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Proceedings of a symposium held at the University of Vermont, Burlington, September 16-17, 1983, in recognition of the contributions by women scientists.

Edited by Margaret M. Harris and Ann M. Spearing

ABSTRACT

Proceedings of a symposium sponsored by the Civil Rights Action Committee of the Northeastern Forest Experiment Station and the University of Vermont School of Natural Resources to provide a forum for the presentation of current research in natural resource fields by women scientists.

RESEARCH IN FOREST PRODUCTIVITY, USE, AND PEST CONTROL

Proceedings of a symposium held at the University of Vermont, Burlington, September 16-17, 1983, in recognition of contributions by women scientists.

Sponsored by

USDA Forest Service, Northeastern Forest Experiment Station,

University of Vermont, School of Natural Resources

Edited by

Margaret M. Harris

Ann M. Spearing

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FOREWORD

In 1982 the Northeastern Forest Experiment Station and the Northeastern Area State and Private Forestry set aside a portion of their Civil Rights budget to fund a number of special projects. It had been a high priority goal of the Forest Service to promote, enhance, and endorse Civil Rights activities, and the Special Project Fund was an innovative addition to the existing Civil Rights Affirmative Action Plan.

On September 24, 1982, the staff of the Burlington Laboratory of the Northeastern Forest Experiment Station responded to the call for special project proposals and submitted, in cooperation with the faculty of the School of Natural Resources of the University of Vermont, a request to support a seminar for women natural-resource professionals. Although there are more women in forestry than ever before, the numbers of women who are principal researchers, forestry professors, and forest managers are still small compared to the numbers of men in these jobs. Furthermore, because they have entered forestry in significant numbers only recently, women forest researchers have not been highly visible. Therefore, a proposal was drafted to organize a symposium which would serve as a forum for women foresters to share their work and set up professional communications among women in the various forestry agencies. It was further intended to provide an outlet for recent research findings.

Admittedly, the ratio of women to men in forestry is small, but when we began our search for qualified women researchers, we found many candidates in federal, state and private employment. It was difficult to choose among the very capable and highly recommended professionals.

The final agenda covered a full day and a half, with a mix of formal presentations, panel discussions, and audience questions. It is our intention, in publishing these proceedings, to make available to the public the research work of a few of the women natural-resource scientists in the United States. Perhaps this publication will also serve to attract others to any future symposia of this kind and encourage the interest of students in environmental curricula.

The program committee thanks the many people who contributed their time and efforts to the success of the symposium. Particular thanks go to Moe Douglas at the University of Vermont School of Natural Resources and Elizabeth Crosby, U.S. Forest Service, Burlington, for editorial and secretarial work and to the personnel from the U.S. Forest Service office in Washington, D.C., for their support of our endeavors. Finally, we wish to thank all the speakers, panel members, and guests who made it all happen.

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PREDICTING RESPONSE OF FOREST DEFOLIATORS TO INSECTICIDES[1]

Molly W. Stock[2] and Jacqueline L. Robertson[3]

Abstract.--This report describes an approach we are using to understand differences in response of forest insects to control efforts with insecticides. Why, for example, does spraying kill some insects but not others? Why does a certain chemical work sometimes but not other times? To help answer these questions, we are integrating results of basic research on insect biology, toxicology, ecology, and genetics. A computer model has been developed that incorporates information on extrinsic variables (chemical, dose, rainfall) and features of the insects themselves (species, developmental stage, genetic level of susceptibility). Using this model, cumulative effects of key variables can be simulated and predictions of population response made. We have found, for example, that for the Douglas-fir tussock moth, timing of spray application is crucial when acephate is used. For carbaryl, it is particularly important to know the genetic makeup of the population to be sprayed. For the western spruce budworm, timing of spray is not as critical as dose. This model is permitting more accurate forecasts of insecticide efficacy and will enable forest managers to use chemical control more judiciously.

