon responded with a flush of microbial activity. This observation is in agreement with the conclusions of several authors who suggest soil organic matter is directly linked to ecosystem sustainability (Jurgensen and others 1997, Kimmins 1994, Morris and others 1997). In fact, Jurgensen and others (1997), in a discussion of dry inland forests, emphasize that "the maintenance of adequate soil organic matter levels is critical for sustaining forest health and productivity" based on its many biological, physical, and chemical functions. Obviously, managers can't overlook the added function of organic matter (forest floor) as potential fuel for wildfires in dry forests. There is no easy answer to the question of how much decaying material (wood, branches, litter) should remain on a given site. Instead, it requires an assessment at a local scale, with input from soil, fire, and silviculture specialists.

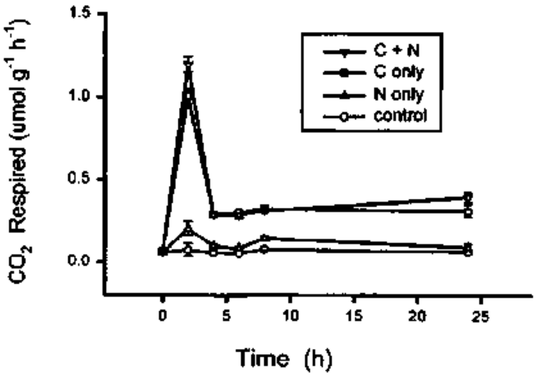

Figure 6—Carbon limitation in central Oregon soil. Microbial respiration was measured after the addition of available carbon (glucose) and/or nitrogen (ammonium nitrate) at optimum concentrations.

CONCLUSION

Picture a forest without a soil microbial community. With a build-up of organic material incapable of decomposing and no continuous supply of plant available nutrients, the forest would be unsustainable to say the least. Yes, this is a ridiculous concept, but it serves as a method to visualize the importance of microorganisms. They are out of sight for sure, but should not be out of mind or taken for granted.

Several concepts were introduced with regard to the function of microorganisms in moisture-limited forests. Foremost, the microbial community appears more tolerant of stress and disturbance in comparison with other forest biota. This does not mean microorganisms are unresponsive to silvicultural manipulation however. Results from studies of ponderosa pine forests in central Oregon show a decline in microbial biomass following continuous vegetation control, and underscore the importance of long-term experiments to avoid over-interpretation of short-term findings. Currently there is limited "hands-on" information of microbial processes to assist forest managers as a consequence of our inadequate understanding of microbial ecology. An indirect approach is recommended, therefore, to insure the sustainability of microbial processes: selection of forest management options that protect their habitat needs for site organic matter.

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MANAGING ROOT DISEASES BY MANAGING STANDS

By Walter G. Thies[1]

ABSTRACT

Root diseases are important natural disturbance agents in forest ecosystems in the Pacific Northwest. The common root diseases are caused by fungi. Root disease fungi inhabit roots, rather than soil. This helps them to avoid competition for food with saprophytic soil organisms. At landscape scales and over long time frames, the impacts of root diseases are considerable. Understanding the ecological roles of diseases, their impacts on resources, management influences on them, and their effect on management is crucial to meeting ecosystem management objectives.

Keywords: root diseases, forest pathology, fungi, white rot, brown rot

INTRODUCTION

Root diseases are important natural disturbance agents in forest ecosystems of the Pacific Northwest. Root disease biology, incidence, severity, and impact must be understood and accounted for if ecosystem management objectives are to be met. Root diseases exert a profound influence on forest structure, composition, function, and yield. Root diseases are important gap formers; they create openings of varied sizes in the forest, depending upon the pathogen(s) and hosts present. These gaps are then colonized by a variety of forb, shrub, and tree species depending on site characteristics and seed sources. Whether root disease is perpetuated on the site is a function of the relative susceptibilities of the ingrowth species. If highly susceptible species continue to colonize root disease pockets, their likelihood of reaching large sizes is low. If immune species occupy root disease pockets, inoculum dies out and eventually susceptible species may grow on the site again without being influenced by root disease. If intermediately susceptible species colonize pockets, root disease inoculum will be perpetuated on the site and influence vegetation development according to relative species susceptibilities. This may mean reduced growth, increased levels of butt decay, and increased chance of windthrow and mortality. Basically, root diseases influence species composition by selectively killing some species and allowing others to survive. Species diversity may increase or decrease depending upon location. Production of special forest products such as berries, boughs, and mushrooms may be increased. Root diseases influence structure by reducing the likelihood that some trees will achieve large sizes, or at the very least, slowing the process. Stocking levels may be reduced in discrete areas or across the stand depending on the distribution of inoculum and tree species present. Root diseases create standing dead trees that may be important for wildlife habitat. The very nature of the decay associated with some root diseases would suggest that many snags will be short-lived, that is, they may remain standing for only a short time compared to trees killed by other agents. Root diseases also create down woody material that is important for habitat, water holding capacity, and nutrient cycling.

Accepting the effects of root disease may be consistent with meeting resource objectives in the immediate future; mortality and spread rates, in general, are low and impacts are not usually dramatic in the short-term. However, root disease impacts over time and space must be considered in planning. Defining the pathogen(s), inoculum concentration and distribution, and population of host species of an area could be critical. There is a legacy of large acreages where susceptible species were planted on sites with high inoculum levels. Whether or not these stands are entered for thinning treatments, are interplanted with resistant species, or are left alone, will depend on the desired future condition of the sites. For example, if the objective is to grow large trees as quickly as possible, either to achieve late successional stand structural characteristics or to satisfy harvest volumes, plantations with high levels of laminated root rot that are predominantly Douglas-fir may not be capable of meeting goals.

Knowledge of the occurrence and level of root disease in an area is required to make reasonable predictions of root disease impacts. Surveys, stand examinations, and resource inventories must include collecting a minimal level of information on root disease. This includes the identity of the root diseases present, tree species composition, size, and stocking, the proportion

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[1] Walt Thies is a forest pathologist, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, OR 97331.

and species of trees affected, how the root disease is distributed in the area, and an estimate of area affected. With this information, a clear picture can be drawn of current root disease conditions, enabling prioritization of treatments. Future impacts can also be predicted with these data using tools such as the Western Root Disease Model Extension to the Forest Vegetation Simulator (Frankel 1998).

COMMON TRAITS OF ROOT DISEASES

It is not within the scope of this paper to provide details about the many root diseases in Pacific Northwest forests. However, there are some generalizations that apply to most pathogens that will help managers better understand diseases:

1. The common root diseases are caused by fungi.
2. Root disease fungi live belowground most of their lives but they are root, not soil, inhabitors. The special ability of these organisms to penetrate and colonize healthy root systems enables them to avoid competition for food with saprophytic soil organisms.
3. Root disease fungi cause dysfunction in root systems by killing cambial tissue, disrupting the transport system, or consuming cellulose, thus causing loss of structural root integrity.
4. Most cause white rots although a few may cause brown rots. White rot fungi can breakdown both cellulose and lignin, thus causing pits. Brown rot fungi breakdown the cellulose leaving the brown lignin untouched.
5. Most attack and invade only living tissue but once the tree is dead they become saprophytic and can remain within the dead root system for a long time, in many cases decades.
6. Because they occupy the root system, which can be fairly massive, these fungi have a good food base and a high inoculum potential with which to attack other hosts.

FACTORS IMPORTANT TO ROOT DISEASE MANAGEMENT

To start planning, a manager needs to know three general factors about a root disease found on a particular site: host species, fungal survival or inoculum longevity, and means of spread. I won't spend more time on host species except to say that most diseases are fairly host specific or have a well-defined host range, avoid particular hosts and the disease will not develop.

Fungal Survival

Many root disease fungi can survive for decades after the host tree has died. Perhaps the longest survivor is the pathogen causing laminated root rot.

In very large stumps this fungus can survive for 50 to 100 years. Longevity of the pathogen inside roots may be attributable in large part to zone lines commonly formed by this and many other fungi in colonized wood. Zone lines are formed as protective barriers to unfavorable conditions and other decay fungi or antagonistic organisms; they are visible as black lines when decayed wood is cut. The process by which a pathogenic fungus converts from a long-term saprophytic existence inside an old root, to a pathogenic form on the surface of a root able to initiate an infection on a new host, is not well understood. Thus, any stump or root with an internal viable pathogen should be viewed as a potential source of inoculum and a threat to adjacent host trees. The regional exception to long-term survival of root pathogens is black stain root disease; the causal fungus dies within 1 to 2 years of tree death. However, this disease is spread by insects and management strategies aim to minimize spread by timing stand entry to life cycle of the insects.

Methods of Spread

Selection of an appropriate management strategy for root diseases depends in large part on the method of spread of the fungus involved. The following are the four common methods of spread, and an example disease.

1. Root-to-root: Laminated root rot—Virtually all spread of *Phellinus weirii* is by mycelia on or within roots with little if any by windblown spores. The fungus does not grow through the soil. The fungus persists on the site in the large roots and stumps of dead or cut trees and appears to effectively wall itself off in the infested wood by a protective hyphal sheath, seen as dark zone lines in cut wood. The pathogen continues to live saprophytically in dead roots for 50 years or more. Infection in a young stand begins when roots of young trees contact residual infested stumps and roots from the preceding stand. The infection spreads between living trees through root contact. As roots decay, a tree dies standing or is robbed of structural support and is windthrown. Nearly all root diseases can spread from an infected tree to a healthy tree when their roots are in contact.
2. Insect: Black stain root disease—Black stain root disease is caused by the fungus *Leptographium*

wageneri (perfect stage *Ophiostoma wagenen,* rarely found). This disease is unique among the root diseases affecting forests of the Pacific Northwest because it is spread by root feeding insects, and it is a vascular wilt disease that does not actually cause a decay of root or stem tissue. Although long distance spread involves insect vectors, once introduced into a tree the fungus can move to new trees across root contacts or by growing up to 15 cm through the soil. Tree to tree spread is not dependent on hosts of low vigor, and centers may expand radially at a rate of nearly 5 feet per year. Insect spread involves root-feeding bark beetles and weevils. Fruiting bodies of the fungus form in the egg-laying galleries of the insects, and the sticky spores that are produced adhere to the insects and are dispersed by them. The spore-carrying bark beetles and weevils feed and breed in roots of low-vigor trees so occurrence of black stain root disease centers in disturbed areas probably reflects vector preference for stressed or injured trees.

3. Water: Port Orford cedar root disease—Port-Orford-cedar root disease, caused by *Phytophthora lateralis,* an introduced fungus, is a severe threat to Port-Orford-cedar on sites favorable for the pathogen. The pathogen is an Oomycete, or "water mold" and is spread by water-borne spores (zoospores) in either water or contaminated soil. Port-Orford-cedar grows in a narrow coastal strip in southern Oregon and northern California. It grows on a wide variety of sites including streambanks, bogs, coastal sand dunes, deep productive soils, and dry sites. Port-Orford-cedar needs a consistent supply of water and is an important species in riparian ecosystems. The pathogen is spread mainly by people moving infected seedlings and infested soil to disease-free sites. Livestock and wildlife may move the pathogen in soil on their feet but that is believed to be a minor factor in most situations. A much greater threat is the movement of soil on tires and machinery from an infested area to a noninfested area during road building or logging activities. Zoospores of the fungus, which can swim a short distance, move in water films in the soil, and are attracted to the uninjured root tips of cedar. They are totally dependent on free water for infection and spread and cannot survive in dry soil. Natural spread is virtually all downslope or downstream in water moved by gravity.

4. Air currents: Annosus root disease—Annosus root disease is caused by the fungus Heterobasidion annosum (previously *Fomes annosus)* which can infect its hosts in two ways: by mycelial growth across root contacts and by windblown spores. Spore infection of freshly cut stumps is the primary way that new infection centers start. In coastal stands, stumps can become infected any time of the year. After growing vegetatively down through the stump and root system, the fungus can move to adjacent trees across root contacts, but does not grow through the soil. Infection centers can expand at one foot per year. The fungus can remain viable in large stumps for at least 50 to 60 years but in small (less than 6 inch dib) stumps the fungus dies out within a few years. The fungus can also infect wood exposed when living trees are wounded. When this fungus colonizes and injury the rate of spread is two to three times greater upward than downward.

DISEASE MANAGEMENT PLANNING

Although no universal system exists for integrating root disease management into land management decisions, some variation of the following decision ladder may be useful for including root disease management in selecting appropriate management scenarios for Pacific Northwest forests.

1. ESTABLISH MANAGEMENT OBJECTIVES: The choice of options will likely vary depending on the objectives. Examples include variations on fiber production, wildlife habitat enhancement, alternative forest products, or some combination of these.

2. GET A HISTORICAL PERSPECTIVE: Determine the historical appearance of the stand: tree species (not what was planted), relative stand structure, composition, and age. Determine the diseases that were and are present, and their distribution. Equally important for some diseases is the availability or probable future availability of inoculum from nearby stands.

3. PROPOSE MANAGEMENT STRATEGIES: Use available models to evaluate the effects of the proposed strategies over time. An example is the western root disease model which can currently be used to address laminated root rot, annosus root disease, and armillaria root disease and their interactions with bark beetles. Simulations designed around one of these three root diseases can be used to approximate others. Stands can be grown to evaluate various cultural treatments and "play" with options. In the absence of models, use local data to project the impacts of various scenarios. Growing a forest takes a long time, and it is important to consider the cumulative effects of various actions and inactions.

4. INTEGRATE: Integrate the decision for managing disease with the needs for managing other resources on the site. Try to integrate the activities on the site with those planned for adjacent sites.

Through this integration, attempt to project impacts to the next larger scale. For example, try to project how the actions planned for this stand will, through time, impact other activities in the watershed.

Managers should expect that there will be some failures to meet desired future conditions. The best laid plans have some built-in uncertainty. In general, we can't control diseases. This is especially true of root diseases given their hidden inoculum. And, where controls are available, they are generally too expensive to use on large areas. When we try to manage diseases we are really engaging in risk reduction. Managing forests is a very long-term enterprise, and changes may occur that are well beyond our reasonable planning horizon. Examples include changes in local weather conditions or the unexpected appearance of other disturbance agents which alter the outcome of our applied management strategy.

TAKE HOME MESSAGES

1. Pathogens are a natural and perhaps essential part of the forest ecosystem.
2. The presence of root disease does not necessarily mean that the soil or forest is unhealthy.
3. Root diseases contribute to plant and animal diversity.
4. Losses are a social not a biological term.
5. Take measures against introducing exotic diseases.
6. Include root disease management considerations early in the planning process.

SUMMARY AND CONCLUSIONS

Forest tree diseases have profound influence on stand structure, composition, and function in Pacific Northwest forests. They are among the most important disturbance agents operating in the forest ecosystems of the Pacific Northwest, even though their effects are often not spectacular at any given point in time. At landscape scales and over long time frames, the impacts of root diseases are considerable. Understanding the ecological roles of diseases, their historical and current distributions, their impacts on resources, how management influences them, and how they affect management, is crucial to meeting ecosystem management objectives. Unless diseases are included as a planning consideration, it is unlikely that ecosystem management strategies will be successful in achieving desired future conditions.

QUESTIONS FROM THE FLOOR

Q: "What insights do you have on effects of subsoiling and disease spread and/or effects of compaction and root damage."

A: Considering the amount of subsoiling that is apparently being done, we know precious little about the effects. I can suggest a few general observations or comments:

1. It is unlikely that there will be much movement of inoculum as a result of subsoiling.
2. Subsoiling equipment should stay as far from living trees as practical.
3. Any subsoiling is likely to injure roots. In some cases armillaria root disease has been associated with subsoiling activities. The injuries may present opportunities for annosus root disease to get started, especially in true firs. But, in general, it is unlikely that subsoiling is going to cause any catastrophic increase in root disease.
4. Hard data is not available but we would expect that subsoiling in the vicinity (within 200 meters) of black stain root disease centers would attract the beetle vectors of the fungus and initiate new centers.
5. My recommendation is that every plan for subsoiling should carry with it a plan and a commitment of funds for a monitoring effort to determine which if any diseases increase. In general that has not been done and is an essential part of evaluating the efficacy of subsoiling. There are many pathologists available who could assist in developing monitoring plans.
6. In 1993 a study was initiated in Region Five to examine the effects of subsoiling on Jeffrey pine on the Milford Ranger District, Plumas national Forest, in northern California. The study and some results are reported in two papers: (a) Otrosina, W. J.; Sung, S.; White, L. M. 1996. Effects of subsoiling on lateral roots, sucrose metabolizing enzymes, and soil ergosterol in two Jeffrey pine stands. Tree Physiology 16:1009-1013. (b) Kliejunas, J. T.; Otrosina, W. J. 1997. Progress report: Effects of subsoiling study, Milford Ranger District, Plumas National Forest. USDA Forest Service, Pacific Southwest Region, Forest Pest Management Report Number R97-01 10 pp.

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ROLE OF SOIL ORGANISMS IN RESTORATION AND APPLICATIONS TO MANAGEMENT

STRUCTURE AND FUNCTION OF BIOLOGICAL SOIL CRUSTS

Jayne Belnap[1], John Williams[2] and Julie Kaltenecker[3]

ABSTRACT

Biological soil crusts are found throughout the world. They are generally dominated by cyanobacteria, lichens, and mosses. When moistened, cyanobacteria move through soils, leaving sticky sheaths behind. Sheaths connect loose soil particles, contributing soil resistance to wind and water erosion. Abandoned sheaths are found up to 10 cm down in soils, providing stability at depth. Moistened sheaths absorb ten times their volume of water. Crusted surfaces roughened by frostheaving slow rainfall runoff, thus increasing infiltration.

Crusts can reduce germination of exotic annual grasses. They contribute nitrogen to desert ecosystems, where nitrogen often limits productivity. Plants growing in crusted areas often have higher levels of many nutrients than plants in non-crusted areas.

Many land uses are incompatible with crustal integrity. Cyanobacterial fibers have little resistance to compressional stress. Crushed crusts contribute less nitrogen to soils. Impacted soils are susceptible to both wind and water erosion, leading to soil loss and burial of nearby crusts.

Recovery is generally very slow. Rates depend on climate; size, timing, and intensity of disturbance; and soil type. In areas with less stable soils and less rainfall, full recovery may take over 250 years, even with small disturbances. Soils with more inherent stability or areas with greater rainfall will recover more rapidly.

Keywords: cryptobiotic soil crusts, microphytic, microbiotic, soil erosion, germination, nutrient cycles, deserts

INTRODUCTION

In arid and semi-arid lands throughout the world, the cover of vegetation is generally sparse or absent. Open spaces between the higher plants are not bare of autotrophic life, but usually covered by a community of highly specialized organisms. This soil surface floral community consists of cyanobacteria, green algae, lichens, mosses, microfungi, and other bacteria. Cyanobacterial and microfungal filaments weave throughout the top few millimeters of soil, gluing loose soil particles together, forming a biological crust which stabilizes and protects soil surfaces from erosive forces (Belnap and Gardner 1993). These crusts occur in all hot, cool, and cold arid and semi-arid regions. They may constitute up to 70% of the living cover (Belnap 1994) and have only recently been recognized as having a major influence on terrestrial ecosystems. These communities are also referred to as cryptogamic, cryptobiotic, microbiotic or microphytic soil crusts (Harper and Marble 1988).

Globally, this consortium of soil biota has many similarities in species composition, structure and function, in spite of occurring in unconnected and seemingly dissimilar environments. Crusts are found in an astonishing variety of higher plant communities throughout the world, ranging from deserts to tundra.

WHAT BIOLOGICAL CRUSTS ARE NOT: PHYSICAL SOIL CRUSTS

Non-biotic soil surface crusts are a major structural feature in many arid regions. Their properties and manner of formation have been studied for many years, primarily because of their detrimental effects to agriculture crops. These crusts are transient soil-surface layers that are structurally different than material immediately beneath. Rainfall onto unprotected soil surfaces is what forms most physical crusts. Surface aggregates are broken apart by raindrops. Smaller particles wash into spaces between larger particles, thus clogging soil pores and reducing infiltration rate by as much as 90%. In general, rain-

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[1] Jayne Belnap is a Research Ecologist for the US Geological Survey, Biological Resources Division, Forest and Rangeland Ecosystem Science Center, Canyonlands Field Station, 2282 S. West Resource Blvd., Moab, UT 84532.

[2] John Williams is a hydrologist for the USDA-ARS in Pendleton, OR 97801-0370.

[3] Julie Kaltenecker is a biologist for the Idaho State Office, Bureau of Land Management, 1387 S. Vinnell Way, Boise ID 83709.

formed crusts are less than 5 mm thick. This layer is often harder than the rest of the soil because it is drier and compounds such as salts, lime and silica have been deposited at the surface as water evaporates. With large pores absent, these crusts increase water runoff and soil erosion, and prevent the emergence of seedlings.

Crusts may form on soil of almost any texture except coarse sandy soils containing very low silt and clay (Lemos and Lutz 1957). Conditions that make surface soil especially susceptible to crusting are low organic matter, high silt and high sodium. These characteristics are all related to soils with low structural stability and soil aggregates easily broken down under the impact of water. Soil aggregate structure is also reduced by the hooves of grazing animals or machinery. Such compacted surfaces have reduced infiltration rates and increased surface runoff and function hydrologically in a manner similar to raindrop-induced crusts.

Using intensive grazing to break up these crusts has short-lived results, as the soil surface is resealed after the first minutes of an intense rainstorm. Management systems that promote soil surface protection (through plant and biological soil crust cover) and increases in soil organic matter produce the only lasting solution to physical soil crust reduction (Blackburn 1983).

BIOLOGICAL SOIL CRUST DISTRIBUTION

Many of the dominant cyanobacteria and soil lichens have a cosmopolitan distribution, and crustal communities can have similar growth forms. For instance, the same soil lichens dominate soils crusts of both the Sonoran and Great Basin deserts of the western United States and areas of South Africa and Australia, while vascular plant species and climate varies greatly between these regions. Crusts are generally flat, and sometimes covered with a layer of pebbles in hot deserts of the world, such as the Atacama, Sonoran, Chihuahuan and Australian deserts. Where freezing temperatures are common, frost heaving often results in crusts with pedicels up to 10 cm high, such as seen on the Colorado Plateau, Great Basin and the Arctic.

In the western US, overall biological crust cover is greatest in low elevation inland sites (<1000 m) compared to mid-elevation sites (1000-2500 m). This results from reduced vascular plant cover, leaving more surface available for colonization and growth of crustal organisms. Crustal organisms have reduced water and nutrient needs relative to vascular plants, and can withstand the harsh growing conditions found in plant interspaces. The positive relationship between biological crust cover and available soil surfaces has been demonstrated in other studies (Anderson and others 1982a; Eldridge 1993a; Harper and Marble 1988; Johansen 1993; Rogers 1972).

Crusts in cool deserts are dominated by the non-heterocystic cyanobacterium *Microcoleus vaginatus* (Belnap and Gardner 1993). *M. vaginatus* is a large, highly mobile filamentous species that lacks heterocysts, the structurally differentiated, oxygen-excluding cells where cyanobacterial nitrogen fixation generally takes place. In contrast, most crusts in warm deserts are dominated by heterocystic cyanobacteria such as *Lyngbya* and *Nostoc,* with no single species dominating the microflora. These species are much smaller and less mobile than *M. vaginatus.* Common co-dominant lichens in both warm and cold deserts are *Collema* sp. and *Placodium* sp.

Likelihood of well-developed lichen crusts is increased with increasing moisture by factors that increase soil surface stability. Factors that increase soil surface stability are 1) more closely-spaced plants; 2) flatter areas (depositional rather than erosional surfaces); 3) limited surface rocks, roots and/or light plant litter to slow water and or wind and to keep hooves off surface; 4) soils with more inherent stability (silt/clay >sandy>shrink-swell clay); and 5) more stable microhabitats (under shrubs, away from small washes). More stable soils support greater cover and more varied populations of cyanobacteria, lichens and mosses. Very sandy soils and high shrink-swell clays (such as Mancos shale) have low inherent stability, and as a result, generally only large filamentous cyanobacteria that are highly mobile can survive in these soils (such as *M. vaginatus).* However, if the very sandy soils are sufficiently stabilized by these cyanobacteria, other smaller species can then colonize them (such as *Scytonema* and *Nostoc)* and lichen and mosses may be found under vascular plants, where some protection from sediment burial is provided. In soils such as Mancos shales, some mosses and lichens can be found occasionally on northern slopes. Extremely shallow soils colonized by *M. vaginatus* are also often stable enough to support most soil species of lichens and cyanobacteria found in a given area. As soil stability increases, these rich communities of cyanobacteria, mosses and lichens become more widespread, covering all surfaces not occupied by vascular plants or rocks.

Time since disturbance also influences the composition of crusts. The composition of biological soil crusts changes through time in a manner analogous to transitions occurring generally during terrestrial plant succession (Johansen and others 1984). As is typical of primary succession of vascular plants, nitrogen-fixing organisms appear first. The species appearing earliest in the crustal succession are cyanobacteria and algae (Anderson and Rushforth 1976; Johansen and others 1981, 1984; Harper and Marble 1988). The ubiquitous cyanobacterium, *M. vaginatus,* can colonize within just days of soil disturbance if soils are wet. Mosses and lichens colonize later, with the lichens *Collema* and *Catepyrenium* generally the first to appear.

MICROSTRUCTURE

Lichens and mosses are easily seen without aid of magnification. However, much of the structure and function of crusts is dependent on cyanobacteria, green algae, and microfungi. All these are often too small to be seen without a microscope. In most desert soils, cyanobacteria contribute the most to crust microstructure.

Cyanobacterial filaments confer structural integrity to the soils in which they occur. When wetted, the sheath of filamentous cyanobacteria swell, expelling the living filaments and leaving behind empty sheath material. These filaments often string sand and clay particles together, much like fibers in fiberglass. Depending on environmental conditions and soil textures, cyanobacterial sheaths may be found at depths of 10 cm below the soil surface (Belnap and Gardner 1993). As aeolian and water-borne materials are trapped in the polysaccharide sheaths of cyanobacteria on the soil surface, old sheaths are gradually buried. Thus, influence on water-holding capacity and soil stability may extend far below the depth to which light can penetrate, unless sheaths are crushed. If sheath-soil connections are broken by trampling or vehicles, these sheaths are no longer living and therefore cannot be repaired.

Measurements of the bumpy surface topography of undisturbed crusts show that few bumps are greater than 8 mm across, with cyanobacterial filaments ramifying throughout the micropedicels. The volume of cyanobacterial filaments per unit soil surface coverage is thus increased greatly in areas where microtopography of the soil surface is very complex, while still preserving photosynthetic capabilities. The roughened soil surface also provides habitat for microfauna, which are responsible for humus production (Gayel and Shtina 1974; Danin 1978).

ECOLOGICAL ROLES

Carbon Fixation

Biological soil crusts are an important source of fixed carbon on sparsely vegetated areas common throughout the West (Beymer and Klopatek 1991). While vascular plants provide organic matter to soils directly underneath them, large interspaces between plants have little opportunity to receive such input. Carbon contributed by soil crusts help keep plant interspaces fertile, and thus provide energy sources for other microbial populations.

The dominant components of biological soil crusts are photosynthetic organisms, and require sunlight. When soils are dry, the bulk of the cyanobacterial biomass is at 0.2-0.5 mm, with bundles found down to 4 mm where sufficient light for net carbon gain is available but UV exposure is reduced. When soils are moistened, *M. vaginatus,* which lacks UV-protective pigments, can be seen migrating to the surface for short time periods. Species with UV-screening pigments, are commonly found on the soil surface (Garcia-Pichel and Belnap 1996).

Recently, ecophysiologists have studied photosynthetic patterns in the lichen species present in biological soil crusts (Lange and others 1997, 1998). They have found that soil lichens have several different strategies to gain carbon. While photosynthesis is activated at low water content for all species, species varied in their response to higher water content. Some species, such as *Collema,* showed dramatic drops in carbon fixation at water contents over 60-80%. Other species showed little, if any, depression at high water contents. Water-holding capacity varies between lichens, which will also influence time of carbon fixation for a given species. Photosynthetic rates are also dependent on temperature (Lange 1980; Lange and others 1997; Nash and others 1982a, b; Rychert and others 1978). Most crustal species increase photosynthetic rates with increasing temperatures up to about 26-28 C, after which rates decline.

Differential responses to timing and amount of precipitation and temperature may mean species composition will shift in response to predicted climate changes. Many areas that are currently winter-rain dominated are predicted to receive increases in summer rain. Effects on species composition may be currently reflected in the different composition of biological soil crusts in the Sonoran (summer rain-dominated) vs the Mojave, Colorado, Colorado Plateau, and Great Basin deserts (winter-rain dominated). Winter-rain deserts have a rich flora of soil lichens and the cyanobacterial flora is heavily dominated by *Microcoleus.* In contrast, the summer rain-dominated Sonoran desert has only a small subset of the lichens found in winter-rain deserts, while the cyanobacterial flora is a complex community co-dominated by up to 10 species.

Nitrogen Fixation

Nitrogen concentrations are known to be low in desert ecosystems relative to other ecosystems. Total atmospheric input over the past 10,000 years has been conservatively estimated about 3 kg N m^2 (ignoring cyanobacteria inputs), with 77% lost through wind erosion, ammonia volatilization, nitrification, and denitrification (Peterjohn and Schlesinger 1990). Extensive surveys in cold deserts have revealed only a few nitrogen-fixing plants (Farnsworth and others 1976; Wullstein 1989). Since nitrogen can limit net primary productivity in many desert ecosystems, normal nitrogen cycles are critical to the fertility of semi-arid soils and in preventing desertification (Dregne 1983).

Cyanobacteria and cyanobacterial-containing soil lichens can be an important source of both fixed nitrogen for plants and soils in desert ecosystems (Evans and Ehleringer 1993; Belnap 1995). Most biological soil crusts in the western US are dominated by nitrogen-fixing cyanobacteria and lichens *(M. vaginatus, Scytonema myochrous, Nostoc* sp.) and the soil lichen *Collema.* All these species are capable of both light and dark nitrogen fixation (Paerl 1990). Nitrogen inputs from biological soil crusts have been estimated from 1 to 100 kg ha^{-1} annually (Harper and Marble 1988). The lowest estimates are almost ten times atmospheric input estimates by Peterjohn and Schlesinger (1990). Nitrogen fixation is highly dependent on past and present water and light regimes, as well as species composition (Rychert and others 1978; Belnap 1996), with maximum fixation at approximately 26°C and above 20% moisture. Past disturbance history is also a critical factor in determining fixation rates (Belnap 1995, 1996).

Five to 88% of N fixed by *Nostoc* has been shown to leak into the surrounding substrate (Belnap and others 1997; Magee and Burris 1954). Nitrogen leaked from these organisms is available to nearby vascular plants (Mayland and Macintosh 1966). Vascular plants growing in biologically crusted areas show higher tissue concentrations of nitrogen when compared to plants in uncrusted soils (Harper and Pendleton 1993; Belnap 1994, 1995; Belnap and Harper 1995). Since rainfall and dewfall events in desert areas are often too small to promote plant growth, but do stimulate microbial community activity, biological soil crusts can be the dominant nitrogen source for the ecosystem. As with carbon, crusts contribute nitrogen to soils both under plants and in plant interspaces, thereby counteracting the tendency of nutrients to concentrate around perennial plants.

Effects on Vascular Plants

Germination and establishment—The presence of crusts can affect vascular plant germination and establishment. While small cracks and crannies on the soil surface are sufficient for small-seeded plants to lodge and germinate, most large-seeded plants need some cover by soil or vascular plant litter. In deserts where plant litter is often limiting in interspaces, large native seeds generally have self-burial mechanisms (such as hygroscopic awns) or through rodent caching. Plants adapted to loose moving soils (such as sand dunes) or deep litter (forests) accomplish this passively. However, exotic species may lack such adaptations. As crusts stabilize soils, germination can be inhibited in sites with well-developed crusts and low plant litter, as was recently demonstrated for the annual exotic grass *Bromus tectorum* in both the field and laboratory (Belnap, Kaltenecker unpublished data). Once the seeds germinate, biological soil crusts show no barrier to seedling root penetration (Belnap, Pendleton and Meyer unpublished data).

Seedling germination *per se* has not been shown to limit species density or presence in desert plant communities. Harper and Marble (1988) and Eckert and others (1986) showed seedling establishment and survival greater on crust-dominated soils than on soils lacking crusts. Experiments done with both fine and coarse-textured soils demonstrate that seedling establishment and survival for both forbs and grasses can be much higher in crusted areas when compared to areas where the crust had been removed (Belnap 1993; Harper and St. Clair 1985; St. Clair and others 1984; Lesica and Shelley 1992). No study has shown a negative relationship between crusts and vascular plant growth. Rather, many studies worldwide suggest that vascular plant cover is most often controlled by water and/or nutrient availability rather than other site factors (Dunkerley and Brown 1995; Mabbutt and Fanning 1987; Tongway and Ludwig 1990).

Some authors have suggested that there is a negative relationship between cover of biological crusts and vascular plants. However, in a recent study (Belnap and others, in review), little correlation was seen between vascular plants and crustal cover at coastal and mid-elevation sites. At more arid low-elevation sites, correlations between vascular plant cover and cover of crustal components was generally positive. This relationship suggests that the presence of plants aids the survival of crustal components, perhaps due to microclimate conditions associated with perennial vegetation (such as decreased soil surface temperatures and increased surface moisture due to shading). Rather than crusts inhibiting plants, it appears more likely that crust occur in spaces where vascular plants cannot grow and keep them out. Numerous other authors have reported crusts either do not compete with vascular plants (Anderson and others 1982a; Beymer and Klopatek 1992; Jeffries and Klopatek 1987; Kleiner and Harper 1972; 1977a, b) or actually enhance vascular plant cover (Carleton 1990; Dadlich and others 1969; Graetz and Tongway 1986; Ladyman and Muldavin 1994; Ladyman and others 1994; Lesica and Shelley 1992; Muncher and others 1988; Rosentreter 1986).

Nutrient levels in vascular plants—Plants growing on crusted soil often show higher concentrations and/or greater total accumulation of various essential nutrients when compared to plants growing in adjacent, uncrusted soils. In southeast Utah, leaf tissue nitrogen in annual, biennial and perennial species was 9-31% higher in crusted areas. Dry weight were greater as well (Belnap 1995; Belnap and Harper 1995). This was verified with greenhouse experiments (Harper and Pendleton 1993). Other authors have obtained similar results with other species (Brotherson and Rushforth 1983; Shields and Durrell 1964).

Several mechanisms have been postulated to explain this effect. Crusts accumulate nutrient rich fine soil and organic matter (Fryberger and others 1988; Campbell and others 1989; and Gillette and Dobrowolski 1993). Material that blows across biological soil crusts can become trapped, either accumulating within low pockets in the microtopography or stuck by exudate on algal sheaths. Algal sheaths are phototropic, and if not buried too deeply, will push through loose soil and organic matter, trapping or entangling the soil in the process (Campbell and others 1989). Danin and others (1989) proposed a positive feedback loop based on this process in which nutrient-rich microsites develop, leading to germination and growth of vascular plants, which in turn contribute to a reduction in erodibility and an increase in the accumulation of washed or wind blown soil.

Cyanobacterial sheath material is often coated with negatively-charged clay particles. Positively charged macro-nutrients bind to these particles, and are thus prevented from leaching from the soil profile (Belnap and Gardner 1993). These clay particles are more nutrient-rich than sand (Black 1968). Lange (1974) demonstrated that compounds in the gelatinous sheath material of half the cyanobacteria species studied were able to chelate elements essential for their growth (e.g., iron, copper, molybdenum, zinc, cobalt, and manganese). Four of the five genera shown to possess this ability *(Anabaena, Anacystis, Lyngbya,* and *Nostoc)* are represented by common species in the biological crusts of western North American deserts (Shields and Durrell 1964). It is also possible that nutrient differences are a result of a thermal effect, as dark crusts would be warmer that lighter uncrusted soils, and uptake of nutrients would occur at a higher rate. Herbivores and other consumers benefit directly from the enhanced nutrient status of these ecosystems (Belnap and Harper 1995). Indirect effects include positive correlations between soil mycorrhizae and microarthopod populations with the presence of well-developed biological soil crusts (Harper and Pendleton 1993; Belnap unpublished data).

Water Relations

The effect of biological soil crusts on soil water relations is highly variable between different regions, soils and climatic regimes. Crustal development (e.g., cyanobacterial, lichen, moss), climatic regimes, the amount of surface roughness, time since destructive disturbance, soil texture, and soil structure can all heavily influence hydrologic cycles at a given site. Soil texture is especially important and can override any effect of biological soil crusts. For instance, soils with high shrink-swell clays have low infiltration rates, and sandy soils have high infiltration rates, regardless of the biological soil crusts present.

Research results conducted under a variety of soil and climate conditions around the world show the variable, and interactive, effects of biological soil crusts and soil properties. While the presence of the mucilaginous cyanobacteria can decrease soil permeability, increased surface roughness can increase water pooling and residence time. Consequently, in cool and cold deserts where frost-heaving is common and biological soil crusts greatly increase soil surface roughness, the presence of biological soil crusts may increases the amount and depth of rainfall infiltration. Under sagebrush mounds in a clayey-skeletal, montmorillonitic soil in southern Idaho, sites with a high cover of biological soil crusts in coppice and moss-grass microsites had significantly higher infiltration rates than adjacent bare or vesicular dominated soils (Blackburn and others1990; Johnson and Gordon 1986; Pierson and others 1 994a and b; Johnson and Rosentreter 1988). (However, this result was complicated by the presence of more plant litter under the shrubs than in plant interspaces, which may have been responsible for this increase). In a Utah sandy loam soil, infiltration rates increased with increased lichen-dominated crusts (Loope and Gifford 1972), and 3-year-old algal crusts decreased time to ponding, although infiltration rates, once runoff began, were the same with or without the crust (Williams and others 1995b).

In warm deserts, where frost-heaving is not present and biological soil crusts are flat, infiltration rates appear to depend more on soil type and climatic regimes, and so are site-specific. Reduced infiltration rates as a result of biological soil crust cover have been reported for sandy soils in Arizona (Brotherson and Rushforth 1983), Australian sandy soils (Bond 1964; Eldridge 1993a,b; Rogers 1977; Stanley 1983; and Graetz and Tongway 1986), and Israeli sandy soil (Yair 1990). In New South Wales, Australia, infiltration rate increased on a transect through a sandy-loam soil as grazing decreased and biological soil crust cover increased. However, comparison with adjacent ungrazed soils with a continuous cover of lichens and mosses showed reduced infiltration (Eldridge 1993b). Infiltration studies conducted on sandy soils of

Oklahoma and Kansas (Booth 1941) and silt-loams and clayey silt loams in Arizona (Faust 1970, 1971) failed to find any influence of biological soil crusts on infiltration rates.

Conversely, components of biological soil crusts rapidly swell (Shields and Durrell 1964) up to 13 times the dry volume (Campbell 1977), potentially closing flow pathways through soils. Scanning electron microscopy shows sufficient openings in sandy loam soils for water flow (Belnap and Gardner 1993) but concentration of silt and clay particles, combined with swelling will restrict infiltration even in sandy soils when wet (Verrecchia and others 1995). The hydrophobic nature of some microphytes have been speculated to contribute to soil surface sealing (Bond 1964); however, other authors have experimental evidence that shows these organisms to be highly hydrophilic (Kidron personal communication).

The influence of biological soil crust on effective hydraulic conductivity (Ke: the rate at which water moves through the soil profile under field conditions) is also variable. Lichen-dominated crusts in Utah decreased Ke (Loope and Gifford 1972). Lichen and algal crusts in Australia were associated with high Ke (Greene and others 1990). Algal crusts in Utah and non-disturbed Nevada crusts had no discernible influence on Ke (Williams 1993; Dobrowolski 1994).

Though overall infiltration of precipitation is critical for plant growth, where water infiltrates can also be critical in maintaining plant community structure. Recent work done on banded vegetation has shown that water infiltration and runoff patterns can be important in maintaining vegetative community structure in hyper-arid zones. Banded vegetation occurs in very flat areas where rainfall is too low to support homogenous distribution of vegetation; instead, plants are concentrated in bands that occur perpendicular to the flow of water. These bands capture water, nutrients and fine soil particles. The bigger the bands, the more effective they are in resource capture; however, their overall size is limited by rainfall and nutrients. Biological soil crusts cover inter-band soils. When these inter-band biological soil crusts are disrupted, water infiltration increases between vegetated areas. This results in less water reaching the vegetated bands, causing large die-offs. This was also seen in Israel, where vegetation died when water infiltration was increased in plant interspaces (Zaady, personal communication).

The effect of biological soil crusts on soil moisture is also variable. Soils under biological soil crusts showed deeper water penetration into the profile and greater availability during drought (Brotherson and Rushforth 1983; Abrahams and others 1988). The ability of the crust to seal the soil surface and reduce evaporation due to high clay and silt concentrations in the crusts has been repeatedly proposed (Danin 1978; Brotherson and Rushforth 1983; Williams and others 1995b) and recently supported by research specifically designed to address the issue (Verrecchia and others 1995). However, this can vary. In Utah and Mexico, soil moisture was less under disturbed crusts than intact crusts (Harper and Marble 1988; Meyer and Garcia-Moya 1989). Increased soil temperature, through the absorption of solar energy by black crusts, may increase soil moisture evaporation rates (Harper and Marble 1988).

As can be seen above, the impact of crusts on hydrologic cycles is highly site-specific. While much of this variation is probably due to soil and crust differences, this is difficult to assess due to lack of standardized data collection methods and better descriptions of soil, crust and climate characteristics at each study site.

Soil Stabilization

Wind and water can be major erosive forces in deserts, as sparse vegetation leaves large soil spaces unprotected by plant litter or vegetative cover (Goudie 1978). These interspace soils in deserts is most often stabilized by rocks or biological soil crusts. Biological soil crusts play an important role in both preventing soil loss and facilitating soil accretion. They contribute to aggregate stability, surface and subsurface organic matter, soil structure and soil surface microtopography as a result of physical and chemical attributes (Booth 1941; Fletcher and Martin 1948; and Shields and Durrell 1964). Contribution to aggregate stability can be visually assessed on both a micro- and macro-scale (Belnap 1994; Belnap and Gardner 1993).