INTRODUCTION

Biological systems are enormously complex. To deal with them effectively, as scientists and as human beings, we must first simplify them, trying to understand one small part at a time, then putting these pieces of knowledge together, bit by bit, to build a solid edifice of understanding. At the same time, we must continually seek ways to view our ideas and our perceived understanding in new ways, from different perspectives. We must continually rearrange our knowledge, as we add to it, so that it more closely approximates reality. Ultimately, what we seek is to be able to predict, to take our understanding of a limited area of the universe and to extrapolate accurately to other areas of the universe.

The history of forest entomology and approaches used to study forest insects today reflect all of these aims. Forest entomologists began, about 100 years ago, by describing and categorizing the insects they discovered. Little consideration was given to their relationships to the forest and to each other. However, as the necessity for more intensive management of forests resulted in the practical science of forestry, so has forest entomology become more practical in orientation. Other factors have also influenced the development of modern approaches in forest entomology and have opened up new areas of study. Important discoveries, such as that of chemical communication, and technical advances, such as computer-aided data processing, have revolutionized the ways that we study insects and the perspectives with which we view them. Perhaps most significant has been the evolution of integrated approaches to problem-solving. Interdisciplinary research efforts are now more the rule than the exception; we work less and less productively in isolation from each other. There is also a much greater awareness of interactions among the various facets of the ecosystem.

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[1] Paper presented at the symposium, Research in Forest Productivity, Use, and Pest Control, Burlington, Vermont, 16-17 September 1983.

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Yet many of the questions that forest managers and forest scientists are asking today are very similar to the questions that have been asked for the past several decades. For example, why do outbreaks of forest insects occur in some places and not others? What starts an outbreak and what causes the natural decline in numbers at the end of an outbreak? Why does spraying kill some insects but not others? Why does a certain chemical work sometimes but not other times?

In spite of the importance of these questions, and the extraordinary amount of time, effort, and money that has gone into answering them, not much progress has been made. Part of the problem lies in the great complexity of the system we are trying to understand. To simplify our understanding of the interactions between insects and their environment, Clark et al (1967) developed the life system concept (Fig. 1). According to this scheme, an organism's success, measured by its numbers and persistence, results from the interaction of the genetic makeup of its component individuals with the effective environment.

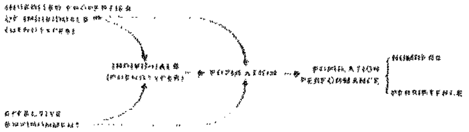

Figure 1.--The life system, showing the relationship between genotype and environment.

Conceptually, the life system is very satisfying; in practice, it is not particularly easy to work out which, of all the variables, constitute the "effective environment" or how to characterize the genetic makeup of the population. But this scheme has helped show us that some of the problems we have had in acquiring answers to our questions may arise from a focus on the environmental aspects of the system, at the expense of an understanding of the genetic or intrinsic components of insect populations. As Wellington (1977) pointed out,

> For decades, a "population" has been viewed as a passive, monolithic lump of protoplasm, out of which chunks are carved by all the lethal agents assailing it. The comparative . . . practical values of any agent have been judged primarily by the size of the chunk it removes . . . . That preoccupation has prevented us from recalling that the pests which concern us most have been surviving in very hostile environments much longer than we have been trying to destroy them.

We are asking, How can we kill more of them?, when we should be asking more relevant questions, such as, What adaptations allow them to evade extinction? And we have paid for our resulting ignorance every time a conventional pest control program has failed.

Because it is being recognized that our view of insect control is rather one-sided, there has been an increasing attention to the attributes that promote species survival, on population variation--the "other half" of the life system. In our research, we set out to understand relationships between genetic and toxicological variation among forest insect populations. Our work focused on two of the questions posed above: Why do insecticides kill some insects and not others, and why are chemicals effective sometimes but not other times? Our aim has been to develop a realistic scheme for accurately predicting results of insecticide application in field situations.