As seen in the microstructure chapter, polysaccharides extruded by the cyanobacteria and green algae, in combination with lichen and moss "rootlets", entrap and bind soil particles together, increasing the size of soil aggregates. As soil aggregates get larger, they are heavier, have a greater surface area, and are therefore more difficult for wind or water to move. In both wet and dry soils, these structures can be seen firmly gluing soil particles together at up to 7 cm below the soil surface. The presence of biological soil crusts enable otherwise loose sandy soils to stay in place on steep slopes, and stabilize pockets of very shallow soil (Bond and Harris 1964; Marathe 1972; Gayel and Shtina 1974; Danin and Yaalon 1980; Schulten 1985; Graetz and Tongway 1986; Campbell and others 1989; Danin and others 1989; Belnap and Gardner 1993). Rough microtopography also slows both wind and water erosion by creating a still air boundary layer to protect against wind erosion. Providing detention dams creates pooling and slowed flows, thus giving sediment time to settle out of the water and reducing sediment loss

(Brotherson and Rushforth 1983; Alexander and Calvo 1990). The degree to which different types of crusts protect the soil surface from both wind and water erosion is: bare soil < algal crust < lichen/moss crust (Belnap and Gillette 1997, 1998; Kinnell and others 1990; Eldridge and Greene 1994; Tchoupopnou 1989). Biological soil crusts are unambiguously effective in reducing wind erosion of soil (Belnap and Gillette 1997, 1998).

EFFECTS OF DISTURBANCE

Many uses of deserts result in impacts to the biological soil crusts. The largest impacts come from driving off-road with vehicles, including military and civilian vehicles; trampling by livestock and people; and various mining activities. Effects of these activities are especially noticeable at sites with highly erodible soils with high topographic relief.

Species Composition

Surface disturbance also results in changes in species composition of soil crusts. While multiple species of soil lichens and mosses, as well as 4 or more species of cyanobacteria can be found in untrampled areas on most soil types, no lichens and only one species of cyanobacteria are generally found in directly-adjacent trampled areas (Belnap 1995). Changes in species composition has implications for both soil stability and nutrient inputs.

Microtopography

Trampled surfaces are generally flat, whereas untrampled interspace surfaces can support cyanobacterial pedicels from 1-7 cm high (depending on climate of the site). Flattened surfaces do not slow water or wind velocity, nor does sediment have an opportunity to settle out; thus, more sediment is lost from trampled sites than untrampled sites. Water residence time on smooth surfaces is shorter, and water infiltration reduced (Harper and Marble 1988).

Soil Stability

Different soils have different intrinsic soil strengths that vary with moisture content. Arid soils with little tendency to form inorganic aggregates (e.g., sandy soils) are more susceptible to stresses when dry, while soils with inorganic crusting are more susceptible to impacts when soils are wet. Trampling greatly accelerates desertification processes through increased soil loss and water runoff. Soils in arid regions are often highly erodible, and soil formation is extremely slow, taking 5,000 to 10,000 years (Dregne 1983).

Crustal components are brittle when dry and the connections they make between sand grains easily crushed. Therefore, compressional disturbances, such as those generated by animal, people and vehicular traffic, can severely affect the ability of crusts to stabilize soils (Belnap and Gillette 1997, 1998; Williams and others 1995a). Damage to the underlying cyanobacterial sheath material is non-repairable, since living cyanobacteria are no longer present at these depths to regenerate filament and sheath materials.

Water erosion from plots with biological soil crusts, undisturbed for two to three years, was significantly less than from plots without crusts in Utah and Idaho (Williams and others 1995b; Loope and Gifford 1972; Blackburn and others1990; Pierson and others1994a, b). Lower erosion rates were not simply due to decreased runoff, strongly suggesting that the reduced erodibility was attributable to conditions unique to the coppice and moss-grass microsites. Globally, many authors have reported that the presence of biological soil crusts reduces soil susceptibility to water erosion through reduced raindrop erosion and sediment loss from sites (Alexander and Calvo 1990; Beymer and Klopatek 1992; Eldridge 1993; Eldridge and Greene 1994; Foth 1978; Harper and Marble 1988; Ladyman and Muldavin 1996).

All studies have shown that crust cover reduces wind erosion on all soil types by requiring much higher wind speeds to initiate soil particle movement (Belnap and Gillette 1997, 1998; McKenna-Neuman and others 1996; Williams and others1995a). Resistance to wind erosion parallels biological crust development. Well-developed crusts (with lichens and mosses) on all soils tested conferred the greatest erosion resistance, when compared with less-developed crust. Compressional disturbances to the crusts greatly decrease resistance to wind erosion for all soil types, regardless of the disturbance regime or soil type, as cyanobacteria and lichens are brittle when dry and crush easily. Vehicle tracks result in greater damage than hoof prints on a given soil type. After 10 years of recovery, sandy soils tested in southeast Utah were still susceptible to wind erosion at commonly-occurring wind speeds (Belnap and Gillette 1997, 1998).

Decreases in the wind resistance of soils is directly associated with increased sediment movement (Leys 1990; Williams and others 1995a). Nearby biological soil crusts can be buried by blowing sediment, resulting in the death of the photosynthetic organisms (Belnap 1995, 1996). Because over 75% of the photosynthetic biomass, and almost all photosynthetic productivity, is from organisms in the top 3 mm of these soils, very small soil losses can dramatically reduce site fertility and further reduce soil surface stability. In addition, many plants have relatively inflexible rooting depths, and often cannot adapt to rapidly changing soil depths.

Nutrient Cycles

Nitrogenase activity can be dramatically reduced in soil crusts after experimentally-applied disturbance (Belnap and others 1994; Belnap 1995, 1996). Disturbance by human feet, mountain bikes, four-wheel drive trucks, tracked vehicles (tanks), and raking all resulted in an immediate 40-80% reduction in nitrogenase activity. After 6-9 months, nitrogenase activity had dropped still lower in the disturbed areas than the initial measurements, with treatments showing an 80-100% reduction in nitrogenase activity.

Crust disturbance can result in large decreases in soil nitrogen through a combination of reduced input and elevated losses (Peterjohn and Schlesinger 1990). Current long-term studies demonstrate a 42% decrease in soil nitrogen and 34% decrease in plant tissue nitrogen 25 years following release from grazing. The greatest long-term impact of disturbance may be on the soil microbial pool: plant-available nitrogen can decrease almost 80% following disturbance. This has large implications for ecosystems that are dependent on biological crusts for nitrogen, such as the Colorado Plateau (Evans and Ehleringer 1993; Evans and Belnap 1 999). Reduced fertility of systems is one of the most problematic aspects of desertification (Dregne 1983).

Albedo

Albedo is also of concern in semi-arid and arid systems. When trampled surfaces were compared to untrampled surfaces, there was up to a 50% increase in reflectance from 0.25 to 2.5 μm (Belnap 1995). This represents a change in the surface energy flux of approximately 40 watts/m^2. Large acreages of trampled areas can lead to changes in regional climate patterns in many regions (Sagan and others 1979).

Changes in surface albedo will result in changes in soil temperatures. Trampled surfaces have significantly different surface temperatures than untrampled surfaces. For example, trampled surfaces in southeast Utah were found to be 23°C cooler than adjacent crusted surfaces. In the winter, surface temperatures of well-developed crusts were up to 14°C higher than ambient air temperature (Belnap 1995). Surface temperatures can be very important in desert systems. Nitrogenase activity is heavily temperature dependent, with lower temperatures resulting in lowered activity levels (Rychert and others 1978). Altered soil temperatures can be expected to affect microbial activity, plant nutrient uptake rates and soil water evaporation rates. Soil temperatures have been shown to affect seed germination time and seedling growth rates for vascular plants. Timing of these events is often critical in deserts, and relatively small delays can reduce species fitness and seedling establishment which may eventually affect community structure (Bush and Van Auken 1991). Food and other resources are often partitioned among ants, arthropods and small mammals on the basis of surface temperature-controlled foraging times (Doyen and Tschinkel 1974; Crawford 1991; Wallwork 1982). Many small desert animals are weak burrowers, and soil surface microclimates are of great importance to their survival (Larmuth 1978). Consequently, altering surface temperatures can affect nutrient availability and community structure for many desert organisms, thus increasing susceptibility to desertification.

Fire

High intensity fire will burn biological crusts, resulting in reduction of visible cover, biomass, and species diversity (Callison and others 1985; Greene and others 1990; Johansen and others 1993). The extent of damage depends on the type of plant community in which the crust occurs, the distribution of fuel and thus fire intensities (Johansen and others 1993). Arid and semiarid communities historically had patchy plant distributions, resulting in discontinuous fuel with biological crusts between (Whisenant 1990). Biological crusts provide little fuel to carry a fire through interspaces, thereby acting as "refugia" to slow the spread of fire and decrease its intensity (Rosentreter 1986). Unburned islands of vascular vegetation and biological crust provide propagules for reestablishment of the community in burned areas. Johansen and others (1993) observed that the structural matrix of the crust was left intact following fire, maintaining stability against erosive forces during the recovery period for vascular plants and the biological crust.

Exotic annual grasses, primarily *Bromus* sp., have invaded semiarid and arid landscapes throughout western North America, homogenizing fuel distribution and drastically altering fire regimes (Whisenant 1990; Peters and Bunting 1994). Increases in both fuel amount and continuity have resulted in large, continuous fires. For example, natural fire return intervals for *Artemisia tridentata* ssp. *wyomingensis* communities on the western Snake River Plain are greater than 60 years (Whisenant 1990). These have been modified to intervals of five years or less, with some areas burning annually. Salt-desert shrub communities rarely burned under pristine conditions. In addition, fire seasons have become longer than the historical average due to the presence of dry fuel from late spring until the onset of cool weather and fall rains. Biological crusts are lost from the community if fire return intervals are shorter that the period required for the crusts to recover (Greene and others 1990; Whisenant 1990). Lichens and mosses are lost if annual grasslands are allowed to dominate. Increases in both live plant density and litter amount result in little open space, repressing the recovery of a diverse biological crust (Kaltenecker 1997).

Timing and Intensity of Disturbance

Only a few studies discuss season of use and attendant impacts on biological soil crusts. In addition, past disturbance regimes are generally not reported. Marble and Harper (1989) found heavy grazing treatments (17 sheep days/acre, applied over 1-2 days) in early winter did not significantly affect biological soil cover and composition or vascular plant cover and composition. When the grazing season was extended to late winter, both biological soil crust cover and species richness declined significantly. Differences are attributed to insufficient soil moisture in late winter/early summer to permit regrowth of biological soil species. This reduction in biological soil crust cover coincides with Lusby's (1979) findings that extending the grazing season from February 15 to May 15 resulted in increased runoff/erosion from depletion of biological soil crusts. Continuous grazing has been shown to be deleterious to biological soil crusts. Jefferies and Klopatek (1987) showed a near complete destruction of the crust on a site heavily grazed year-long, compared to similar pristine and light-moderate winter gazing on sandy blackbrush sites in southern Utah and northern Arizona. Brotherson and Rushforth (1983) showed large reductions of both biological soil crust and vascular vegetation on continuous moderate to heavily grazed sites in northern Arizona.

Likewise, intensifying physical impacts through short duration grazing strategies is also deleterious to biological soil crusts. While this is reported to be beneficial to vascular plant communities in some ecosystems dominated by summer moisture such as in Zimbabwe (Savory and Parsons 1980) and the Great Plains region of the U.S., it is not beneficial to either native vascular plants or biological soil crusts in areas where precipitation is predominantly received in the winter, such as the Mojave, Great Basin, Colorado Plateau or Columbia River Basin (Johansen 1986). Platou and Tueller (1985) suggest that the natural grazing system that evolved in the Great Plains closely resembles high-intensity short duration grazing, while the natural grazing system in the shrub-steppe is more similar to rest-rotation grazing in the winter only (Mack and Thompson 1982; Parmeter and Van Devender 1995; Hormay 1970).

EXOTIC PLANTS

Introduced annuals such as *Bromus tectorum* (cheatgrass) and *Taeniatherum asperum* (medusahead) appear to impose long-term threats to biological soil crust communities. Surveys in these plant communities show that the rich perennial moss/lichen community has generally been replaced with annual mosses and cyanobacteria. The mechanisms by which the presence of annual grasses negatively affects the biological soil crusts is not clear, but could include a decrease in available soil surfaces (via increased cover of vascular plant and plant litter); increased soil disturbance by small rodents responding to an increase in seed availability; increased fire frequency; increased soil turnover by increased populations of soil fauna; and/or increased soil disturbance by plant surface roots.

REGIONAL THREATS

Many regional factors influence ecological processes in deserts. Atmospheric nitrogen deposition from power plants and/or car exhausts, increased UV-B radiation from ozone reductions, and changes in land-use patterns are likely to cause large changes in the integrity and sustainability of ecosystems in the southwestern US. Inherent low resource availability and species diversity of these ecosystems (Verstraete and Schwartz 1991) make them especially susceptible to even small changes in critical ecosystem processes that determine species composition and primary productivity. However, large changes in nitrogen and carbon dynamics may occur because components of biological crusts may be very sensitive to these global changes (Garcia-Pichel and Bebout 1996; Beymer and Klopatek 1991; Evans and Belnap 1999).

Arid ecosystems may be more severely impacted by increased atmospheric nitrogen deposition than more mesic ecosystems. Historic rates of nitrogen input and overall nitrogen availability are low so even small changes in rates of deposition represent a significant change in the nitrogen cycle. Nitrogen derived via long-distance pollution transport from major urban regions and from power plants may contribute significant amounts of N to ecosystems still recovering from more than a century of grazing impacts. Nitrogen deposition could in part offset the reduced N inputs resulting from plant invasion and previously-impacted or recovering cryptobiotic crusts; alternatively anthropogenic N deposition may aggravate N loss through increased ammonia volatilization and denitrification.

RECOVERY FROM DISTURBANCE

Natural Recovery Rates

The recovery of biological crusts and vascular plants appear to occur in concert, rather than as individual "steps" in the recovery process (Danin and others 1989; Johansen and others 1993; Kaltenecker 1997). The biological crust stabilizes the soil surface and increases nutrient availability to enhance reestablishment vascular plants (Belnap and Harper 1995; Williams and others 1995). Vascular plants also protect the soil surface. In addition they provide shading and curb wind speed at the surface, providing conditions conducive to development of the biological crust (Danin and others 1989). As the community develops, the shaded areas under plant canopies and open interspaces between plants allow diversification in the crust. Microsites created by the uneven topography of the crust serve as safe sites for vascular plant seeds.

Species composition-Recovery rates of biological soil crusts depend on the type and extent of disturbance, the availability of nearby inoculation material, as well as on the temperature and moisture regimes that follow disturbance events. Recovery time is faster when crustal material is not removed, as pieces of remaining organisms remain to re-inoculate recovering surfaces. Therefore, although most damage is done with the initial impact, recovery will be faster if disturbances are not repeated. Timing of the disturbance is also important. Damage is less severe when crusts are wet. In addition, if damage occurs when rain is imminent, then crustal organisms have opportunity to reattach themselves before being blown away or buried. However, if disturbances occur before a long dry period, reattachment is not possible and much crustal material may be lost or too deeply buried for recovery. Size of disturbance can be important, especially if crustal material has been lost from the disturbed site. As inoculant must come from adjoining areas, the size of the perimeter area relative to the internal surface area of the disturbance can heavily influence recovery rates. In addition, recovery is slower if soils in adjacent areas are destabilized. Sediments from these areas can either bury adjacent crusts, leading to their death, or provide material for "sandblasting" nearby surfaces, thus increasing wind erosion rates and slowing recovery (Belnap 1995; McKenna-Neumann and others 1996).

Cyanobacteria or green algae recover first. *Microcoleus* is generally the first species to appear. Cyanobacteria are mobile, and can often move up through disturbed sediments to reach needed light levels for photosynthesis, while slow-growing lichens and mosses are incapable of such movement. Instead, they require stable soil surfaces for growth, and colonization of these components generally takes place after surfaces have been stabilized by cyanobacteria. *Collema,* a nitrogen-fixing lichen, is generally the first lichen to appear.

Cyanobacterial and green algal communities can recover quickly, especially in regions where effective precipitation is relatively high. As these organisms are metabolically active only when wet, the recovery process is more rapid in regions where soil surface moisture lasts for a relatively longer period of time. For instance, green algal communities recovered within two years of a summer wildfire in the lower Columbia Basin (Johansen and others 1993). This relatively rapid recovery is credited to cooler, wetter conditions relative to the more southerly locations. This includes areas that receive a majority of annual precipitation as cool-season moisture. Other influential factors might include mild temperatures, with the majority of moisture occurring as rain rather than snowfall. Sites with fine-textured soils such as silt loams retain surface-soil moisture for a longer period than do coarse-textured, sandy or gravelly soils.

Estimates of time for visually-assessed recovery have varied from 5 to 100 years (Anderson and others 1982b; Jeffries and Klopatek 1987; Callison and others 1985; Cole 1990). However, Belnap (1993) showed that many components of recovery can not be assessed visually. Assuming linear recovery rates, recovery was estimated to be 35-65 years for cyanobacterial biomass, 45-85 years for lichen cover, and 250 years for moss cover in scalped 0.25 m^2 plots surrounded by well-developed crusts. Since recovery time is dependent on presence of nearby inoculant, larger disturbed areas will take longer to recover. Several studies have demonstrated that inoculation can hasten recovery (Tidemann and others 1980; Ashley and Rushforth 1984; Belnap 1993).

Nitrogen-fixation-On the Colorado Plateau, recovery of nitrogenase activity levels in experimentally-disturbed areas is slow. In areas where crusts were removed, no nitrogenase activity was detectable after 9 years. N content of soils was much lower when compared to adjacent control plots. In areas disturbed with 4 wheel drives, no recovery could be documented after 2 years (Belnap 1996). Thirty years after release from grazing, soil and plant N and nitrogenase activity levels were found to be significantly lower when compared to an area that was never grazed (Evans and Belnap 1999). Similar results were found for disturbances in the Mojave desert. Analysis oj recovery rates for dated disturbances show 2000 years may be required to restore N inputs at old tank tracks and old ghost towns. Recovery of nitrogenase activity in experimentally-disturbed areas in the Great Basin and southern New Mexico show much faster recovery trajectories of 20-30 years (Belnap and Herrick unpublished data).

Albedo-Restoration of normal surface albedos and temperatures will depend on the restoration of cyanobacteria, lichens and mosses. While cyanobacteria form a dark matrix in which other components are embedded, dark mosses and lichens contribute up to 40% of the cover in an undisturbed crust (Belnap 1993). Consequently, recovery of surface albedos will depend on climate and soils.

Fire-Time required for post-fire recovery of the biological crust depends on a number of factors, including the size and intensity of the fire, the composition of the crust (i.e., which types of organisms are dominant), general climate of the area and weather immediately following the fire, soil characteristics, pre-fire condition of the biological crust and plant community, and post-fire disturbances (Belnap 1993; Johansen and others 1993). Small or low intensity fires result in a mosaic of burned and unburned vegetation, thereby providing vascular plant and biological crust propagules to colonize the burned areas. Mosses dominate biological crusts in the northern Great Basin within two to five years following fire if the community is not converted to annual grasses (J. Kaltenecker, unpublished data). Although the lichens that codominate are slow-growing and may take several decades to reach pre-fire cover values, considerable diversity is apparent within about one decade. Recovery may be enhanced in areas that burn late in the dry season, as opposed to early-season fires. Historically, fires occurred in late summer when the native bunchgrasses were dry enough to burn. Consequently, the period of time between burning and cooler, moister weather during which resprouting of vascular vegetation and growth of the biological crust occur was probably less than two months long. Since invasion of exotic annual grasses, fire seasons have increased in length by one to two months. The longer interim before conditions conducive to regeneration increases the vulnerability of the soil surface to destructive impacts: trampling or crushing by humans, livestock, or vehicles and the erosive forces of wind or brief, high intensity summer rain storms.

Enhanced Recovery Rates

The use of inoculants to speed up recovery of crusts works well (St. Clair and others 1986; Lewin 1977; Tidemann and others 1980; Ashley and Rushforth 1984). In an experiment reported from SE Utah, all measured responses were significantly enhanced by inoculation (Belnap 1993, 1995, 1996).

EVOLUTIONARY HISTORY OF DISTURBANCE

Soil and plant characteristics of low and mid-elevation Colorado Plateau ecosystems suggests that they probably evolved with low levels of soil surface disturbance by ungulates. These characteristics include limited surface water, sparse vegetation, the presence of biological soil crust which are easily disrupted by trampling, and the dependence of these ecosystems on nitrogen provided by the biological soil crusts (Evans and Ehleringer 1993; Evans and Belnap 1999). Dung beetles, present globally in other systems with large ungulate populations, are lacking (Mack and Thompson 1982). Limited surface water would have kept ungulate populations small and generally limited to winter use of lower elevations, as is seen today (Parmeter and Van Devender 1995). Winter use results in lower impacts to biological crust (Marble and Harper 1989) as soils are wet or soon to be wet. Dominant bunchgrasses that lack adaptations to grazing such as tillering, secondary compounds, or high tissue silica content (Mack and Thompson 1982; Martin 1975; Stebbins 1981). In addition, shallow soils and limited precipitation limits the distribution of burrowing vertebrate and invertebrate species. Thus, these systems may depend more heavily on soil surface integrity for natural ecosystem functioning than other regions. As a result, these deserts may be more negatively affected by soil surface disturbances than deserts that evolved with higher levels of surface disturbance.

CONCLUSION

Unfortunately, many activities of man are incompatible with the presence and well-being of biological soil crusts. The cyanobacterial fibers that confer such tensile strength to these crusts are no match for the compressional stresses placed on them by increased anthropogenic activities. Crushed crusts contribute less nitrogen and organic matter to the ecosystem. Impacted soils are left highly susceptible to both wind and water erosion. Raindrop erosion is increased, and overland water flows carry detached material away.