From the toxicological perspective, laboratory experiments--because they are less expensive and inherently more controlled than field trials--have traditionally been used to estimate results of field application of insecticides. Early laboratory studies emphasized testing of chemicals by directly applying them to fully exposed insects, then extrapolating results to suggest field application rates. This procedure is inherently inaccurate because measurement units in topical application bear little, if any, relationship to those actually reaching insects in the field. Factors such as shielding of insects by foliage, dilution of chemicals by rainfall, differential response within and among populations, and ingestion of the chemical by feeding on sprayed foliage must also be considered. Over time, laboratory bioassays have become increasingly sophisticated, incorporating evaluation of the effects of all these variables. At the Berkeley USDA Forest Service laboratory, a comprehensive data base on the toxicological response of two important forest defoliators--the Douglas-fir tussock moth (Orgyia pseudotsugata McDunnough) and the western spruce budworm (Choristoneura occidentalis Freeman) has been systematically accumulated over the past 15 years.

It is now clear, from these and related studies, that genetic variation in population response should be considered when chemical control is used. In these two species, we found not only differences in tolerance (a general term used to describe the natural variation in response occurring among populations of a species) but also apparent resistance (a term conventionally used to describe the response of insect strains actually modified by insecticide usage). Tests on Douglas-fir tussock moth populations revealed a two-fold difference in response to carbaryl (expressed as ratios of LD_{50}s) when just four populations were examined (Stock and Robertson 1979). To determine whether these differences had an underlying genetic basis, we tested sibling groups (offspring from single-pair matings in the laboratory) and found significant variation among groups (in one case, a 12-fold difference). Similar work with the western spruce budworm revealed a three-fold difference in tolerance to acephate between a field population from Idaho and a laboratory colony (Stock and Robertson 1980). Response of budworm sibling groups also varied nearly three-fold. More recent studies (see Robertson and Stock, these proceedings) have shown that some western spruce budworm populations are 18 times more tolerant of carbaryl than others.

Further research has been aimed at understanding the specific genetic and physiological mechanisms underlying differential population response. Once an insecticide enters an insect's body, it is subject to degradation by a variety of enzymes. Whether or not death occurs is directly related to the efficiency of key enzymes in the detoxification process. The role of esterases in the hydrolysis of organophosphate toxicants, such as acephate, resulting in formation of nontoxic products, is well known. Insect esterases are highly polymorphic; in some groups, as many as 20 alleles have been observed at one esterase locus. Variation in these enzymes has been linked to variation in response to organophosphates in a number of insect species (e.g., Beranek 1974, Pasteur and Sinegre 1975, Sudderuddin 1973). Commonly present among the esterases are silent (null) alleles which code for inactive enzymes or no proteins and which may also be associated with differences in tolerance among groups. Differential response of at least two insect groups, including the western spruce budworm, has been related to frequencies of null alleles at an esterase locus (Stock and Robertson 1982, Tsakas and Krimbas 1970). Insect esterases have thus provided a rich source of experimental material for the study of insecticide effects.

The technique we used to identify differences in esterases within and among populations is electrophoresis, the separation of charged molecules in an electric field. Proteins produced by different gene forms at a chromosome locus commonly differ slightly in overall charge. Thus, when they are put into an electric field, they will migrate in one direction or other at a speed related, in part, to their charge, and the different gene products will separate out (Fig. 2). In practice, homogenate of individual insects is absorbed onto small paper wicks and inserted into a starch gel medium. Then an electric current is applied for a few hours and the proteins move through the starch gel medium. Separate slices of the gel are then stained with substrate-specific stains which color those areas of the gel where the different products of a particular gene type have localized. One can then see bands on the gel, a direct visualization of genetic similarities and differences among individuals in a population, and quantitative information is obtained for comparison of groups. Such data are particularly useful for evaluating overall population or species relationships in taxonomic and evolutionary studies, or for comparisons of specific gene types, such as the esterases in toxicological work.

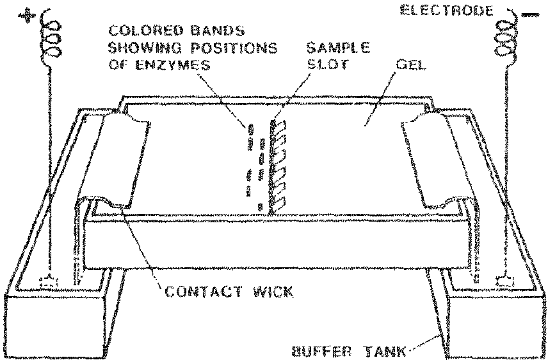

Figure 2--Schematic diagram of the technique of gel electrophoresis.