Soil erosion in arid lands is a major threat worldwide. Beasley and others (1984) estimated that in rangeland of the United States alone, 3.6 million ha has some degree of accelerated wind erosion. Relatively undisturbed biological soil crusts can contribute a great deal of stability to otherwise highly erodible soils. Unlike vascular plant cover, crustal cover is not reduced in drought, and unlike rain crusts, these organic crusts are present year-round. Consequently, they offer stability over time and in adverse conditions that is often lacking in other soil surface protectors. Unfortunately, disturbed crusts now cover vast areas in the western United States as a result of ever-increasing recreational and commercial uses of these semi-arid and arid areas. Therefore, the tremendous land area currently being impacted may lead to significant increases in regional and global soil erosion rates.

QUESTIONS FROM THE SYMPOSIUM FLOOR

Q: Are herds of wild horses, donkeys, and burros compatible with the stability of semi-arid landscapes?

A: This depends on population numbers, densities, timing of use, and intensity of use of both native and introduced large mammals. Before the advent of wells, irrigation and other water developments, availability of free surface water, along with predators and forage availability, naturally limited large mammal populations, as well as season of use in dry areas. We have disrupted these natural limitations through water development, predator control, conversion of grasslands to shrublands, irrigation and other activities. Coinsequently, soil surfaces in arid and semi-arid systems are, in general, receiving much greater use than they have in the past. Increased densities and year-round use will compromise the stability of these surfaces.

Q: Our current situation is millions of acres where crusts have been disturbed by past 100-150 years of land use. Society still demands products and land use. Is it possible to restore crusts on a large scale and still meet societies demands for land use?

A: It is possible to restore crusts on a large scale. However, it is also important to realize that there are many areas that have excellent crust development, and conservation is much easier and cheaper than restoration. Land use does not have to be incompatible with healthy crusts. It is more an issue of social values, and we need to reassess what values are most important to us as a society.

Q: When saying "disturbance" was/is there any distinction in levels/intensities? i.e. any vs. high disturbance; truck track spinning tires vs. motorcycle or bicycle tires, etc.

A: Most damage occurs with the first disturbance. Repeated disturbance will increase compaction, which has other consequences for hydrologic cycles, soil food webs, and vascular plants. Continous disturbance, such as wheeled vehicles produce, are more problematic than discrete disturbances, such as footprints, if water is channeled along the disturbance.

Q: So why did the cheatgrass establish in Virginia Park with the optimal crust conditions present?

A: Cheatgrass requires humidity to germinate. In this dry, arid region, humidity is achieved by very minimal burial by soil or organic matter, which does not generally happen in a heavily crusted, native bunch grassland, where soils are stabilized and surface litter is minimal. However, rainfall in the fall of 1994 was very unusual here. Instead of our normal rainfall pattern, it rained almost daily for several weeks, and was very cloudy and cool. We speculate that the increased humidity allowed the cheatgrass to germinate. Through experimentation, we have replicated this in the lab.

Q: On radical disturbances - what can we do to enhance crust colonization?

A: Inoculation works really well on all disturbances. The downside is that you need to disturb other crusts to obtain material. We try to stay in touch with proposed construction projects and get there before the bulldozers to salvage crusts.

Q: Will colonization occur mostly through wind blown spores or some other mode?

A: Cyanobacteria colonize mostly through wind-blown material. Lichens and mosses vary with species, but my observations are that reproduction is mostly vegetative, when pieces from adjoining areas break off and roll in.

Q: Can we artificially transport - transplant? Please refer to Jane's ecology cookbook.

A: Yes. It is simple. You can scalp off the top 2 mm of soil. If collected when dry and kept dry, crustal organisms will stay alive for years.

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THE ROLE OF SOIL ORGANISMS IN RESTORATION

Michael P. Amaranthus[1], Efren Cazares[2] and David A. Perry[3]

ABSTRACT

The soil biological community is inevitably impacted on degraded sites, and much remains to be learned about these impacts. This myriad of soil organisms and their interactions profoundly affect forest restoration through capture and uptake of nutrients, nitrogen fixation, protection against pathogens, maintenance of soil structure, and buffering against moisture stress. The best approach for managers is prevent degradation of the soil biological community. The vast majority of soil organisms live and work in rhizospheres, humus, rotten wood, and the upper mineral soil which are powerhouses of soil biological activity and thus are essential substrates for maintaining site resilience. Although there is no "magic bullet" for enhancing restoration, there is great opportunity to use soil organisms as "tools." Research is now underway to identify organisms best adapted to specific environmental and biotic conditions and to assess the potential for "managing" these organisms. Incorporating the concept of the "living soil" in evaluation of site restoration is part of a new, expanding view of forest ecosystems. Understanding soil organisms and putting them to wise use, practicing foresters can better not only maintain populations of beneficial organisms on site but also achieve restoration success.

Keywords: soil restoration, soil organisms, ectomycorrhizae, disturbance, reforestation

INTRODUCTION

In widely varying ecosystems throughout the world, removal of indigenous vegetation through clearcutting, mining, urbanization, shifting cultivation, or overgrazing has led to deterioration in productive capacity, often accompanied by alterations of plant communities that appear permanent. Degradation is well documented in moist tropical forests (Arnason and others 1982), in the semiarid Miombo woodlands of southern Africa (Maghembe 1987, personal communication), in the montane coniferous forests of northern India (Sharma 1983), and in montane forests of North America (Amaranthus and Perry 1987, 1989). Despite widely varying community types and environmental conditions, the loss of soil organisms has been linked to the decline of these ecosystems.(Perry and others 1989). Reestablishing beneficial soil organisms has facilitated restoration of some sites, and is likely to aid restoration of others as well. The soil biological community is inevitably impacted on degraded sites, and much remains to be learned about these impacts. Which organisms are important to site recovery following disturbance? How do management activities affect these populations? What are the rates of recovery? Can these organisms be "reinoculated" to improve restoration success? Answers to these important questions have come slowly, deterred by difficulty in identifying organisms, enormous variability within and among sites, and unresolved methodologies (Trappe and Bollen 1979). However, our growing knowledge of the workings of this complex belowground forest system has already enabled us to better predict the consequences of our actions.

In this paper we (1) briefly review the variety, abundance, and interactions of organisms in forest soils, (2) examine the important functions of these organisms in the context of restoration (3) consider the factors that adversely affect populations of beneficial organisms-and thereby restoration-on managed forest lands, and (4) look at the potential for managing soil organisms to enhance restoration activities.

VARIETY, ABUNDANCE, AND INTERACTIONS OF SOIL ORGANISMS

The life forms residing and interacting in forest soil range from the smallest, most primitive living organisms all the way up the evolutionary ladder to mammals. Estimates of the types and numbers of these organisms, which vary in function and are strongly interdependent, are staggering. For example, 10-100 million bacteria and actinomycetes, 1000-100,000 fungal propagules, and several kilometers of

[1] Michael P. Amaranthus is a research biologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Box 440, Grants Pass, OR 97526.

[2] Efren Cazares is a research associate, Department of Forest Science, Oregon State University, Corvallis, OR 97331.

[3] David A. Perry is a professor, Department of Forest Science, Oregon State University, Corvallis, OR 97331.

fungal hyphae can be present in a single gram of forest soil (Bollen 1974). Mites and nematodes can number from thousands to hundreds of thousands per square meter of surface soil, and larger soil organisms such as worms, insects, and animals from 10 to well over 100 (Dindal 1973). The resulting biomass reflected in these numbers is immense. For example, in the Pacific Northwest, the soil of an old-growth Douglas-fir *[Pseudotsuga menziesii* (Mirb.) Franco] stand can contain some 4,200 kg/ha (3700 lb/acre) dry weight of fungal mycelium and 5,400 kg/ha (4800 lb/acre) of mycorrhizal tips alone (Fogel and Hunt 1983).

The balance of forest-soil organisms can shift dramatically in response to fluctuations of chemical, environmental, and biotic factors caused by natural disturbance or management-related activities such as timber harvest, site preparation, mining, overgrazing, land clearing and fertilization (Perry and Rose 1983, Amaranthus and Perry 1987). Although some soil organisms thrive in the aftermath of disturbance (Pilz and Perry 1984), those that cannot compete may decline, lose vigor, or disappear altogether (Perry and others 1982, Harvey and others 1986, Amaranthus and Perry 1987). The final equilibrium of soil organisms may or may not facilitate rapid revegetation of the site.

To assess the potential impact of disturbance, we must understand where the vast majority of soil organisms live and work. Humus, rotten wood, and the upper mineral soil are the powerhouses of soil biological activity (Harvey and others 1979, 1986) and thus are essential substrates for maintaining forest productivity. Densities of fine roots in these substrates and populations of organisms near these root surfaces are higher than in surrounding soil (Rambelli 1973). It is in the rhizosphere, the 2-3 mm zone surrounding root surfaces, that biological activity is greatest. Fine roots maneuvering through the soil exude carbohydrates, amino acids, and other compounds that stimulate the growth of microflora such as bacteria, actinomycetes, and fungi, which in turn produce their own compounds that either stimulate or repel other soil organisms. Microflora are also prime food for "grazer" herbivores such as mites, nematodes, and springtails, which themselves fall prey to carnivores such as centipedes and spiders. Saprophytic organisms feed on the dead remains of other microbes and roots accumulating in the rhizosphere and decompose complex organic molecules into basic components. Nutrients released through decomposition, as well as water, are captured and transported to host plants by specialized fungi that colonize root tips in a symbiotic association termed mycorrhizae (Harley and Smith 1983, Read and others 1985). The area immediately surrounding mycorrhizae, the "mycorrhizosphere" (Rambelli 1973), supports its own increased levels of microbial activity. Rhizosphere and mycorrhizosphere populations may vary among plant species and are further influenced by season and host maturity (Foster and Marks 1967).

Litter and woody materials are also important centers of activity. Plant tissue fallen to the forest floor is attacked by soil organisms called "detritivores". These organisms, including mites, millipedes, snails, and beetles, tear and chew holes in fresh litter, increasing its surface area and utilizing its more soluble components. The remnants are decomposed by other soil flora and fauna. Wood fallen to the forest floor is attacked by beetles and a succession of fungi that "digest" the cellulose and lignin. Insects, earthworms, amphibians, reptiles, and mammals likewise concentrate in and around this woody debris, enhancing site productivity by mixing and aerating the soil and by transporting and excreting nutrients and the spores of mycorrhizal fungi from one microsite to another (Maser and others 1978).

Woody debris is a dynamic component of the forest soil. It provides a storehouse of moisture and is an energy source and refuge for microorganisms critical to forest restoration. A significantly higher proportion of mycorrhiza activity occurs in decaying wood compared to soils (Harvey and others 1979). The relative importance of woody debris in supporting feeder roots may be greater on dry sites than on moist sites. During periods of adequate moisture, humus supports the highest level of ectomycorrhiza activity; but during periods of drought, soil wood becomes the most active site (Harvey and others 1986). Thus, the wood component appears most important on low-productivity sites where moisture is limited or where indigenous levels of woody debris are low. Wood on the forest floor forms long-lasting, moist microsites that may aid forest recovery. Following intense wildfire in southwest Oregon, decaying logs retained 25 times more moisture than surrounding soil (Amaranthus and others 1989). Such decaying logs may expedite forest recovery by providing important refuge for roots and associated mycorrhizal fungi of pioneering vegetation. However, accumulated woody debris, if overly abundant, represents a fuel hazard and increases the potential for wildfire. So there can be too much as well as too little woody debris. A balance must be struck between fuel management guidelines and protection of large woody debris if forest productivity is to be maintained.

An appreciation of the importance of the plant-soil relationship can be acquired from looking at the amount of energy plants divert to soils. In temperate forests, from 50 to 80% of the net carbon fixed in photosynthesis goes to roots and associated organisms such as mycorrhizal fungi (Fogel and Hunt 1983, Perry and others 1987). Energy flowing into the soil supports a diverse community of soil organisms which in turn influence plant growth through effects on nutrient cycling, water uptake, pathogens, and soil structure.

Energy flowing to soil organisms may have a specific cost/return for participating host plants. This is likely to vary in time and space and with changes in the physical and biotic environment. Different organisms do different jobs for different hosts in different environments. Some organisms, like mycorrhizal fungi and nitrogen fixers, benefit host plants in clearly definable ways. Others may benefit hosts only during periods of environmental extremes, at certain points in plant development, following disturbance, or indirectly by influencing important ecosystem properties such as soil structure. Maintaining native populations of soil organisms helps minimize site degradation by assuring a diversity of plant responses to unpredictable or varying environments.

IMPORTANT FUNCTIONS OF SOIL ORGANISMS

Nutrient Cycling

Most woody host plants require soil organisms to facilitate adequate nutrient uptake. Mycorrhizae enhance such uptake not only by increasing the absorbing surface area of roots but also through active physiological mechanisms. Ectomycorrhizal fungi release enzymes which increase the availability of phosphorus to higher plants (Williamson and Alexander 1975, Ho and Zak 1979, Alexander and Hardy 1981). This "extraction" process also extends to other nutrients and enters them into the forest nutrient cycle. Mycorrhizal fungi, common to members of the Pinaceae, release compounds (chelating agents called siderophores) that are especially important in iron nutrition (Graustein and others 1977, Powell and others 1980). Perry and others (1982) found lower levels of siderophores in soils from both burned and unburned clearcuts than in undisturbed forest soil from 8 of 10 widely scattered sites in southwest, central, and east-central Oregon; the reduction in siderophores was related to poor iron nutrition of Douglas-fir seedlings. See Allen (1991) for a general overview on the ecology of mycorrhizae.

Conservation of nutrient capital is necessary to prevent site degradation. Few nutrients leach out when populations of soil organisms are healthy and active. This is particularly significant for soluble forms of nitrogen (N) such as nitrate, which is mobile and susceptible to leaching. Soil organisms form an intricate web to capture and assimilate N into complex organic compounds and then slowly release them into the ecosystem. This capture, assimilation, and release are critical to the nitrogen capital of forest soils.

Nitrogen Fixation

Inadequate nitrogen is a common limitation on degraded sites. Loss of N due to timber harvest, removing harvest residues, and site preparation (especially intense burning) often exceeds natural inputs to the forest (Perry and Rose 1987). Perhaps the most practical and economical means of replenishing this loss is through biological fixation of nitrogen in the soil (Domingo 1983, Gordon and Avery 1985).

Symbiotic N fixation can add substantial amounts of nitrogen continuously to Pacific Northwest forests (Wollum and Youngberg 1964, Trappe and others 1968). Common nodulated plants such as lupine, alder, and snowbrush *(Lupinus, A/nus,* and *Ceanothus* species) form a mutually beneficial relationship with certain bacteria and actinomycetes that convert ("fix") atmospheric N_2 into ammonium N. This fixed nitrogen is released into the roots of host plants, thereby increasing N concentrations in living tissue (Tarrant and Trappe 1971). As N is returned to the soil by litterfall and washing of leaves by rain, other species—including tree species valued for timber-reap benefits.

Through asymbiotic N fixation, "free-living" organisms contribute to the nitrogen pool. Nitrogen-fixing bacteria have been found in association with wood-rotting fungi in coniferous forest residues (Larsen and others 1980). *Azotobacter* and *Clostridium* species fix nitrogen under conditions characteristic of the rhizosphere, where oxygen levels are low (Giller and Day 1985). Fixation by these and other species, such as the bacterium *Azospirillum,* may be enhanced by or may totally depend on mycorrhizal fungi (Amaranthus and others 1990). Use of these free-living organisms to improve nitrogen levels is now receiving considerable attention and deserves further research.

Protection Against Pathogens

Both symbiotic and free-living soil organisms can protect trees against soil pathogens. Several mycorrhizal fungi protect pine *(Pinus)* species and Douglas-fir from pathogens such as *Phytophthora cinnamomi, Fusarium oxysporum,* and *Rhizoctonia solani* (Wingfield 1968, Marx 1973, Marx and Krupa 1978). The protective mechanisms include physical barriers against root penetration by pathogens, excretions of antibiotics, and stimulation of other pathogen-inhibiting rhizosphere organisms (Zak 1964, Marx 1972). Rose and others (1980) found that a free-living *Streptomyces* species from the rhizosphere of snowbrush *(Ceanothus velutinus* Dougl.) antagonized three common root pathogens, *Phellinus weirii, Fomes annosus,* and *Phytophthora cinnamomi.* Some nonmycorrhizal fungi also may inhibit pathogens; for example, the fungus species *Trichoderma* can reduce the incidence of root rot in pine seedlings (Kelly 1976).

Soil Structure

Soil structure often declines on degraded sites (Borchers and Perry 1992). Mycorrhizae and other microbes affect soil structure by producing humic compounds (Tan and others 1978), accelerating the decomposition of primary minerals (Cromack and others 1979), and secreting organic "glues" (extracellular polysaccharides) that bind soil particles into water-stable aggregates (Sutton and Sheppard 1976, Forster 1979, Tisdall and Oades 1979, 1982). The importance of the first two processes to soil fertility and plant nutrition is well documented. The third-aggregate stability—also is important because the stability of pores, essential for the movement of water and air required by plant roots and soil organisms, is predicated on the stability of aggregates formed when mineral grains and homogeneous clays are linked by organic glues (Lynch and Bragg 1985, Emerson and others 1986). When the flow of organic materials is interrupted, soil aggregation-and ultimately forest sites are degraded.

Examination of aggregates from granitic soils on a high-elevation site in the Klamath Mountains of southwest Oregon illustrates this decline. This site, logged in 1968, has not become reforested despite several attempts (Amaranthus and Perry 1987). Now dominated by grasses and herbs, it supports different microflora than found associated with conifers. Scanning electron micrographs show that soil structure in the clearcut and adjacent, undisturbed forest differs drastically: an abundance of relatively large (>50 microns) pores and fungal hyphae in the forest soil contrast with a scarcity of large pores and fungal hyphae in the clearcut soil. Degradation of soil structure in clearcuts is likely to make reforestation difficult, especially on potentially droughty sites. More research is needed on how best to stabilize and maintain soil structure after harvest.

Soil Moisture

Some soil organisms, especially mycorrhizal fungi, seem to benefit associated plants when soil moisture is limited (Mikola 1970). Mycorrhizae are important in water uptake, storage, and transport (Reid 1979). Mycorrhizal fungi substantially increase the surface absorbing area of colonized roots, directly increasing the total soil volume roots can explore for water. They also prevent gaps between roots and soil, preserving "liquid continuity" during drier periods. Differentiated "vessel hyphae" can act as specialized channels for water transport to the host plant (Read and others 1985).

FACTORS ADVERSELY AFFECTING POPULATIONS OF BENEFICIAL ORGANISMS

What reduces populations of beneficial organisms on disturbed forest land? How do reduced populations affect forest revegetation? Under what conditions are forest sites most likely to be impaired? Final answers are as yet unknown, but recent studies provide sufficient evidence for reasonable speculation.

Much of the research on reductions in populations of beneficial organisms after disturbance has focused on ectomycorrhizae. Although information on other organisms is scanty in the Pacific Northwest, mycorrhizal fungus populations may serve as indicators of the health and vigor of other associated beneficial organisms. Mycorrhizae provide a biological substrate for other microbial processes. For example, in a Douglas-fir system, mycorrhizae provided 50% of the annual biomass returned to the soil and 42% of the annual nitrogen release (Fogel and Hunt 1983). Microbial activity generally is stimulated in soil surrounding ectomycorrhizae (Oswald and Ferchau 1963, Rambelli 1973)-an effect that likely extends along the vast expanse of ectomycorrhizal fungal mycelia in the soil. Numerous authors have reported reductions in mycorrhiza populations due to forest disturbance (Harvey and others 1980, Parke 1982, Perry and others 1982, Amaranthus and others 1987). However, the degree of reduction and its impact on forest restoration vary widely and depend on many factors.

Type and Severity of Disturbance

The most widespread activities which alter both the aboveground and belowground environments and which therefore potentially impact populations of soil organisms are timber harvest and site preparation. In the Pacific Northwest, clearcutting and prescribed burning are the common harvesting and site-preparation practices. Soil nutrient status, moisture, temperature, pH, and organic matter content, litter inputs, and species composition affect the growth and occurrence of soil organisms (Harvey and others 1980)--and all of these are influenced by harvesting and site preparation. Clearing vegetation and disturbing the forest floor remove nutrients and reallocate them within the ecosystem. Harvesting host trees eliminates the photosynthate source for dependent ectomycorrhizal fungi and associated microbes. Converting a mature forest to a clearcut typically increases soil temperatures once the protective canopy is gone. Prescribed broadcast burning increases soil pH, creates a nutrient flush, and can reduce litter and duff levels (Amaranthus and McNabb 1984). Soil organic matter, humified material, and decaying wood are centers of microbial activity and can substantially diminish as a result of intense fire. Changes in aboveground community composition alter the form of root exudates and litter leachates.

Wright and Tarrant (1958) found fewer ectomycorrhizae on Douglas-fir seedlings growing in burned, compared to unburned, clearcuts. The greatest reductions were associated with the hottest burns. Thus, not only the type of activity, but its severity, is critical. Parke (1982) compared mycorrhiza formation in soils from burned and unburned clearcuts of 36 "difficult to regenerate" sites in northwest California and southwest Oregon. Douglas-fir and ponderosa pine *(P/'nus ponderosa* Laws.) seedlings grown in soils from the burned clearcuts formed 40% fewer ectomycorrhizae, and seedlings grown in soils from the unburned clearcuts 20% fewer ectomycorrhizae, than seedlings grown in undisturbed forest soil. Yet it is difficult to generalize about effects of burning on microbial populations because they are highly dependent on duration and intensity of fire as well as soil and site conditions (Perry and Rose 1983).