On the basis of combined genetic and toxicological work of this type, we were able to categorize Douglas-fir tussock moth and western spruce budworm populations as inherently susceptible (i.e., most die), tolerant (many don't die), or resistant (few die) to acephate and carbaryl. However, while interesting and potentially useful, all this earlier work was a far cry from being able to say how effective an actual spray program was going to be; further integration of the toxicological and genetic information was needed.

In collaboration with Dr. Jo Ellen Force at the University of Idaho, and Dr. Carroll Williams at the USDA Forest Service, Berkeley, we recently developed a probability model to integrate information on variables known to affect insecticide efficacy in field applications and to simulate their cumulative effects. Model input includes insect species (Douglas-fir tussock moth or western spruce budworm), chemical (acephate or carbaryl), dose applied, genetic response level (susceptible, tolerant, or resistant), age of insects (larval instar distribution), and foliage moisture condition (dry or wet from rain at various intervals just prior to or after spray).

A few examples of model output are shown here. For a carbaryl-tolerant Douglas-fir tussock moth population sprayed under dry conditions, low doses (70-140 g/ha) are most effective during the first 6 days after the caterpillars are first seen, and then after about 4 weeks (Fig. 3). Higher doses of carbaryl are effective any time. For carbaryl-susceptible Douglas-fir tussock moth populations, lower doses result in much higher mortality (Fig. 4).

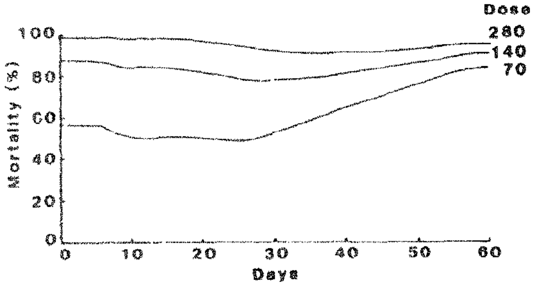

Figure 3.--Simulated mortality of carbaryl-tolerant Douglas-fir tussock moth treated with 3 dose levels of carbaryl in relation to days after egg hatch.

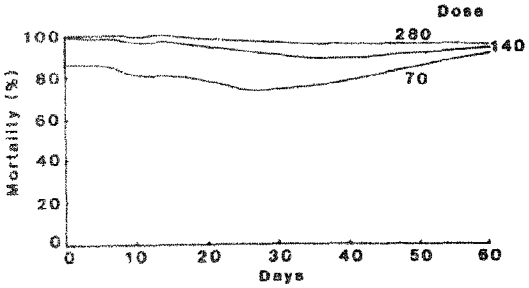

Figure 4.--Simulated mortality of carbaryl-susceptible Douglas-fir tussock moth treated with 3 dose levels of carbaryl in relation to days after egg hatch.

For acephate-tolerant western spruce budworm (the most common population type), low doses are nearly as effective as high doses during the 5th week after emergence (Fig. 5). When western spruce budworm are sprayed with carbaryl under dry conditions, mortality showed a consistent pattern regardless of dose (Fig. 6). Mortality fell steadily over development.

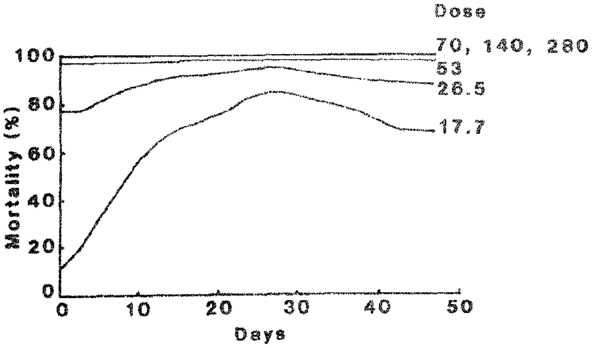

Figure 5.--Simulated mortality of acephate-tolerant western spruce budworm treated with 6 doses of acephate in relation to days after emergence of second-stage larvae from hibernacula.