Because ectomycorrhizae predominate in the organic layers of the soil (Trappe and Fogel 1977, Harvey and others 1979), the degree of organic matter lost from a site can influence mycorrhiza populations. Harvey and others (1979) found more than 87% of the active ectomycorrhizal fungus types in humus and decaying wood in a mature Douglas-fir/larch *(Larix)* forest. Moreover, the physical consumption of humidified material affects not only ectomycorrhizae but an array of other beneficial organisms tied to site restoration. Habitat for small mammals that are important in distributing fungal spores of several belowground mycorrhizal fungi (Maser and others 1978) also can be lost. Thus, numbers, diversity, and activity of beneficial soil organisms can be reduced by repeated removal of organic matter from a site.

Minimizing soil compaction helps maintain healthy populations of soil organisms by preserving soil structure (Amaranthus and others 1996). Pore space is essential for the movement of oxygen and water into soil and the flushing of carbon dioxide out of it; microbial activity is drastically altered when levels of these basic elements become extreme. Undisturbed forest soil is rarely saturated because large pores allow for rapid downward percolation of water. However, when soils are compacted, large pores are destroyed and water movement through soil is reduced. Soil compaction greatly influences the types and activities of soil organisms sensitive to excess soil moisture. Thus, the adverse response of plants to compaction reflects both indirect effects on microbes and direct effects on the plants themselves. Careful selection and skillful implementation of harvest methods to minimize compaction increase the potential for maintenance of beneficial soil organisms.

Topsoil is a reservoir of both nutrients and fungal spores and other propagules important for mycorrhiza formation. Loss of this biological reservoir by erosion will inevitably impair restoration. Reeves and others (1979) found that the dominant species in a sagebrush *{Artemisia)* community in Colorado all were mycorrhizal. When topsoil was severely disturbed and eroded, numbers of mycorrhizal propagules were greatly decreased (Moorman and Reeves 1979), and nonmycorrhizal weedy species could successfully reestablish. Little is known about the effects of soil erosion from deforested areas, but the density and diversity of mycorrhizal inocula are reduced.

Climatic Conditions

Climate influences seedling growth and ectomycorrhiza formation (Harvey and others 1980, Pilz and Perry 1984). The importance of early mycorrhiza formation in dry areas has been emphasized (Parry 1953, Mikola 1970). Dry climates may limit the activity of mycorrhizal fungi by decreasing the length of time for spore production, germination, and optimal mycelial growth, which in turn can decrease the chances for planted seedlings to become colonized. Seedlings in moist climates may be able to survive longer without mycorrhizae than those in dry climates, increasing their chances of becoming colonized. Fungal symbionts differ in their capacity to function in periods of either low or "excessive" soil moisture, and impaired function will subsequently affect growth of associated plants (Mexal and Reid 1973, Slankis 1974, Theodorou 1978). Moisture content also affects uptake of certain nutrients by mycorrhizae (Gadgil 1972).

Seedlings growing in cold climates may also require rapid, early mycorrhizal colonization to take advantage of the short growing season and obtain the necessary nutrients and water to survive the long cold season and early frosts. In studies in the Klamath Mountains of northwest California and southwest Oregon, Amaranthus and Perry (1987) found that mycorrhiza formation most strongly influences seedling survival and growth on sites limited by both moisture and temperature.

Biotic Conditions

What factors influence a seedling's potential to form mycorrhizae on disturbed forest sites? Numerous factors directly and indirectly influence the potential for mycorrhiza formation, including seedling physiology, environmental conditions, and abundance of soil microorganisms and propagules (Perry and others 1987). Modification of these conditions may influence a seedling's ability to form mycorrhizae. Mycorrhizal potential following disturbance such as clearcutting and slashburning depends primarily upon (1) the balance between mortality and input of mycorrhiza-forming propagules (such as spores and hyphae of mycorrhizal fungi); (2) the recovery of host plants, which provides the energy to stabilize populations of mycorrhizal fungi and allows them to grow and colonize nonmycorrhizal roots of surrounding plants; and (3) the diversity of fungus species, which buffers the mycorrhizal community against environmental changes following disturbance.

Much remains to be learned about the importance of aboveground species composition and arrangement to belowground biological functioning. It is increasingly apparent, however, that an ectomycorrhizal fungus can link some plant species with fungal mycelia (Bjorkman 1970, Read and others 1985, Finlay and Read 1986). In the natural forest environment, ectomycorrhizal fungi supported by nonconiferous hosts can actively colonize conifer seedlings. Root-chamber analysis of the development of ectomycorrhizal mycelium has shown that expanding hyphal fans not only act as nutrient-absorbing structures but also colonize nonmycorrhizal feeder roots in host-plant combinations within and among species. Using radioactive labeling, Finlay and Read (1986) have demonstrated the free movement of carbon among plants connected by mycorrhizal mycelia. Clearly, the existence of "pipelines" for distributing materials among plant species has important implications for forest regeneration.

Little is known of the persistence and distribution of ectomycorrhizae in the absence of living hosts. It has been suggested (Hacskaylo 1973) that ectomycorrhizal fungi do not persist long in the absence of host-supplied substrates. In the Klamath Mountains of northwest California and southwest Oregon, sites that have been logged and burned are often rapidly invaded by woody shrubs (Gratkowski 1961). Many of these shrubs, members of the Ericaceae and Fagaceae, form mycorrhizae with many of the same fungi as do members of the Pinaceae (Molina and Trappe 1982). This mechanism of natural redundancy preserves mycorrhiza diversity during periods of rapidly changing community structure.

Amaranthus and Perry (1989) transferred small amounts of soil from a Pacific madrone *{Arbutus menziesii* Pursh) stand to planting holes at three locales-a site cleared of whiteleaf manzanita *(Arctostaphylos viscida* Parry), a meadow cleared of annual grasses, and under Oregon white oak *(Quercus garryana* Hook) —on which Douglas-fir seedlings were grown. In the first year, they found more rapid mycorrhizal colonization of Douglas-fir feeder roots, and dramatically improved seedling survival and growth, on the site cleared of manzanita than in the meadow under similar soil, moisture, and temperature conditions. In the second year, Douglas-fir seedling performance continued to increase dramatically on the site cleared of manzanita compared to the other two locales. Rapid mycorrhiza formation, especially on sites that are difficult to regenerate, increases the chances that succeeding species will become established.

Some woody shrub species may act as reservoirs not only of mycorrhizal fungi but of other microflora as well. Significantly higher rates of nitrogen fixation-and increased seedling survival and growth-were found in association with the roots of Douglas-fir seedlings in a stand cleared of whiteleaf manzanita than in a meadow cleared of annual grass (Amaranthus and others 1987). *Azospirillum,* an N_2-fixing bacterium, was isolated within the mycorrhizae of Douglas-fir at the manzanita site. Whiteleaf manzanita occupies particularly hot, dry sites where fire is frequent. Because high N losses can accompany intense fire, natural mechanisms by which N is returned to the soil are important to site restoration. Quite likely, the N fixed and gradually accumulated in association with mycorrhizae is biologically important for individual conifers over their long life.

We suggest that conifers and some woody shrubs form successional guilds, in which the rapidly sprouting pioneer members of the guild maintain the guild's shared soil microflora, forming a biological time bridge between old and new conifer stands. In the long run, maintaining diversity of soil microflora by pioneering shrubs may optimize conifer performance during the varied conditions likely over a rotation.

Effect of Mycorrhizal Hosts Shifts Over Time

Many grass species and shrub species such as *Ceanothus* and *Rubus* (e.g., blackberry, salmonberry) form vesicular-arbuscular mycorrhizae (VAM) (Rose and Youngberg 1981, Trappe unpublished data). On sites long dominated by VAM species, space availability and the ectomycorrhizal fungi needed by members of the Pinaceae may gradually disappear, and the soil microbial complex associated with ectomycorrhizae will shrivel. Occurrence of VAM in some members of the Pinaceae has been reported, however, the ecological significance remains undetermined (Ccizares and Trappe 1993, Ccizares and Smith 1996). Invasion of sites by nonectomycorrhizal plants over years can seriously affect reforestation (Amaranthus and Perry 1987) and yield, particularly in the case of ectomycorrhizal tree species growing on difficult sites where seedlings must establish ectomycorrhizae early to survive. Changes in soil microflora associated with nonhost species could affect patterns of decomposition; nutrient and water retention, availability, and uptake; and the balance between pathogens and pathogen-inhibiting organisms.

How long soils retain their mycorrhizal colonization potential in the absence of living hosts is unknown. Ectomycorrhizal spores and hyphal fragments have remained metabolically active after 2 years in Scandinavian forests, though the number of active fragments dropped dramatically over that period (Persson 1982, Ferrier and Alexander 1985). In the Pacific Northwest, mycorrhiza formation generally decreases as the length of time between disturbance and reforestation increases (Pilz and Perry 1984, Perry and others 1987).

POTENTIAL FOR MANAGING SOIL ORGANISMS ON DEGRADED SITES

Survival and growth of tree seedlings inoculated with the ectomycorrhizal fungus *Pisolithus tinctorius* have been enhanced in some areas (Marx 1975, Marx and Krupa 1978). However, the generally disappointing performance of *P. tinctorius* in the Pacific Northwest (Alvarez 1982; M. Castellano and J.M. Trappe, unpublished data, USDA Forest Service, Pacific Northwest Research Station) suggests that there is no "magic bullet." Because of the wide variety of soil, climatic, and biotic conditions characterizing temperate forests, it is improbable that a single fungus could benefit all host species and adapt to all conditions. For example, the types and activities of soil organisms associated with young conifers may be quite different from those associated with mature forests (Mason and others 1983, Amaranthus and Perry 1987). On an old, high-elevation, nonreforested clearcut, soil inoculum transferred from a plantation significantly increased survival and growth of Douglas-fir seedlings compared to soil inoculum transferred from adjacent, mature forest. Likewise, soil organisms needed to help seedlings establish on difficult sites may differ from those which sustain site productivity over a forest rotation.

In the Pacific Northwest, Douglas-fir seedlings growing in containers in nurseries have been successfully inoculated with the mycorrhizal fungus *Rhizopogon vinicolor* when its spores were added to irrigation water (M. Castellano, unpublished data, 1986). Although not all fungal symbionts can be inoculated in this manner, success was attained with this promising species. *R. vinicolor* is commonly found in clearcuts on young Douglas-fir seedlings and can improve seedling tolerance to drought (Parke and others 1983). Preliminary results upon outplanting indicate that seedlings inoculated with *R. vinicolor* also grow better (Castellano and others 1985).

Inoculating seedlings with beneficial soil organisms in bareroot nurseries has similar potential for improved outplanting performance. However, mycorrhizae adapted to outplanting sites are often lacking in modern bareroot nurseries (Trappe 1977). High fertility levels and routine fumigation, which are common in nurseries, reduce mycorrhizal fungus populations. Methods to increase mycorrhiza formation and diversity on seedlings in the nursery need further attention. Selecting the appropriate organisms is also critical. Seedlings colonized by a diversity of soil organisms adapted to conditions in the outplanting environment may outperform seedlings colonized by less diverse populations adapted to nursery conditions (Trappe 1977).

Much remains to be learned about the potential benefits of reintroducing soil organisms that benefit plants into degraded soils. Some, perhaps many, restoration projects will be aided by this approach and the evidence for this optimism is strong. However, even where it does benefit restoration, reintroducing beneficial organisms is not some kind of magic bullet that will allow the rest of the ecosystem to be ignored. The best advice for those working in reclamation is to try. One does not have to be a scientist, or even have a high school diploma, in order to experiment. All it takes is common sense —perhaps backed up by a little intuition and access to the proper soil organisms.

Forest managers should be aware that the restoration-enhancing attributes of soil organisms are the product of diverse, complex interactions within natural systems that have co-evolved over millenia. Thus, the best management approach is to minimize drastic or cumulative impacts to the forest environment so as to retain populations of beneficial organisms. To do this, forest managers should:

1. Minimize disturbance severity-that is, intense burns, extensive soil compaction or erosion.

2. Emphasize retention of site organic matter.

3. Emphasize rapid revegetation of sites by indigenous host species and associated beneficial soil organisms.

4. Recognize that sites with harsh environments such as cold or drought are most susceptible to restoration losses.

A new era is emerging in our understanding of forest ecosystems. Incorporating the concept of the "living soil" in our evaluation of site restoration is part of this new, expanding view. Although much remains to be learned, we are making progress at a rapid rate. By understanding soil organisms, practicing foresters can better achieve short-term management goals while ensuring site restoration and recovery. The challenge to forest managers is to assimilate the growing body of information concerning soil organisms in forest ecosystems and put that information to wise use.

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SOIL ORGANISMS-APPLICATIONS FOR NATIONAL FOREST MANAGEMENT

Karen Bennett[1]

ABSTRACT

Maintaining health and vigor of ecosystems requires definition of thresholds. Soil quality standards, developed by the US Forest Service Regions, focus on limiting area of impact, protecting physical soil properties, and maintaining some level of organic matter. Soil compaction and puddling, displacement and erosion and severe burning are specific indicators of detrimental conditions. Monitoring results show that many practices can meet soil quality standards, but repeated entries, with ground based equipment, often don't meet standards. Soil microorganisms may be good early warning indicators of declining conditions. Better understanding of below ground communities is important for ecosystem sustainability. Collaboration between the scientific community and managers needs to improve.

Keywords: soil quality standards, compaction, displacement, severe burning, monitoring, ecosystem sustainability

The controversies we face in the management of the National Forests is not new. Preservation versus utilization of our nations resources was debated in the halls of congress and throughout society since before the authorization of the National Forest System in the late 1800's. It will continue to be a topic of discussion for centuries to come. Miners, ranchers, loggers, environmentalists, scientists, economists and society as a whole, all see a different value in and from the forest. Everyone wants a piece of the resources, some want it all, and all are motivated by differing needs and desires.

We are no longer an isolated nation in these debates. It is now recognized that our land management decisions not only have national implications, but affect global resources and global economies. There has not been a greater declaration of concern for global forest resources than at the Environmental Summit in Rio. From that summit emerges these criteria:

1. Maintain the productive capacity of forest lands
2 Conserve biological diversity
3. Maintain the forest contribution to the global carbon cycle
4. Conserve and maintain soil and water resources
5. Maintain ecosystem health and vigor.

The National Forest System and especially forests in the Pacific Northwest, being among the most productive ecosystems in the world, have a responsibility to uphold these environmental criteria. Recent forest planning efforts including the Northwest Forest Plan and the Interior Columbia Basin Ecosystem Management Project capture these concepts and the future of forest conservation depends on their implementation at a global scale.

No one who depends on the utilization of renewable resources can deny the ultimate importance of these guidelines. Ranchers want a productive forage base, forest industries want a sustainable timber base, everyone wants clean water and a healthy environment. Can we have it all? Can we utilize products from the forest while maintaining biodiversity and protecting soil and water resources? At what level do we maintain the health and vigor of ecosystems? At what spatial and temporal scales? This is where the debates begin.....This is where the agreement erodes.....This is where the thresholds need to be defined.

Our ability as humans to establish thresholds of ecosystem sustainability has a rather poor track record. Eric Ekholms book "Losing Ground" provides a critical perspective on this issue. Remember the Cedars of Lebanon? The great timbers that were utilized by royalty for centuries for their castles and their ships? Now in their place, a rocky shallow soil - eroded by centuries of deforestation and overgrazing supports only forb and shrub species. No **one noticed the decline!**

The health and resilience of the forests in parts of Europe today is drastically declining. Disease and poor growth of trees is the norm after centuries of timber harvest and the removal of forest litter for fuel and farm compost. Nutrient cycling processes were truncated. **No one noticed the decline!**

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[1] Karen Bennett is Soil Scientist and Watershed Program Manager, USDA Forest Service, Siuslaw National Forest, Box 1148, Corvallis, OR 97339.

Our counterparts in Australia, where a 30 year rotation produces their commercial timber crop, have proven that soil compaction and loss of organic materials through silvicultural practices has resulted in a decline of a whole site class in productivity in just one rotation. **No one noticed the decline!**

How much degradation is acceptable to fulfill societal needs? Where do we define our thresholds?

Many ecosystem processes depend upon the condition of the soil resource. It was recognized shortly after passage of the National Forest Management Act that we as managers, needed appropriate, implementable standards with which to protect soil resources. As a result, we have soil quality standards in place. Although each Region differs slightly in the specifics of the standards, the concepts are generally the same:

- **limit the amount of area that is impacted,**
- **protect soil physical properties, and**
- **maintain some level of organic matter** on or **in the soil surface.**

These standards were designed with at least two specific intentions. They had to be appropriate and they had to be implementable. Appropriate means they have to be true indicators of detrimental soil conditions. As such, they represent the best scientific understanding of the factors that effect the sustainability of the soil resource that we have today. Implementable means that someone has to be able to measure and detect the resource condition without extensive and expensive procedures. This is also the reason why we focus on changes to soil physical properties, since they can be easily measured and infer that these changes have implications for soil chemical and biological properties as well. Not only do we have a clear set of standards in place, we also have standardized monitoring techniques that insure valid conclusions are drawn from monitoring efforts.

Look at the indicators:

Severe burning means that the temperature extremes and duration of fire on an area had to be significant enough to literally oxidize the soil, result in red soil colors and drive humic acids down into the soil profile.

Compaction and puddling deal with changes in soil structural properties. The standard is a 15 or 20% increase in bulk density. There is currently debate about the adequacy of this measurement versus soil resistance to penetration. However, the point is that the strength of the soil, or the amount of pore space, is changed to a point where growth of above ground plant species is negatively affected.

Displacement/Erosion allows the loss of 50% of the A horizon of soils.

As defined, these indicators measure degraded soil conditions. By the time these levels of soil disturbance can be detected, there has truly been a long-term degradation of the soil resource. These are not conservative standards. It is the spatial limitation to 15% of an activity area that make them acceptable from an ecosystem sustainability view point.

These Soil Quality Standards establish our thresholds! We are legally required to implement these standards to fulfill the intent of long-term soil protection in the National Forest Management Act. How are we doing?

The verdict is mixed. Where skyline logging or aerial logging systems, small landings and a restricted road networks are employed, our monitoring reports show that we generally are able to meet the standards, the most common soil disturbance has been associated with hot slash burns and subsequent dry-ravel erosion. But in areas where ground based logging systems are employed, especially if this is the second or third entry onto that same piece of ground, monitoring has shown that we cannot consistently meet our soil standards. Compaction and displacement of the surface soil horizon are typically the dominant soil disturbing factors. Recent Forest monitoring reports show that close to 60% of the units logged by ground based equipment exceeded Regional standards.

Why can't we implement our standards? The variety of resource issues that get juggled in each environmental analysis are numerous and complex. Most resource managers focus on the signatures of forest or rangeland health that they see expressed in the above ground systems. As soil scientists, we are trained to see the minute, to see small changes in landscapes, on soil surfaces and in the soil profile. We look for these changes because those changes help us to define soil characteristics. We focus on these changes whether it's a change in landscape position, in depth of the litter layer, or in deformation of soil structure, to help us interpret soil resource conditions. Others do not see these subtle changes, they are not trained to look for these changes. They can see dying trees, they can see wildfire, they can see results from harvesting trees, from piling and from burning slash. It is the condition of the above ground environment that, in their minds, either positively or negatively affects the ecosystem for which they have management responsibility. They cannot see the effects on the below ground ecosystem. Therefore, they question the validity of the soil quality standards when balanced against the management of other resource conditions which are readily apparent. As a result, there is no consistent assurance that soil quality standards will be implemented. It is difficult to be concerned about a system that you cannot see. It is easier to believe that every soil is resilient and that it will recover on its own. The need for us to be educators is well defined or we will all be **waiting for the decline** in ecosystem productivity.

We must become communicators, we must act as educators. Our responsibilities as soil resource managers, are to interpret the implications of degraded soil systems on ecosystem productivity so that wise management choices can be made. It is not an easy task, it is not the role which the majority of us chose as a career path. But unless we effectively communicate and educate, the message will continue to go unheard.

Being the educator implies many things, it implies that we are educated ourselves, that we know the systems in which we are working. We must be able to stratify landscapes and define driving processes. We need to know inherent constraints and how they differ for different environments. We must discover important ecological links. We must define and highlight sensitive areas, separate out the resilient areas. We cannot do all that alone, soil scientists understand certain parts of the ecosystem, other professionals - geologists, hydrologists, ecologists, foresters... understand different parts. Pool the knowledge to develop this understanding. Working together to understand a landscape is an education in itself, **take time to do it.!**

The current revision of the soil quality standards adds some guidelines which direct each Forest or ecoregion to establish local standards of appropriate levels of coarse and fine woody debris for various spatial and temporal scales. Step forward, **lead those efforts,** investigate the systems you work in and develop some common understandings with your peers and managers.

In addition, collaboration with the scientific community must continue to improve. Together we can focus on appropriate forest management questions and initiate some sound management advice. Apart we may develop separate conclusions. As resource specialists we constantly have to disclose environmental effects of our management activities. We've heard the experts at this conference hesitate to answer the same questions we are asked to answer every day. We can't wait for results from a 200 year experiment to help us understand the intricacies of the ecological components we are manipulating everyday. As a community we must move cautiously ahead, insuring that we keep the critical parts of the ecosystem intact.

Scientists and forest managers need to work together to assess our current soil quality standards which speculate that if physical soil properties are protected,the habitat for below ground communities will thrive. If our mission is to sustain ecosystem productivity, do we need to wait for physical indicators to tell us our systems are degraded? Soil microbial populations quickly alter based on current environmental conditions. Microbes are adept at manifesting "survival of the fittest"! - whichever organisms are best adapted to a given environmental condition flourish, others decline or are eliminated from the system. Our ability to utilize microorganisms as early indicators, as a warning system for environmental degradation may help us to alter management practices or employ some restoration techniques before we are able to notice the decline through above or below ground indicators. If soil microbial parameters are sensitive biological markers that can be used to assess changes in soil quality, then we should be using them.

We know that below ground communities are important to ecosystem sustainability, they are vital. We do not understand the intricacies of below ground systems, we may never understand. That should inspire us to ask questions, to explore, to investigate. Think of how our management decisions would change if we could identify subtle changes in microbial communities that forewarn us of unacceptable changes in the environment. The Forest Service and Bureau of Land Management manage an incredible laboratory, quite a diverse laboratory. A laboratory from which a multitude of data could be assembled. The task remains for us to build a library of information, collect soil resource information and be able to interpret the results for different ecological units.

Before we embark on such a venture, we need to determine objectives for data collection and how to meet those objectives. We need to determine the soil physical, biological and chemical parameters that may help us answer ecosystem sustainability questions. Then we would need to design and organized a method to fund and implement the data acquisition. Embarking on such a venture would be a long-range strategic process, possibly tied in with our ecological unit inventories. Collaboration is the key, discovery is the impetus. If we don't strive to get more insights into these below-ground systems, we will we be asking these same questions 70 years from now with no more insight than we have today.

We need to start thinking about how below ground communities are affected by our management activities. We know that these complex and diverse communities are susceptible to specific stimulations and to specific stresses. We need to be able to disclose this information in our activity assessments and we need to be able to understand the implications of changes in these communities as we look toward restoring our ecosystems **so that we will notice the decline!**

SOIL ORGANISMS-APPLICATIONS TO BUREAU OF LAND MANAGEMENT RANGELAND MANAGEMENT

Mike Pellant[1]

ABSTRACT

Livestock grazing management on public lands administered by the Bureau of Land Management (BLM) has evolved from a commodity oriented approach to an ecological approach that still includes sustainability of uses such as livestock grazing. The role of the soil organisms in rangeland management has received little agency attention until recently. The implementation of Standards for Rangeland Health in 1 997 has focused management attention on soil organisms relative to their roles in nutrient cycling, energy flow, and the hydrologic cycle. The challenge for land managers is to both understand the functions of soil organisms and to apply this knowledge to improving the health of public rangelands managed by the BLM.

Keywords: soil organisms, soil biological crust, rangeland management, standards for rangeland health

INTRODUCTION

The management of public lands by the Bureau of Land Management (BLM) is influenced by climatic, biological, socioeconomic, and political forces. Over half of the 264 million acres managed by the BLM are considered rangelands (USDI 1996b) and are managed for multiple uses (livestock grazing, recreation, aesthetics, watershed protection, and wilderness values) according to the Federal Policy and Management Act (FLPMA) of 1976. Rangelands are non-forested lands dominated by herbaceous species, succulents and shrubs. As used herein, rangelands are a kind of land, not a use of land by herbivores such as livestock.

Prior to FLPMA, the emphasis on much of the public rangelands was commodity oriented with an emphasis on sustained forage production to support a stable livestock industry. Recently, the BLM's grazing regulations were changed to reflect a more ecological approach to livestock management on public lands. These new regulations indirectly incorporate soil organisms into the management of public lands since a cornerstone of this initiative is maintaining or improving the functioning of ecological processes (nutrient cycle, energy flow, and hydrologic cycle).

The term soil organism includes a multitude of organisms from bacteria to badgers. I will focus my discussion on two components, 1) soil biological crusts (surface dwelling lichens, mosses, cyanobacteria, bacteria, algae and fungi) and, 2) subsurface microorganisms (bacteria, actinomycetes, fungi and algae). This emphasis is taken because these two components are closely tied to soil stability (hydrologic cycle) and the nutrient cycle and energy flow.

My focus on the role of soil organisms in the management of public rangelands is directed toward two topic areas. One is the implementation of the new grazing regulations entitled, "Standards for Rangeland Health" and the other is the effect of wildfires and rehabilitation practices on soil organisms. This is not an inclusive discussion list, but it includes two topics with which I am most familiar with relative to the role of soil organisms in BLM rangeland management.

STANDARDS FOR RANGELAND HEALTH

Before discussing the Standards for Rangeland Health, I will provide a brief perspective on historical grazing management policy and monitoring and inventory procedures. This perspective is important in order to understand the significance that the recently implemented Standards for Rangeland Health are having on public land management, especially in regards to the role of soil organisms in rangeland management.

Historical Perspective

Formal grazing management of western public lands began with passage of the Taylor Grazing Act in 1946 which, in part, addressed the degradation of rangelands by livestock. Prior to the passage of this Act, livestock numbers, stocking rates and season of use was largely unregulated resulting in overgrazed and degraded rangelands. Accelerated loss of soil and reduced

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[1] Mike Pellant is a rangeland ecologist, Bureau of Land Management, 1387 S. Vinnell Way, Idaho State Office, Boise ID, 83709.

rangeland productivity were also problems. The Taylor Grazing Act set up the framework to resolve these issues by a process of rangeland adjudication and adjusting livestock numbers through a forage allocation process. Ecological processes, including the role of soil organisms, were not considered in forage allocations, therefore management decisions, monitoring, and inventory protocols were designed primarily to measure and allocate forage for livestock.

Most early monitoring and inventory efforts focused on the livestock carrying capacity of rangelands or the degree of accelerated erosion on degraded rangelands. In 1937, an Interagency Range Survey Committee, composed of representatives of the major land management agencies, agreed on a procedure to conduct range surveys to determine livestock forage production and watershed protection (Wagner 1989). Rangeland inventories in the BLM are still focused on biomass production of vascular plants with no measures of production or abundance of soil organisms taken.

Rangeland monitoring studies have traditionally focused on the trend or direction of change in composition or condition of "key" plant species (USDI 1996a), which are generally plants preferred by livestock. For example, the Parker 3-step method (in use in the 1950's) directed that plant vigor ratings should be focused on those plants which carry most of the grazing load (Wagner 1989). The objective of most rangeland trend studies has been to determine whether livestock forage species are vigorous and if they were increasing or decreasing in abundance. Again, soil organisms were not measured nor were they considered in the interpretation or evaluations of monitoring data.

The functional status of the ecological processes and specifically the soil organisms that contribute to these processes were seldom considered in designing monitoring or inventory strategies prior to the incorporation of rangeland health standards into BLM rangeland management in 1995. A transition is occurring at this time as management strategies and inventory and monitoring procedures are being modified to better incorporate rangeland health attributes into protocols.

What Are the Standards for Rangeland Health?

New BLM grazing regulations implemented on February 22, 1995 entitled, "Fundamentals of Rangeland Health" (43 Code of Federal Regulations Part 4, Subpart 4180) changed the emphasis of livestock management and monitoring from "livestock forage and erosion" to looking at the overall "health" of rangelands. Rangeland health is defined as "the degree to which the integrity of the soil and ecological processes of rangeland ecosystems are maintained" (National Research Council 1994). The ecological processes include the water cycle, energy flow and nutrient cycle and are closely related to the integrity of the plant community and site stability. These standards were refined to fit local conditions by public "Resource Advisory Councils" in each State in concert with BLM technical specialists.

Soil organisms, especially the above ground and visible soil biological crusts, are integrally linked to the ecological processes, therefore they are included in evaluations of rangeland health. The role of soil organisms in the functioning of the ecological processes is well established (Whitford and Herrick 1995). I will now present a few examples of these roles specific to rangelands.

Nitrogen fixation is a key process in nutrient cycling. Rychert and others (1978) stated that the biological crust performed the majority of nitrogen fixation in some desert ecosystems. Other soil organisms, primarily bacteria and fungi, are important in the decomposition process converting litter into organic carbon. Ninety per cent of this mineralization of carbon is carried out by soil organisms such as bacteria and fungi (Swift and Anderson 1993). Many plants in arid zones are benefitted nutritionally by mycorrhizal fungi which absorb and translocate nutrients from the soil to the host plant (Wicklow-Howard 1989). Whitford and Herrick (1995) summarize the ecological benefits provided by soil organisms as decomposition, nutrient immobilization and mineralization, storage and release of water and nutrients, nitrogen fixation, and denitrification, production of plant growth factors, and nutrient uptake by mycorrhizae. Thus, the importance of soil organisms in nutrient cycling, energy flow and the water cycle is well established. The dilemma for land managers is to measure or describe the functional status of the soil organisms contributing to the functioning of the ecological processes over large landscapes.

Incorporating Standards for Rangeland Health Into Grazing Management Practices

The Standards for Rangeland Health, including the associated "Guidelines for Grazing Management" (S&G's) are now incorporated into the management of all public lands. I will use Idaho as an example of how one state is incorporating soil organisms into public rangeland management to maintain or obtain "healthy rangelands" via the S&G's. The Idaho S&G's were developed by the three Resource Advisory Councils (RAC's) with technical assistance from BLM. The RAC's recognized that soil organisms, especially the biological soil crusts, were important in maintaining ecological processes in properly functioning condition.

The final Idaho S&G's (USDI 1997) reflect this point in that soil organisms were specifically mentioned in:

> *Standard 4 (Native Plant Communities) includes the following indicators for a healthy, productive, and diverse plant community where the ecological processes are properly functioning:*
>
> > *Native plant communities (flora and* ***microbiotic crust*** *(emphasis added)) are maintained or improved to insure the proper functioning of ecological processes and continued productivity and diversity of native plant species.*

The Guidelines for Grazing Management are the management prescriptions that should be considered if the Standards for Rangeland Health are not met, not making significant progress and if livestock management is the reason for non attainment of the Standard. Guideline 8 states:

> *Apply grazing management practices that maintain or promote the interaction of the hydrologic cycle, nutrient cycle, and energy flow that will support the appropriate types and amounts of* ***soil organisms*** *(emphasis added), plants and animals appropriate to soil type, climate and land form.*

The next step in implementing S&G's is to determine if current grazing management practices are in compliance with the S&G's. An interdisciplinary team evaluates selected landscapes using both qualitative assessments and available monitoring and inventory data to make these determinations. Since information on all aspects of the ecological processes is not available, "indicators" must be used as surrogates for the direct assessment of the status of ecological processes including soil organisms. An indicator is an element of an ecosystem that is used as an index of those attributes that are too difficult or expensive to measure. There is no one indicator of ecosystem health; instead a suite of key indicators should be used for an assessment (Karr 1992). A partial list of indicators of the functional status the ecological processes and therefore by inference the functional status of soil organisms includes:

1) The presence of leguminous plants that fix nitrogen in association with root nodules.
2) Lichens and cyanobacteria that fix nitrogen.
3) Adequate litter and roots (relative to site potential and climate) available for decay by soil organisms.
4) Normal rates of soil and organic matter loss via erosion as opposed to accelerated erosion that removes organic matter and thus soil organism substrate at a nonsustainable rate.

These indicators are evaluated by first visiting an ecological reference area (ERA) and reviewing the appropriate ecological site (range site) description for the site. This ERA serves as the benchmark for conducting assessments on other, similar sites being evaluated. This allows the interdisciplinary team to get familiar with the amount and distribution of biological soil crusts, leguminous plants, litter, and natural rates of erosion prior to conducting evaluations on landscapes with similar potential to the ERA.

If allotment evaluations reveal that the Standards for Rangeland Health are not being met, the authorized officer (manager) must make changes in livestock management using the Guidelines for Grazing Management prior to the start of the next grazing season. Relative to soil organisms, changes in grazing management practices, if needed, will probably be focused on soil biological crusts rather than the smaller, subsurface obvious soil organisms for several reasons. Soil biological crusts are visible and the impact on them by livestock is evident. The effects or impacts of livestock grazing on soil organisms below the soil surface are much less obvious. Second, research on the effects of livestock on the survival and recovery of soil biological crusts, although minimal, is better and more available than similar research on soil organisms below the soil surface in the Great Basin Desert.

For example, winter grazing appears to be less detrimental to soil biological crusts followed by spring grazing when the soils are moist (Marble and Harper 1989; Memmott and others 1998). Late spring and summer grazing when the soils are dry are the most detrimental to crust health and recovery. Of course grazing management changes must also consider the vascular plant community along with soil organisms. Herein lies the challenge of managing rangelands to insure the maintenance or obtaining of properly functioning ecological processes. In some Great Basin plant communities, summer grazing (after seed ripe) may be favorable for grass and forb species but not for the biological soil crust and possibly for other soil organisms. Good management strategies for livestock grazing will require a better understanding of the impacts of livestock grazing on soil organisms.

WILDFIRES AND REHABILITATION PRACTICES

Wildfires have a major impact on resource values in the Great Basin, particularly in southern Idaho where wildfires are large and frequent. The BLM mitigates the harmful impacts of wildfires on public lands by applying rehabilitation practices that include, but are not limited to, reseeding, protection from livestock grazing, and installation of erosion control structures ("gully plugs," contour furrows, and check dams). An interdisciplinary team evaluates wildfire impacts on vascular plants to determine if reseeding is needed or if the natural recovery process can repopulate native plants on a burned site.

The impacts of wildfires on soil organisms are rarely evaluated on burned areas for several reasons. First, the purpose of the BLM's Emergency Fire Rehabilitation (EFR) program is to mitigate the adverse impacts of wildfires on watershed function and to reduce risks to private property in a timely and cost-effective manner. Restoration of ecological processes, including soil organisms, is not within the scope of the EFR Program. Secondly, little is known about the impacts of wildfires on soil organisms and the appropriate technology to restore desired soil organisms on large burned areas is not practical.

However, several cooperative studies sponsored by BLM and the Biology Department, Boise State University are providing some insight into the link between soil organisms, wildfires, and post fire recovery of vascular plants and biological soil crusts in the Snake River Plain. Wicklow-Howard (1989) determined that a high severity wildfire caused a significant reduction in vesicular-arbuscular mycorrhizae (VAM) concentration compared to a low severity wildfire in a Wyoming big sagebrush community in Southwestern Idaho. However, this effect lasted less than two growing seasons. In a later study to further elucidate the relationship between VAM and reestablishment of sagebrush on burned rangelands, Gurr (1993) hypothesized that a summer burn released sufficient nutrients so that inoculating sagebrush seedlings with VAM was unnecessary.

More recently Kaltenecker (1997) studied the effects of wildfire and rehabilitation on biological soil crusts in Wyoming big sagebrush *(Artemisia tridentata)* sites with high potential for cheatgrass invasion. She determined that reestablishment of a plant community structure similar to that of the native plant community (widely spaced perennial plants with open interspaces) was necessary for recovery of the biological crust, and that vascular plant and biological crust establishment were synergistic. This was based on evidence of high cover of biological crust in ungrazed, rehabilitated communities, with diversity of lichens and mosses only slightly lower than that found in unbumed sagebrush communities. High plant densities, litter accumulation, and the lack of open interspaces in communities dominated by cheatgrass created conditions that were not conducive to establishment of a fully developed biological crust.

One area where soil organisms have proved to be beneficial to the success of rehabilitation projects is the addition of *Rhizobium meliloti* innoculant to leguminous species, primarily dryland alfalfa *(Medicago sativa),* included in rehabilitation seed mixtures. I have observed that innoculated dryland alfalfa appears to establish better than non innoculate legumes.

SUMMARY

Soil organisms, especially the biological soil crusts, are receiving more attention on public lands administered by the BLM with the implementation of State S&G's. With this increased attention comes the need for a better understanding of the effects of grazing and other uses on soil organisms. Science must play an important role in supporting management decisions relative to changing livestock practices to support soil organisms and therefore rangeland health. Existing science must be made available to resource specialists and managers now to insure that management decisions are based on the best available science. In addition, new studies are needed to fill information gaps relative to the effects of management practices on the role of soil organisms in rangeland health. This research is needed quickly and must be distributed to resource specialists, managers and the public in both technical and nontechnical formats.

In addition to the need for an increased research in this area, managers need to begin incorporating soil biological crusts into rangeland monitoring and inventory programs. Soil biological crusts can be easily incorporated into rangeland monitoring and inventory programs. In Idaho, cover and frequency of soil biological crust components (mosses and lichens) are recorded along with vascular plants in some rangeland trend studies. Rangeland management decisions will improve as this baseline information on soil biological crusts is accumulated and incorporated into new grazing management strategies.

The last issue that I would like to address in this summary is the polarization that is occurring between some "environmental" and "commodity" users of the public lands over the importance of soil organisms in the management of public rangelands. Again I will focus on the soil biological crusts since most of the current controversy surrounds this component of the soil organism community. One extreme perspective of the "pro biological crust" public was provided by Hogan (1994). He states that loss of "cryptogams" has greatly contributed to the loss of half of the topsoil on arid lands and the solution is, "total removal of livestock from western North American arid lands." The media is promoting the controversy by printing stories with titles of "West tramples key asset into dust; rangeland 'skin'" (Twin Falls Idaho Times-News, July 28, 1998). On the other side of the coin are Savory and Parsons (1980) who promote grazing practices designed to "break the crust" to increase vascular plant establishment. This management approach recognizes soil crusts as a sign of deterioration on western rangelands that needs to be "broken" by hooved animals in order to promote proper functioning of rangeland ecosystems.

I feel that the middle road must be taken in issues that concern the management of soil biological crusts in particular and of soil organisms in general. Focusing on just soil organisms for changing grazing management practices neglects the functional links between vascular plants, soil organisms and the ecological processes. Litter and roots from vascular plants provide the substrate for soil microorganisms to break down organic material to carbon, while leguminous plants are the host for *Rhizobium* species that provide nitrogen used by the plants. There are many other examples of the linkages between vascular plants and soil organisms that could be cited to illustrate this point (Whitford and Herrick,1996). Singling out one component of the ecosystem for special management is not the best approach for managing rangelands for overall health. Management of our public rangelands for health and productivity will be encouraged if polarization is avoided and rangeland ecosystems are managed as a whole and not divided into their parts to forward different agendas.

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NATURAL RESOURCES CONSERVATION SERVICE-DATABASES AND ANALYTICAL SERVICES

Carol D. Franks[1]

ABSTRACT

This paper is a brief overview of NRCS databases, the National Soil Survey Laboratory (NSSL) soil analyses and characterization, and the National Soil Survey Center's (NSSC) new program in Soil Biology and Soil Carbon. The NRCS soils and plant community databases (NASIS and PLANTS) are discussed (Internet access: NASIS http://www.statlab.iastate.edu/soils/, and PLANTS http://plants.usda.gov/). Current NSSL soil characterization analyses as well as new projects and analyses for the Soil Biology and Soil Carbon program are presented. The Soil Biology and Soil Carbon program augments our existing emphasis areas of Global Climate Change, Carbon Sequestration, Soil Survey, and Technical Soil Services. Benchmark Site Selection is presented as a case study for database development that can be adapted or modified to fit a variety of situations.

Keywords: soil databases, NASIS, plant databases, PLANTS, soil analysis, benchmark sites, organic carbon analyses, microbial biomass, microbial activity

INTRODUCTION

The Natural Resources Conservation Service (NRCS) estimates that our corporate databases are worth $8.5 billion. The NRCS has 6 major databases; soils, snow survey, plants, field office, Natural Resources Inventory (NRI) and others. These individual databases are valued (billions of dollars); soils - $5.0, snow survey - $0.3, plants - $0.2, field offices - $2.7, NRI - $0.2, and other $0.1 (Harward, 1997). Our databases are one of our most important assets. We use them extensively, and we want other groups to have access to them as well. The first section of this paper covers key points about three of our databases, NASIS, PLANTS and the NSSL Soil Characterization database (a subset of NASIS).

The second section of this paper deals with the National Soil Survey Centers new program in Soil Biology and Soil Carbon. Finally, Benchmark Site Selection is presented as a case study that ties together all aspects of database development and can be adapted to a variety of situations.

SOILS DATABASES

The National Soil Information System-NASIS
(http://www.statlab.iastate.edu/soils/)

NASIS is the new NRCS soils database. NASIS replaces our State Soil Survey Database (3SD). NASIS is designed to meet the following objectives:

1. Provide a flexible and dynamic management system for soil data and information.

2. Improve the quality of soil data and information.

3. Improve automated map unit management.

With these objectives in mind NRCS focused on customer data needs. The following areas of database development were emphasized and represent the components of an information management framework: 1) data collection, accumulation and aggregation (from field observations to integrated soil survey maps and interpretations); 2) data management and access; and 3) database application. Key functions and data that NRCS typically uses were also identified. These key functions include coordination, data acquisition and data input. Types of data NRCS uses include soil, water, air, plant, animal and others.

Soils data are currently used in the following applications:

Water Quality Models
Water Balance/Budgets
Engineering Practices
RUSLE - Revised Universal Soil Loss Equation
Agricultural Waste Management

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[1] Carol D. Franks is a research soil scientist, Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NE 68508-3866.