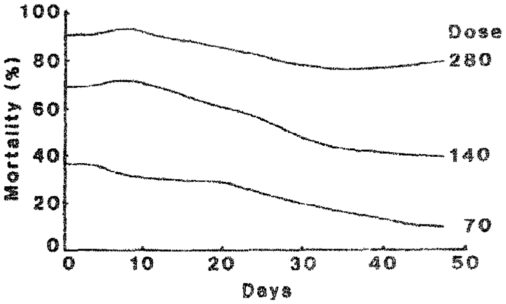

Figure 6.--Simulated mortality of carbaryl-tolerant western spruce budworm treated with 3 different doses of carbaryl in relation to days after emergence of second-stage larvae from hibernacula.

When acephate application to wet foliage was simulated, predicted mortality of insects of either species was drastically reduced for both tolerant and susceptible populations (Figs. 7 and 8).

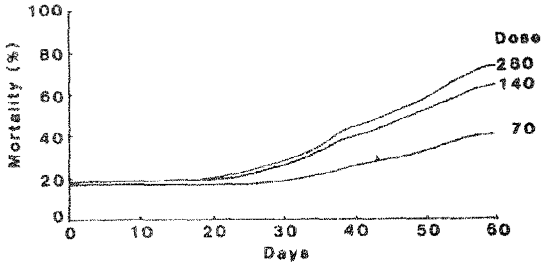

Figure 7.--Simulated mortality of acephate-tolerant Douglas-fir tussock moth on wet foliage to 3 different doses of acephate in relation to days after egg hatch.

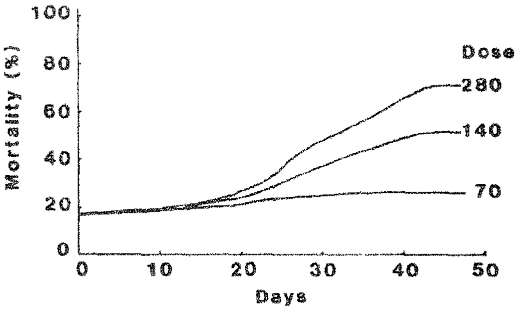

Figure 8.--Simulated mortality of acephate-tolerant western spruce budworm on wet foliage to 3 different doses of acephate (in relation to days after emergence of second-stage larvae from hibernacula).

Several generalizations can be drawn from these simulations. For example, for the Douglas-fir tussock moth, timing of spray application is crucial, especially when acephate is used. When carbaryl is used on the Douglas-fir tussock moth, it is particularly important to know the genetic makeup of the population to be sprayed. If the population is carbaryl-tolerant, spraying near the end of population development will give highest mortality. For the western spruce budworm, timing of spray is not as critical as dose. And if the foliage is wet at the time of spray, or if rain is expected soon after spray application, very low effectiveness will be obtained.

In terms of basic science, the model provides ideas and hypotheses for future research and testing. For example, we now recognize the need to evaluate the effects of host plant foliage on insecticide response. We also realize that the existing information used to predict and stimulate effects of rainfall must be expanded and refined. The model is also helping us provide after-the-fact explanation of why successful or unsuccessful results were obtained by a chemical control effort and, perhaps most important, is permitting more accurate forecasts of insecticide efficacy. Williams and Robertson (1983) found that the model predicts results of actual field applications with 73-95% accuracy. We have just completed development of a generalized, interactive ("user-friendly") model expanded to simulate efficacy of any chemical over time during seasonal development of a western spruce budworm or Douglas-fir tussock moth population. It is written in BASIC and can be operated on a minicomputer. This second-stage model will permit comparison of the effectiveness of a diversity of chemicals when decisions are being made in a control program. Next, the program will be adapted for use with other forest defoliators.

Information obtained with models such as these will enable forest managers to use chemical control more judiciously--choosing to use it when it will be most effective, choosing alternative methods when model output suggests that chemical control will be ineffective. Ultimately, time and effort can be saved, and environmental contamination by toxic chemicals reduced.