Pesticide Management
Interpretive Maps
Conservation Practices
Conservation Practice Effects
Wind Erosion Equations
Grazing Lands Application
Grazing Lands Data System
Environmental Planning
National Resource Inventory

The following are NASIS priorities for new development:

Lab Characterization data model
Convert pedon and lab data
Point/site data collection tool
Spatial analysis
Manuscript generation/management
Official series descriptions
Convert STATSGO Attribute data
NASIS interface enhancements
Generalized export
Improved report functionality
Improved query functionality
Natural resource data gateway
Data aggregation
Data comparison

In order to meet the objectives outlined above, NRCS developed the National Soil Data Access Facility (NSDAF), in conjunction with Iowa State University. NASIS and NSDAF are designed for the following applications; automated geographic tabular natural resource databases supporting conservation planning tools, resource inventory tools and technical procedures, conservation effects tools, and practice design tools. Future data access features will include; a USDA wide area network, including all NRCS offices, NSDAF, U.S. Forest Service, universities and clients.

The National Soil Data Access Facility-NSDAF
(http://www.statlab.iastate.edu/soils/)

The purpose of NSDAF is to serve as a clearinghouse for map unit data, site data, soil geodata, and taxonomic data for data producers and users such as; universities, federal agencies, and the private sector. The guiding principle for NSDAF is that anyone requiring or producing soil geodata shall have the ability to easily determine what exists, the ability to easily access this data, and the ability to contribute data to the National Repository. All NRCS standards for data collection, input and quality will apply to data in this facility.

NRCS National Soil Survey Center and National Soil Survey Laboratory (NSSL) Database

This database includes standard soil characterization analyses for more than 20,000 soils from around the world and throughout the United States. There are four types of standard soil characterization, acid soils, alkaline soils, organic soils and andic soils. These four types of analyses are based on characteristics of the soil sampled. Acid soils typically have pHs less than 7, lower base saturation and can be dominated by aluminum chemistry. Alkaline soils typically have pHs greater than 7, higher base saturation and can contain appreciable amounts of chemical salts such as calcium and magnesium carbonate and sodium chloride. Organic soils typically contain more than 12 percent organic carbon and are often called "peat" or "muck". Andic soils typically formed in weakly weathered volcanic materials dominated by glass (ex: volcanic ash). Listed below are standard analyses NSSL performs on the different soil types.

1. Acid Soils-bulk density, 1500 MPa water retention, particle-size, total carbon, total nitrogen, calcium carbonate equivalent (<2mm), organic carbon (difference method), pH, cation exchange capacity, extractable acidity, aluminum, iron, silica, manganese, and phosphorous (Bray 1).

2. Alkaline Soils-bulk density, 1500 MPa water retention, particle-size, total carbon, total nitrogen, calcium carbonate equivalent (<2mm), organic carbon (difference method), pH, cation exchange capacity, electrical conductivity, and calcium, magnesium, sodium and potassium (from the saturation extract).

3. Organic Soils-bulk density, 1500 MPa water retention, organic fiber content, mineral content, total nitrogen, pH, cation exchange capacity, extractable acidity, iron, silica, aluminum and manganese.

4. Andic Soils-clay mineralogy, glass content, pH, iron, aluminum, silica, manganese, and phosphorous.

PLANT DATABASES

The National PLANTS Database was designed by NRCS to provide a single source of standardized information about plants. This database focuses primarily on plants of the US and its territories. This database includes checklists, distributional data, crop information, plant symbols, plant growth data, references and other plant information. PLANTS reduces costs by preventing the duplication of efforts and by making information exchange possible across agencies and disciplines. These Web pages allow you to query the PLANTS database, download information, and view images of plants.

NRCS PLANTS Database

(http://plants.usda.gov/)

The NRCS PLANTS database consists of six subsets:

1. Agronomy
2. Integrated Taxonomic Information System (ITIS)
3. National Plant Data Center (NPDC)
4. Ecological Site Information System (ESIS)
5. Vegetative Practice Design Application (VegSpec)
6. Plant Materials Program

The Agronomy Projects subset supports various agronomy projects with data and data management software. Supported agronomy projects include the Revised Universal Soil Loss Equation (RUSLE) and Wind Erosion Equation (WEQ) software applications.

The Integrated Taxonomic Information System (ITIS) is a partnership of U.S., Canadian, and Mexican agencies, other organizations, and taxonomic specialists cooperating on the development of an on-line, scientifically credible, list of biological names focusing on the biota of North America. ITIS is also a participating member of Species 2000, an international project indexing the world's known species. ITIS data may be accessed via the Web.

The National Plant Data Center (NPDC) focuses resources on the acquisition, development, integration, quality control, dissemination and access of plant information; NPDC incorporates new plant technology into the agency's automated tools. The NPDC is responsible for the PLANTS database, which focuses on the vascular and nonvascular plants of the United States and its territories.

The Ecological Site Information System (ESIS) contains the ecological site inventory (Range 417) database for Rangeland Data, ecological site inventory (Wood 5) database for Forest Soils, and the Ecological Site Description (Range Sites) database. Currently, the Ecological Site Inventory Database for Rangeland Data is available. Later this summer the Ecological Site Inventory for Forest Soils will be available. The Ecological Site Description database will be available sometime next year (pending data input).

The Vegetative Practice Design Application (VegSpec) provides practice design technology for the preparation of vegetative establishment specifications. The vegetative establishment practices for which VegSpec automates practice design include cover crop, critical area planting, filter strip, pasture and hayland planting, range seeding, tree planting, farmstead windbreak and field windbreak. This application is interactive and fully functional.

The Plant Materials Program develops plant materials and plant technology for the conservation of the Nation's natural resources. Many of today's environmental problems can be addressed effectively through the use of plants. Plant Materials centers and specialists provide state-of-the-art technology to help field offices and land users solve critical natural resource issues. The Plant Materials program strives to meet the change by (1) developing new technology for current conservation needs, and (2) Transferring this information to its customers.

SOIL ECOLOGY AND BIOLOGY PROGRAM-NRCS NSSC

The purpose of this program is to branch out into new areas of soil science in order to enhance our existing Soil Survey Program, support our Global Climate Change Program, support Soil Quality initiatives and develop new soil interpretations and assess management impacts on the soil. To accomplish this task the National Soil Survey Center and the Soil Survey Division are developing this new program in Soil Biology and Soil Carbon. The following outlines areas of emphasis for this new program.

Soil Biology Areas of Emphasis

1. Soil and Ecosystem Function
   Soil Mapping
   Technical Soil Services

2. Soil Quality
   Soil Function
   Microbes and Soil Climate
   Microbes and Plant Communities
   Microbial Biodiversity
   Management impacts
   Database Development

3. Wetland Identification and Function

4. Global Climate Change
   Nutrient Cycling
   Ecosystem Modeling
   Threshold Identification

5. Resource Inventory and Assessment
   National Resource Inventory (NRI)
   Interagency Inventories

6. Field Sampling and Observations
   Near Surface Soil Properties
   Field Sampling Method Adaptation and Development

7. Database Development
   Modeling
   Benchmark Sites-a Framework

8. Soil Characterization
   Lab Analyses Methods
   Adaptation and Development
   Research and Development
   Implementation

9. Soil Interpretations and Management Impacts
   Rangeland
   Cropland
   Forestland

10. Bioremediation

The following section provides objectives for the eleven soil biology and soil carbon projects NRCS is pursuing at this time.

Benchmark sites-A framework to develop a pilot database of microspatial and temporal near surface soil properties and plant communities suitable for use in modeling efforts, based on benchmark sites.

Microbial community fingerprinting-Test the Fatty Acid Methyl Ester (FAME) microbial analysis for use on archive benchmark soil samples dried at 45°C. Resample benchmark sites and perform analyses on fresh samples/ FAME, ergosterol (fungi), total biomass, dehydrogenase activity and C and N mineralization.

Soil food web database-Cooperative effort between NRCS Soil Quality Institute and National Soil Survey Center (NSSC) and Oregon State University (OSU) Soil Microbial Biomass Service. To link microbial data collected to the NRCS interpretive soil database (soil survey map units) through georeferencing. Development of a Logical Data Model and linkage-Completed,

Expanded organic carbon analyses-Test minimum dataset for organic carbon for applicability to NRCS programs and projects. Build a characterization database based on benchmark sites that includes data elements needed in carbon and nutrient modeling.

Microbial activity **and biomass** analyses-Adapt, develop and implement NSSL capability to analyze fresh soil samples for total microbial activity using Chloroform Fumigation Incubation (CFI). In cooperation with ARS test soil samples for the Conservation reserve Program and International Projects.

Field sampling protocols-Document and implement appropriate field sampling methods for all microbial analyses.

Soil chemical, physical, and microbial characterization of benchmark sites-In cooperation with OSU Soil Microbial Biomass Service: analyze fresh soil samples using extraction techniques to determine various biomass measures; NSSL will characterize the same benchmark site thus creating a point/site linkage between the lab characterization and the microbial biomass database under development by OSU; compare NSSL incubation methods to OSU direct extraction methods.

Oregon demonstration project-To test the potential to combine federal inventories such as-NRI, FS-FIA and FSIS, NASS enumerative survey, etc.; test the various plant community inventory protocols in all of the three major land uses; cropland, rangeland and forestland; test repeatability of measurements between field crews through double sampling; field test potential Soil Quality Indicators in a national periodic inventory.

NRST/IRWET database-Use this WEPP dataset to evaluate soil quality and nutrient cycling for the soils sampled.

Wetland ecosystem project-Develop a laboratory analysis to measure anaerobic N or C for use on wetland soils.

Macronutrient cycling-Develop additional laboratory analyses for evaluating C, N and P cycling in soils.

In order to complete these projects, we have developed a variety of new soil analyses: microbial biomass/activity, mineralizable nitrogen, particulate organic matter (POM), organic matter residues (0 horizons and litter), root biomass and labile carbon. These analyses are available on a limited basis for other selected projects. In the future, we hope to offer these standard analyses for the National Soil Survey Laboratory.

Benchmark Site Selection

The following section is an outline for using Benchmark Site Selection. This process can be used and modified to focus research efforts, soil survey efforts, resource inventory efforts or resource assessment efforts to make them more efficient, cost effective and reduce the number of sites needed for evaluation. This comes from work I did for the Rangeland Component of the interagency Water Erosion Prediction Project (WEPP) to develop the new process based WEPP model for erosion prediction (Franks and others 1993).

Why do we need a site selection process? With limited time and resources we must effectively augment existing erosion, soils and hydrology research on plant community ecosystems in order to enhance the modeling effort. This process is based on the concept of a benchmark. Webster's New World Dictionary, 1988 defines a benchmark as a standard or point of reference in measuring or judging quality, value, etc. NRCS has used this standard to develop the concept of a Benchmark Soil. A benchmark soil is one of large extent, one that holds a key position in the soil classification system, or of special significance to farming, engineering, forestry, or other uses. Knowledge of benchmark soils can be applied to other soils with similar properties. The purpose of benchmark soils lists is to focus research efforts on soils that have the greatest potential for expansion of data and interpretations. Lists of benchmark soils are useful in planning for many kinds of studies.

Current benchmark soils lists have limitations because they are based on political boundaries such as counties and states. Typically, such lists emphasize agronomic uses and are limited to 20 or 30 soils per state. However, we can use many of the criteria used in developing benchmark soils lists for other purposes. To this end I have developed the Benchmark Site Selection process (Franks and others 1993). The steps in this process are:

1. Define what constitutes a benchmark for purposes of the study.

2. Review benchmark soil criteria for applicability.

3. Develop new criteria essential to the study.

4. Determine which criteria occur in the national soils database.

5. Access the database.

6. Develop new potential benchmark soils lists.

7. Select soils from this new list which have potential sites where land use history is known and available; has contrasting vegetation states (different plant comminutes or cropping systems); easy access so one can return and conduct further studies later.

8. Identify other limiting factors that effect the site selection process.

The benchmark site selection process is an organized, logical, criteria-based method to assist in the site selection process for field studies. It can be used and modified to enhance site selection for any soil-based research for process-based modeling. All data gathered from all sites must have the greatest potential possible for extrapolation to larger areas, similar plant community sites, and similar soils. The following maps (fig. 1 and 2) illustrate how we used only twelve major sites to collect data that can be extrapolated to similar soils found in the region.

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National Range Study Team (NRST)

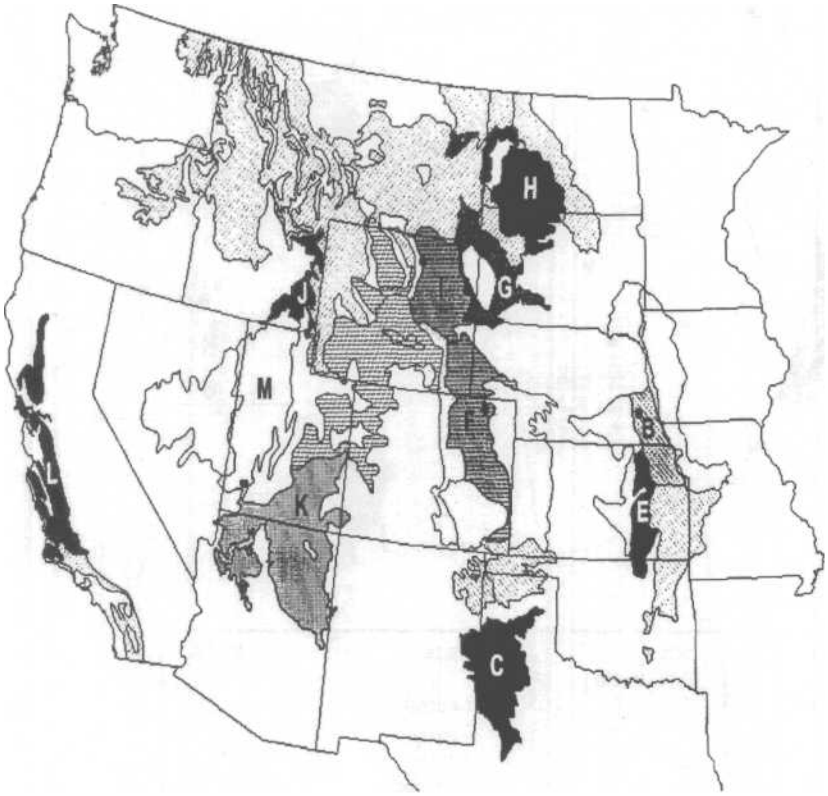
Major Land Resource Areas where NRST sites occur

Site Designation	State	MLRA
B	Nebraska	M106
C	Texas	H77
E	Kansas	H76
F	Colorado	G67
G	Wyoming	G60A
H	North Dakota	F54
I	Wyoming	G58B
J	Idaho	A13
K	Arizona	D35
L	California	C15
M	Utah	D28A

Figure 1-This map shows the geographic distribution of the Major Land Resource Areas (MLRAs) where NRST sites are found. NRST data can be extrapolated to apply to similar soils and plant communities within the designated MLRA. Map source is Major Land Resource Areas of the United States. NRCS, National Soil Survey Center, 1997. Table A defines the respective MLRA for each state.

National Range Study Team (NRST)

Additional Major Land Resource Areas where the soil series found at an NRST site also occurs



Site Designation	State	MLRA	Additional MLRAs
B	Nebraska	M106	107,75,102B
C	Texas	H77	78,78A
C	Kansas	H76	76,106,112
C	Colorado	G67	69,72,49
G	Wyoming	G60A	32,33,58B,34,67
H	North Dakota	F54	53A, 53B, 58B,58A
I	Wyoming	G58B	32,33,34,60A, 67
J	Idaho	A13	43
K	Arizona	D35	39,36
L	California	C15	20
M	Utah	D28A	28B

Figure 2-This map shows the geographic distribution of additional MLRAs where the NRST data may be extrapolated to similar soils and similar regions within these MLRAs. These additional MLRAs were selected because the Soil Interpretation Records (NRCS, National Soils Information System (NASIS), 1997) for the Soil Series found on the NRST sites indicate that these Soil Series also occur within these additional MLRAs. Some MLRAs found on the Soil Interpretation Records were excluded because of poor fit with the plant communities, range cover regions, and range cover types (Shiflet 1994). Map source is Major Land Resource Areas of the United States, NRCS, National Soil Survey Center, 1997. Table C provides the descriptive names of the additional MLRAs.

SOIL ORGANISMS: FUNCTIONS AND PROCESSES-MANAGEMENT IMPLICATIONS. A SYNOPSIS

Martin F. Jurgensen[1]

ABSTRACT

The objective of this symposium was to examine the various roles and functions of soil organisms, and how they relate to forest and range management in the Pacific Northwest. This paper is a synopsis of my perspectives on the main topics of the symposium. They were: 1) why are soil organisms important, 2) management impacts on soil organisms, and 3) management of specific soil organisms. The consensus of the symposium speakers was that forest and range management activities do have pronounced effects on soil organisms, but it was not clear if management-induced changes in population numbers and diversity are important for long-term soil productivity and stability. Until more information becomes available, forests and rangelands should be managed in ways which maintain soil organism populations and diversity, and are consistent with overall management objectives. Management activities, such as maintaining soil organic matter levels and reducing soil compaction, are usually beneficial to both soil organisms and other components of forest and range ecosystems.

Keywords: soil organisms, organic matter decomposition, soil compaction, microbial diversity, timber harvesting

INTRODUCTION

Much has been written about the significance of soil organisms to the functioning of forest and range ecosystems, especially their role in forest health and soil productivity/sustainability (Meurisse - this symposium; Harvey 1994; Hessburg and others 1994). However, many questions are being raised whether soil organisms can be managed, and if they can, should they become an integral part of management activities. It was the objective of this symposium to examine the various roles and functions of soil organisms, and how they relate to forest and range management in the Pacific Northwest (Ypsilantis - this symposium). The papers presented at this meeting covered a wide range of topics - from the very basic (genetic diversity of soil microorganisms) to the very applied (landscape considerations), many of which are published in this proceedings. Rather than give detailed comments on individual papers, I have decided to give my perspective on what I feel were the main topics or focus of the symposium. They were: 1) why are soil organisms important, 2) management impacts on soil organisms, and 3) management of specific soil organisms.

Unfortunately I was not able to read most of the papers published in this symposium proceedings. As often happens, papers published in a proceedings may be quite different than the oral presentations. Therefore, this paper is based on my notes and memory of information given by the various authors at the symposium. Consequently, if I have misinterpreted or misquoted any of the symposium speakers, my apologies.

IMPORTANCE OF SOIL ORGANISMS

Plants

While soil organisms affect many components of forest and range ecosystems, the main focus of papers presented was the impacts of soil organisms on plant communities. The role of particular microbial and faunal groups in organic matter decomposition and nutrient release were high-lighted by Ingham, Norton, Molina, Moore, and Seastedt (this symposium). Since nearly all soil nitrogen is in organic matter and many western forest soils are nitrogen limited (Binkley 1991; Moore 1994), the importance of soil organisms in the nitrogen cycle, especially dinitrogen fixation and nitrogen mineralization, was repeatedly stressed (Myrold; Stark; Prescott - this symposium). Soil organisms also affect plant water availability and aeration by incorporating organic matter in mineral soil horizons (soil structure), and forming large macropore (biopore) channels (Herrick; Belnap - this symposium). The significance of forest pathogens on ecosystem functions and forest health was addressed by both Thies and Harvey (this symposium). The comments by Thies that root disease activity does not indicate an "unhealthy" forest, and

[1] Martin F. Jurgensen is a professor of forest soils, School of Forestry and Wood Products, Michigan Technological University, Houghton, MI 49931

that wood "lost" to pathogens is a social, not a biological concept should be remembered when forest health concerns and management are discussed. No mention was made of growth factors and other plant-stimulating compounds produced by soil microorganisms (Colinas and others 1994), although Ingham (this symposium) mentioned possible beneficial effects of rhizosphere bacteria in protecting roots from disease attack. Mycorrhizal fungi and other soil microflora have been reported to produce antibiotics or other metabolic products which inhibit various root pathogens (Azcon-Aguilar and Barea 1992).

Water

The impacts of soil organisms on water quality was indirectly addressed by the role of soil microorganisms in the nitrification and denitrification processes (Myrold; Stark - this symposium), which would affect the amount of nitrate available for leaching into ground water or surface streams and lakes. I was surprised there was not a greater emphasis on this issue at this meeting, considering the interest in managing riparian zones of western forests. This is of major concern in the southern U.S., where extensive research is being conducted on the biological filtering processes in forest buffer strips along streams and wetlands (Hubbard and Lowrance 1994).

Animals

While animals would be indirectly affected by plant community changes caused by soil organism activity, the direct involvement of mycorrhizal fungi fruiting bodies, as part of the food chain supporting spotted owl populations, was discussed by both Molina and Amaranthus (this symposium). Soil organisms also seem to be an important food source for another endangered species, the red cockaded woodpecker, which is found in old-growth pine stands in the southeastern U.S. After Hurricane Andrew in1989 destroyed many pine stands in the Coastal Plain of South Carolina, it was projected that populations of this woodpecker would plumate. Instead, numbers increased to record numbers in some areas, as the woodpeckers fed on insects associated with the large amounts of coarse woody residue produced by the hurricane[2].

Biodiversity

The concept of soil organism biodiversity as being importance to forest ecosystems and their management is relatively new, and has generated considerable interest and possible concern. While adequate populations of soil organisms are recognized to be necessary in carrying out the various processes needed for plant, water and animal activity (discussed above), maintaining the diversity of these soil organisms has also become an issue (Molina; Spence; Moldenke-this symposium). Soil microorganisms and microfauna are the largest and most diverse of the biological groups, and they are extremely difficult to identify and obtain accurate estimates of population size. It has been estimated that only 1 to 5% of soil microorganisms have been characterized and named (Hawksworth and Mound 1991). Consequently, much effort is going to develop technologies for characterizing the taxonomic and functional diversity of soil organism populations (Busse; Franks - this symposium; Kennedy and Gewin 1997).