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DIFFERENTIAL POPULATION CHARACTERISTICS OF WESTERN SPRUCE BUDWORM[1]

Jacqueline L. Robertson[2] and Molly W. Stock[3]

Abstract.--Western spruce budworm populations differ significantly in their responses to carbaryl, an insecticide currently registered for their control. Although we interpret these differences in population response to be the result of cross-resistance between DDT and carbaryl, the possibility exists that the wide range of tolerance levels represents only natural variation. In either case, the underlying assumption of the insecticide registration process--that population responses are equal or vary only within relatively narrow limits--does not appear to be valid for carbaryl. We examine the evolution of this realization from the general assumptions that guided forest pest control practices beginning with the use of DDT in 1947.

INTRODUCTION

Spruce budworms (Choristoneura species) are among the most destructive defoliators in North America. In the eastern United States and Canada, the spruce budworm, C. fumiferana (Clemens), feeds primarily on balsam fir. White spruce, red spruce, black spruce, larch, hemlock and pines may also be defoliated (Baker 1972). The western spruce budworm, C. occidentalis Freeman, feeds primarily on Douglas-fir and white fir throughout the Pacific Coast States and British Columbia. Other hosts included grand fir, subalpine fir, western larch, Englemann spruce, white spruce, and blue spruce (Furniss and Carolin 1977).

Western spruce budworm larvae feed on buds and new foliage. Sustained heavy feeding may cause almost complete defoliation in 4-5 years. Epidemics may result in decreased tree growth, tree deformation, top-killing, and tree death over extensive areas.

Prior to 1963, when its use was banned, DDT was heavily used for control of both eastern and western spruce budworm. For example, between 1952 and 1963, over 3,300,000 acres of forests in the northern Rocky Mountains were sprayed with DDT (Fellin 1983). The reasons for the frequent use were simple: DDT was readily available; it was cheap; it could be applied from aircraft; and it was effective.

Without DDT, and with the growth of integrated pest management practices for forest insects in recent years, the use of chemical control has decreased dramatically. However, several chemicals are still available for use against the spruce budworm and western spruce budworm. At present, carbaryl is one of the most commonly used insecticides in the United States. It is the active ingredient in such products as Sevin garden dust and flea powder. One reason for this widespread use is carbaryl's low toxicity to mammals and birds. The Sevin-4-oil formulation is registered by the Environmental Protection Agency for use as a forest spray for control of both spruce budworm and western spruce budworm (Hamel 1982).

The basic premise of the current insecticide registration process is that a chemical can be recommended for use at one rate for a given insect species because responses for populations of one species are equal or vary within relatively narrow limits. We have examined this premise in the case of western spruce budworm populations treated with carbaryl and have concluded that it is not

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[1] Paper presented at the Research in Forest Productivity, Use, and Pest Control Symposium, Burlington, Vermont, September 16-17, 1983.

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valid. This premise is the latest in a series of assumptions that have guided forest insect control practices since the introduction of DDT. In our opinion, this assumption should be discarded in favor of a more biologically realistic approach to the use of insecticides as part of the integrated pest management systems for forest insects.

INSECT SYSTEMATICS AND PEST MANAGEMENT: PAST ASSUMPTIONS

Biological classification is a familiar subject. Living things are divided into two kingdoms, plant and animal. Kingdoms are divided into phyla, for example, the phylum Arthropoda. A phylum is divided into classes, for example, the class Insecta. A class, such as the Insecta, is divided into numerous orders. The order with which we are concerned is the Lepidoptera. An order, such as the Lepidoptera, is further divided into families. The spruce budworms are in the family Tortricidae. Other important families with respect to forest trees are the Lymantriidae, including such insects as the Douglas-fir tussock moth and gypsy moth, and the Geometridae, commonly called the inchworms or measuring worms. Families are divided into genera, such as the genus *Choristoneura*. A genus is divided into species, and a species is composed of populations.

From the time DDT began to be used routinely to control forest defoliators in 1947, forest entomologists assumed (on the basis of no data) than any chemical toxic to an insect species in any family would be equally toxic to the other species in that family. This assumption probably resulted from the fact that DDT was toxic to virtually every insect pest from the body louse to the budworm when it was first used and before resistance began to appear. We were the first to question this premise when we compared to responses of various forest geometrids (Table 1) (Robertson et al. 1974). We concluded that the large differences in LD_{50} values, sometimes over 100-fold, clearly showed the risk involved in predicting insecticide toxicity to one species on the basis of data obtained for a different genus in the same family.

We next examined another presumption, that is, that species in the same genus would have equal responses to any chemical. In 1978, we tested species in the genus *Choristoneura* (Robertson et al. 1978). Table 2 is a sample of our results. These data are for carbaryl, and show almost a thirty-fold difference in response between the most and least susceptible species. Our overall results are shown in Table 3. Since the hypothesis of equality (Savin et al. 1977) was not accepted among species for any of the 22 chemicals tested,

Table 2.--Responses of *Choristoneura conflictana* (C), *occidentalis* (O), *lambertiana* (L) and *viridis* (V) to carbaryl

Species	LD_{50}(95%CL)[a]
C	3.65(2.92-4.35)
O	19.9(14.5-26.5)
L	30.6(11.5-44.5)
V	109(6.90-325)

[a] µg/g body weight. 95% CL are 95% confidence limits.

Table 1.--Decreasing order of susceptibility at LD_{50} of forest geometrids[a] to eight insecticides

Insecticide	Most susceptible	Times less susceptible		
		1.3-12	30-60	128- 417
Bioethanomethrin	E	--	P(50)[b]	C(167)
DDT	L	E(1.3)	A(32)	C(142)
Malathion	L	E(7.0)	P(>29)	A(152), C(>417)
Mexacarbate	E	L(2.0)	A(30), C(47)	P(128)
Phosmet	E	--	C(34)	--
Phoxim	E	C(12)	P(38)	--
Pyrethrins	E	L(2.0), P(7.0)	A(40), C(60)	--
Tetrachlorvinfos	E	C(6.9)	A(38), P(38)	--

[a] Abbreviations for species are: A = *Alsophila pometaria*; C = *Calocalpe undulata*; E = *Ennomos subsignarius*; L = *Lambdina fiscellaria lugubrosa*; P = *Paleacrita vernata*.

[b] Value in parenthesis indicates LD_{50} less susceptible species LD_{50} most susceptible species.

Table 3.--Summary of tests of the hypothesis of equal responses among *Choristoneura* species

Type of insecticide	Number tested	Number of species compared	Hypothesis accepted for any chemical?
Carbamate	4	2-6	No
Chlorinated hydrocarbon	1	6	No
Organophos-phorous	11	2-4	No
Pyrethroid	6	2-5	No

we concluded that the genus was not the taxonomic level at which to generalize.

The next level we considered was the species. In 1978, we examined the responses of Douglas-fir tussock moth populations to insecticides. Responses of these populations to carbaryl provide an example of our findings (Table 4).

Table 4.--Responses of California (C), Montana (M), New Mexico (NM), and Oregon (O-1 and O-2) Douglas-fir tussock moth populations to carbaryl

Population	LD_{50}(95%CL)[a]
C	25(21-30)
O-1	56(38-120)
O-2	51(30-170)
M	30 b
NM	160 b

[a] μg/g body weight. 95% CL are 95% confidence limits.

[b] Data too heterogeneous to provide useful 95% CL.

Table 5 shows the overall results of our experiments. Clearly, equal responses were rare. This was our first indication that the generalization that population responses are very similar and usually equal was not valid. However, further work was necessary before we were absolutely certain of this conclusion.