The reasons proposed for conserving soil organism biodiversity are also diverse. One, which appeals to the practical, utilitarian part of human nature, is conservation of the large gene pool present in soil organisms. These organisms, their genes, enzymes, or metabolic bi-products have the potential to benefit society, such as in the mitigation of polluted soil and for antibiotic production. This trend is exemplified by the recent proposal between a drug company and Yellowstone National Park to search for unique microorganisms in hot pools. At the other end of the spectrum is the idea that soil organism diversity should be maintained because "they are there", and have an intrinsic worth in themselves beyond any practical value. Spense (this symposium) noted that biodiversity is a "value choice —a thing of the heart". This concept is best illustrated by the Deep Ecology Platform of Naess and Sessions (in Devall 1993).

Of more significance to forest and range ecosytems and their management is the importance of soil organism diversity to soil productivity and sustainability. Increased plant diversity has been positively correlated with increased ecosystem productivity (Naeem and others 1996; Tilman 1996). Losing one or several plant species from an ecosystem can have pronounced effects on community productivity and nutrient retention (Symstad and others 1998). These have been termed "keystones" species, to signify the important role they have in ecosystem functioning. While the loss of a plant species may have a major impact on ecosystem productivity or stability, this has not been clearly shown for soil organisms. The difficulty in isolating and categorizing the soil microflora into discrete taxonomic units has made this concept seemingly unusable for soil bacteria and fungi. Moldenke (this symposium) used keystone species to describe certain soil fauna active in the decomposition of forest floor litter.

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[2] Personal communication. 1997. Carl Trettin, Center for Forested Wetlands, Southern Research Station, Charleston, SC.

Instead of keystone species Amaranthus (this symposium) proposed using keystone microbial "groups or functions", such as nitrogen-fixing bacteria and mycorrhizal fungi, which are critical for maintaining ecosystem productivity. This concept recognizes that many different groups of soil organisms are active in the same soil process, for example - nitrogen mineralization. This overlap in function or "redundancy" by soil organisms is an important factor in determining what impact forest and range management has on soil ecosystems (Moore -this symposium). Unfortunately, the degree of microbial redundancy for most soil processes is not known (Busse - this symposium).

MANAGEMENT IMPACTS ON SOIL ORGANISMS

Forest and range management can have profound effects on numbers, activity and diversity of soil organisms. These effects are either positive or negative, depending on one's outlook or management objectives. Boyle (this symposium) took an optimistic view on soil resilience, and concluded that management had very little negative impacts on long-term soil functions, except under extreme conditions. Others (Belnap; Bennett; Ingham; Moldenke - this symposium) tended to look more on "the dark side", and concluded very little is known on long-term, management-induced changes of soil organism populations and processes.

Considerable information is available on the impacts of timber harvesting and subsequent site preparation on soil biological populations and activities (Edmonds; Ingham; Moldenke; Molina; Moore; Norton; Visser - this symposium). Similar information is available for grazing on western rangelands (Belnap; Stark - this symposium). The decrease in numbers and types of soil microorganisms and microfauna usually found after harvesting and site preparation is largely a response to lower soil organic matter levels, and changes in soil temperature and moisture conditions (Johnson 1992; Jurgensen and others 1997). Lower C:N ratios and lignin contents in litter from early successional plants established after timber harvesting (Myrold; Prescott - this symposium) could also affect the composition of the microbial communities. Ingham (this symposium) indicated that in western Oregon bacteria populations increased in young successional stands, compared to fungal-dominated soil populations in late seral and old-growth forests. She contends that by reducing soil fungal populations and increasing soil bacteria, clearcutting will decrease site productivity. In contrast, Norton (this symposium) reported that bacteria biomass decreased and the fungi/bacteria biomass ratio increased after a clearcutting. Since bacteria have a more rapid turnover than fungi, she concluded that bacteria are more active than fungi in soil nutrient availability.

Similar to timber harvesting, wildfire or prescribed burning affects the types and numbers of soil organisms by lowering soil organic matter levels and changing plant litter quality (DeBano and others 1998). However, a wildfire in an older, larger stand could increase the amount of coarse woody debris (Edmonds - this symposium). Fire favors the development of soil bacteria by decreasing soil acidity (Norton - this symposium). Of particular significance is an increase of nitrifying bacteria, which increases soil nitrate levels and possible nitrogen leaching losses (Myrold - this symposium). Volatilization losses of soil nitrogen could also increase the activity of symbiotic and nonsymbiotic nitrogen-fixing microorganisms after fire (Jurgensen and others 1997).

Soil compaction by logging equipment would directly restrict the movement of various soil fauna in the mineral soil by decreasing pore size, especially macropores, and the burrowing-ability of larger soil fauna, such as earthworms. Both the soil microflora and fauna would be affected by changes in soil moisture and oxygen levels at higher bulk densities (Startsev and others 1998). All of these factors could account for reported decreases in mycorrhizae numbers and types in compacted soil (Amaranthus and others 1996). How long compaction would impact soil organisms depends on how quickly soil bulk density returns to preharvest conditions. If soil compaction lowers plant growth, the reduction in the amount of organic matter returned as litter and root turnover would also affect soil organism populations and activity. The impact of both soil compaction and soil organic matter levels on long-term site productivity is being investigated on various sites throughout the United Sates and Canada (Powers 1991).

MANAGEMENT OF SOIL ORGANISMS

The main focus of most public and private forest management has been on forest protection and productivity. Consequently, the management of forest soil organisms has dealt mostly with specific groups, which had either detrimental or beneficial effects on tree growth or stand development. Both Thies and Harvey (this symposium) discussed the implications of forest management operations on root diseases, and how this relates to current questions on forest health and productivity. The beneficial effects of mycorrhizal fungi on plant growth is being used in forest nursery management to try and improve the success of out-planted seedlings (Castellano 1996). There have been various attempts to use nitrogen-fixing plants instead of adding N fertilizers to Pacific Northwest forests (Everett and others 1991; Trowbridge and Holl 1992). However, the increased competition from nitrogen-fixing plants when grown in mixed plantings with conifers seems to have limited the widespread application of this management option.

While efforts to manage specific soil organisms for the maintenance or improvement of forest and range productivity will continue, questions are being raised as to whether management activities should also consider soil organism diversity (Busse; Ingham; Moldenke - this symposium). The answer is obvious if organisms are listed as threatened or endangered (Molina - this symposium), or are considered important in the restoration of degraded ecosystems (Belnap; Bennett; Pellant - this symposium). How important soil organism diversity is to overall ecosystem diversity and stability, and whether various management practices (for example, clearcutting or prescribed fire) are detrimental to soil biodiversity is not as clear.

As noted above, any management practice which changes the amount and quality of soil organic matter, raises soil pH, removes nitrogen, or compacts the soil will affect soil organism populations and diversity. Many studies have found reductions in numbers and types of soil organisms immediately following or several years after timber harvesting (Spence; Visser-this symposium). While such short-term results are important, managers also need to know: 1) how different these management-related changes in soil organism populations are from those occurring after natural disturbances (fire, blowdown), 2) whether the pattern of soil organism succession is changed as the new stand develops, and if so, 3) do these changes affect soil productivity or sustainability. This is illustrated in Figure 1, where timber harvesting was assumed to reduce soil organic matter content by different amounts, which resulted in long-term changes in soil organism diversity. Conventional wisdom is that the soil with the greatest number of soil organism types or species after harvest will result in a more diverse soil ecosystem as the stand ages, and be more productive and sustainable than the one with lower initial soil diversity. However, the ability or "redundancy" of many different soil organisms to carry out important soil functions and processes makes this assumption questionable. Does a reduction of 25 in some measure or index of soil diversity mean that soil respiration and nitrogen mineralization will be less, or that soil organisms will be less able to adapt to possible future climate change? How much can soil organism diversity be reduced before such changes occur? Unfortunately, there is very little information on the impact initial changes in soil organisms have on long-term ecosystem diversity, and how important organism redundancy is for soil processes. Spence (this symposium) reported that arthropod populations in a mixed aspen-conifer soil forest one and two years after a wildfire were much different than in an adjacent clearcut, but these differences were not evident after 30 years. In contrast, rhizosphere changes in microflora and microfauna were still present ten years after Douglas-fir trees were injected with chloropicrin or methylisothiocyanate to control *Phellinus weirii* root rot (Ingham and Thies 1997). Moldenke (this symposium) stressed the importance of such long-term studies to assess management effects on soil organism populations and diversity.

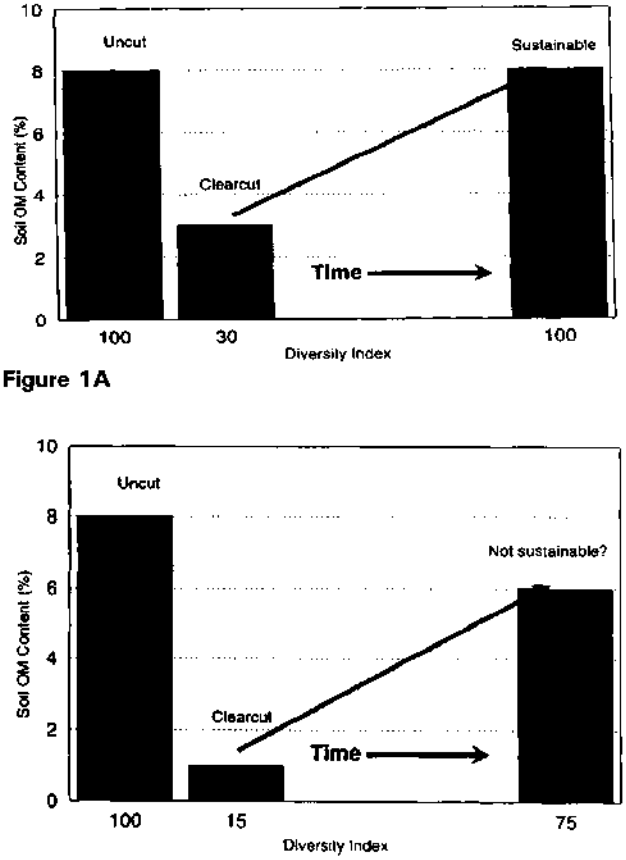

Figure 1A

Figure 1B

Figure 1 —Possible changes in soil biodiversity as related to changes in soil organic matter after timber harvesting: A. Higher soil organic matter content, B. Lower soil organic matter content.

BOTTOM LINE

The overwhelming consensus of this symposium was that forest and range management activities do have pronounced effects on soil organisms. However, it was not clear if these management-induced changes in population numbers and diversity are long-term, and if so, how important are they for soil productivity and stability. Until more information becomes available, it would seem prudent to manage in ways which maintain soil organism populations and diversity, and is consistent with overall management objectives. Fortunately, such management activities are usually beneficial to both soil organisms and other components of forest and range ecosystems. The keys to such management is to maintain or increase the amount of organic matter in or added to the soil, and reduce soil compaction (Busse; Ingham - this symposium). Both of these activities will favor soil organism populations and diversity, and maintain or increase site productivity. Consequently, managers should ask the questions: 1) how will this management activity affect soil organic matter levels and soil compaction now and in the future, and 2) can organic matter losses and compaction be reduced (for example - no dozer piling, the use of forwarders, fencing streams) and still accomplish management objectives. The current focus on ecosystem management with it's emphasis on a wide variety of successional stages, stand densities and plant communities across a landscape should provide various litter types and soil microsite conditions to promote soil organism diversity.

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ABSTRACTS OF PAPERS NOT SUBMITTED

SOIL FOODWEBS

Elaine Ingham[1]

ABSTRACT

The soil foodweb is important because plant productivity increases as soil foodweb complexity increases. An incredible wealth of interactions, complex feedbacks, and less-than-obvious subtleties are hidden in this simple statement. In order to reduce the cost of growing row crops, herbs, shrubs, orchards, and forests, we need to manage soil organisms. We need to be aware that soil organisms exist, to know which ones help which plants grow, and which ones harm those plants. In order to manage those organisms, we need to be able to measure them.

The soil foodweb includes several trophic levels. The first trophic level includes plants and other organisms that fix carbon dioxide into biomass using sunlight for energy. The second trophic level are the bacteria, fungi, root-feeding nematodes and arthropods, which convert plant material into their own biomass, metabolites, and respiratory products. The third trophic level organisms, are the predators of bacteria and fungi, including protozoa, bacterial- and fungal-feeding nematodes, and fungal-feeding microarthropods. Several higher trophic levels may exist (maybe as many as fourth, fifth, sixth, and higher levels) which are predators of the predators, and include many forms of arthropods, worms, insects, and aboveground birds, and mammals.

Bacteria and fungi immobilize N in their biomass, and along with soil organic matter, which these organisms produce, contain the majority of the nutrients in a healthy soil. These nutrients need to be moved from the organisms into plant-available forms at the speed and in the places the plants need them. If mineralization into plant-available forms is more rapid than plants require, the nutrients can be leached or volatilized from the system. Too little mineralization, and the plants will be nutrient limited. The organisms that eat bacteria and fungi turn the nutrients immobilized in bacterial and fungal biomass into plant-available forms. Thus, protozoa, nematodes and microarthropods, are critical players in plant production. But these predators can overeat bacteria and fungi, and so those predators that eat predators of bacteria and fungi are important for keeping balance.

Along with nutrient cycling, a complex soil foodweb keeps disease-causing organisms in check. It also improves soil aggregation, ease of root penetration and water infiltration, and increases decomposition of a greater variety of plant materials, and anthropogenic compounds. As a greater diversity and a greater number of functional groups of organisms occur in the soil, competition with disease-causing organisms is greater.

The soil foodweb greatly influences the production of soil aggregates, soil pores and soil channels. An analogy to building a brick house is useful here. To build bricks, straw and sand have to stick together. Then the bricks are held together with mortar to form walls. The house has structure when the walls are arranged in certain patterns. Different organism groups in the soil foodweb do the same for soil structure. Bacteria glue the clays, silts and sands together into microaggregates. Microaggregates are bound together by fungal hyphae, root hairs and roots. The structure of the rooms are made by the arthropods, insects and earthworms. Only when all the organisms are present and active can roots and water move into the soil with ease.

Soil compaction is a major disturbance of soil aggregation. When heavy machinery moves across the soil, the pores and channels within the soil collapse. As the space in the soil is reduced, the organisms living in those spaces are killed. The applied force and strength of the soil aggregates determines the extent of damage. The greater the force and the stronger the aggregates, the less damage will occur to the soil. One way of looking at this is to say, if a highly complex soil foodweb is present, better built soil aggregates will be present, and the bigger the truck is that can be driven on the land. Alternatively, an assessment of the soil type and the soil foodweb should yield an understanding of how fragile soil structure is, and thus what kinds of vehicles can be used without destroying critically important functions in that soil.

It is critical to understand the benefitis a complex soil foodweb, can give to an ecosystem. It is important to understand what disturbances do to this foodweb, and how to repair that damage if it proves necessary to allow those disturbances to occur.

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[1] Elaine Ingham is an Associate Professor in the Department of Botany and Plant Pathology at Oregon State University, Corvallis, OR 97331.

NUTRIENT & SOIL ORGANISM POPULATION DYNAMICS-THE BASIS OF ECOSYSTEM STABILITY

John C. Moore[1]

ABSTRACT

There are three objectives to this presentation. The first objective is to make explicit connections between the plants and decomposers. Much of ecological theory is based on plant-herbivore-predator models. Differences between terrestrial and aquatic ecosystems notwithstanding, most primary production is not consumed by herbivores, rather it is decomposed by microbes. A thorough treatment of the detritus-decomposer-consumer pathway and linkage of this pathway to the plant-herbivore pathway has yet to be conducted.

The second objective is to formalize an observed connection between changes in community structure, nutrient dynamics and the mathematical stability of an ecosystem (local stability and resilience). My research has demonstrated that communities are composed of stable assemblages of species that share common habitats, food, and life history traits. Within soils, these assemblages are the pathways of trophic interactions and nutrient flux from plant roots, bacteria and fungi. The resilience of these pathways depends on the physiologies of the species within them. The bacterial pathway is more resilient and mineralizes nitrogen at a faster rate than the fungal pathway. Disturbance induces a shift in activity from the fungal to the bacterial pathway resulting in increased decomposition and nitrogen mineralization rates, and thus lower nutrient retention. These changes in nutrient dynamics have been shown to destabilize mathematical models of the ecosystems.

The final objective is to explore the interplay between diversity and function. Linking function to biodiversity requires studying both of them during community responses to disturbance. Traditional approaches identify a duality to diversity and to the mechanisms that govern it, i.e., animal diversity is linked to plant diversity. Where detritus and detritivores fit in is less clear, but will have to be resolved to answer how biodiversity affects ecosystem function. Within soils, there appears to be a balance between taxonomic specificity and redundancy in function. Key taxa are needed for decomposition to proceed, but, following major disturbance, functional diversity recovers before species diversity.

My overall theme is that the energetic organization of communities, as defined by nutrient and population dynamics, forms the basis of ecosystem stability. Five propositions are presented.

PROPOSITION I

The utilization of resources by species is highly diverse and compartmentalized. The ability to shift from one food source to another and between habitats are adaptations that have implications beyond the ability of an organism to persist, but are important at the system and community levels as well.

PROPOSITION II

Ecosystems are organized as a series of quasi-independent interacting energy pathways. The pathways are made up of species that share similar habitat requirements and complimentary life history traits. As a result of this, matter is processed and energy is transferred within the pathways at distinct rates. In soils, these pathways originate from plant roots and detritus. The detritus pathway is divided into a bacterial pathway and fungal pathway.

PROPOSITION III

The species composition of the plant community and decomposer communities are tightly coupled through plant litter quality. Species within the fungal and bacterial pathways have adapted to the chemical composition of the substrates produced by the producer (plant root) pathway.

The importance of litter quality to decomposition is well established. The relationship between plant and soil communities is a function of litter quality. For example, pine forests possess a distinct decomposer community compared to a sage meadow.

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[1] John C. Moore is Associate Professor, Department of Biological Sciences, University of Northern Colorado, Greeley, CO 80639.

PROPOSITION IV

Disturbances alter energy pathways and hence the pattern of energy flow within ecosystems. Nutrient availability to plants and retention within the ecosystem are affected by changes in the activity of energy pathways. In soil, disturbances have a disproportionately large adverse affect on the fungal pathway compared to the bacterial pathway. Nutrient availability and retention were either tied to the activities of the fungal pathway, or is a function of the combined activities of the bacterial and fungal pathways, and how synchronous these activities are with plant growth.

Links between nutrient dynamics and population dynamics are explored through the life histories of the organisms. Evidence is presented from agricultural studies and sites under managed grazing.

PROPOSITION V

The distribution of biomass within a system (trophic structure), and how the system responds to a disturbance (dynamics and resilience) is a function of the rate of energy input and the rate at which energy is transferred among organisms within the system. The relationship between soil communities and how they respond to disturbance to nutrient dynamics is explored.

A series of hypotheses is proposed as follows:

H1: Decomposition rates and nitrogen mineralization rates increase following physical disturbances of soil due to a shift in function away from the fungal pathway to the bacterial pathway.

H2: Nutrient retention decreases in disturbed soils due to changes in the community from a stable to unstable pattern of interactions.

H3: Functional diversity is more resilient than taxonomic diversity due to the high degree of redundancy in function among taxa.

H4: Nutrient retention is enhanced by increased species diversity within the fungal rather than the bacterial pathway due the greater resilience of the bacterial pathway and to the stronger coupling of fungi to resistant plant substrates.

FOREST MANAGEMENT INTERACTIONS WITH SOIL ORGANISMS

James R. Boyle[1]

ABSTRACT

Soil organisms, macro-, meso- and micro-, are involved in the dynamics of matter and energy in forest ecosystems, influencing plant growth, soil properties and other ecosystem components. Critical ecosystem processes, including transformations of organic matter to yield plant-available nutrient ions, and maintenance of soil porosity, are controlled by soil organism activities.

Forest management activities (and "natural" disturbances) alter the physical and chemical environments of soil organisms. Amount and composition of organic matter in forest floors and within soils are changed as plant cover is altered and residues are added. Solar radiation inputs, temperature fluctuations, and water dynamics are influenced by forest management. Changes in organic matter alter availability of energy, carbon and other elements on which soil organism metabolism depends. Diversities and community compositions of soil organisms are therefor changed, as are ecosystem processes.

Forest scientists and managers are well-advised to consider potential changes in critical or limiting ecosystem processes, including those mediated by soil organisms, as they plan, execute and evaluate impacts of forest management. Sustainability of forest ecosystems, simple or complex, intensively- or extensively-managed, is dependent on basic ecosystem processes and components, not on flows of human- defined forest products and values. Soil organisms are among the "hidden" ecosystem characteristics that must be maintained.

[1] James R. Boyle is Professor of Forestry and Soil Ecology, Forest Resources Department, College of Forestry, Oregon State University, Corvallis, OR 97331

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To provide a review of the state-of-the-science about soil organisms for management, a symposium was convened to address soil organism functions and processes and management effects on soil organisms and processes, and to describe some roles of soil organisms in restoration and applications for land management. The focus of the symposium was on Pacific Northwest forest and rangeland ecosystems.

Keywords: Soil organisms, soil quality, nutrient cycling, nitrogen transformation, foodwebs, ecosystem, bacteria, fungi, anthropods, root diseases.

Pacific Northwest Research Station
333 S.W. First Avenue
P.O. Box 3890
Portland, Oregon 97208-3890