Table 5.--Results of tests of the hypothesis of equal responses among Douglas-fir tussock moth populations

Insecticide	Populations tested	Hypothesis accepted for any chemical?
Bioethanomethrin	W,O-1,C,NM	No
Carbaryl	C,O-1,O-2,M,NM	No
DDT	W,C,O-1,O-2,M,NM	No
Mexacarbate	W,C,O-1,O-2,M,NM	No
Phoxim	W,C,O-2,NM	No
Pyrethrins	W,C,O-1,O-2,M,NM	No
Trichlorfon	O-2,M,NM	No

Our next investigation also concerned Douglas-fir tussock moth populations. This time, we considered populations and sibling groups, the genetic products of a single pair mating (Stock and Robertson 1979). We also related genetic characteristics to response. The results of the population tests are shown in Table 6. Once again, population responses were not generally equal. The sibling group responses were very revealing (Table 7). Sibling group responses are highly variable and appear to be the ultimate unit of variation of population response. These responses are related to variation in frequency of an esterase isozyme detectible by electrophoresis.

Table 6.--Responses of Douglas-fir tussock moth populations to acephate and carbaryl

Population[a]	LD_{50}(95%CL)[b]
	1. Acephate
NM	52.4(46.7-57.6)
LFB	51.8(46.2-57.4)
ED	54.4(48.1-59.6)
LAB	55.5(45.0-65.7)
	2. Carbaryl
NM	32.5(15.8-62.6
LFB	25.3 (7.4-48.2)[c]
ED	22.4(12.8-32.5)
LAB	41.8(25.0-87.4)

[a] Abbreviations for populations are: NM = Medio Dia Canyon, Cibola National Forest, New Mexico; LFB = Lowry Air Force Base, Denver, Colorado; ED = east Denver, Colorado; LAB = laboratory colony, Berkeley, CA.

[b] Dosage expressed as μg/g body weight. 95% CL are 95% confidence limits.

[c] Data too heterogeneous to compute 95% CL. 90% CL listed.

Table 7.--Toxicity of acephate and carbaryl to sibling groups of a Douglas-fir tussock moth population

Sibling group no.	LD_{50}(95%CL)[a]
	1. Acephate
3	45.1(b)
4	36.6(b)
5	47.2(39.2-56.4)
9	75.8(63.0-101)
8	147.7(b)
11	54.4(48.1-61.1)
13	76.0(57.9-93.6)
14	54.9(39.4-75.2)
15	59.2(44.7-66.8)
	2. Carbaryl
2	21.3(10.9-31.8)
3	48.8(31.2-168)
6	14.1(b)
7	20.7(b)
11	2.4(b)
12	17.1(b)
14	85.1(b)
15	172.0(b)

[a] Dosage expressed in µg/g body weight. 95% CL are 95% confidence limits.

[b] Data too heterogeneous to provide useful 95% CL.

On the basis of the second Douglas-fir tussock moth population study, we concluded that, from a practical aspect, adoption of routine genetic assays as part of population surveys prior to implementation of control operations could provide estimates of population response to various insecticides. Initially, joint genetic/toxicological assessments might be performed as part of each population survey. Larvae from many randomly selected egg masses could be reared to the fourth instar in the laboratory, their response to a particular insecticide determined, and survivors and control larvae from each sibling group subjected to electrophoretic analysis. Once sufficient data from concurrent genetic and toxicological evaluations were obtained, direct extrapolation from a pre-spray genetic survey to a dosage required for desired level of mortality in the field could be achieved. Ultimately, such matching could minimize overdosing and environmental contamination on one hand, and insufficient levels of control on the other.

DIFFERENTIAL POPULATION RESPONSES OF WESTERN SPRUCE BUDWORM

Over the past three years, we have examined 11 widely distributed population samples of western spruce budworm (Robertson and Stock 1983). The general results of these experiments are shown in Table 8. We have identified five distinct response levels among these populations.

Table 8.--Relative responses of western spruce budworm population samples to carbaryl

Population (State-year)	Tolerance Ratio[a]
Idaho-1981a	1.0
Washington-1981a	1.2
Washington-1980a	1.6
Idaho-1980	1.8
Washington-1981b	2.6
New Mexico-1981	4.0
Arizona-1981	4.2
Idaho-1981b	4.6
Montana-1981a	6.8
Washington-1980b	8.8
Montana-1981b	17.9

[a] LC_{50} population ÷ LC_{50} Idaho 1981a.

The Idaho-1980, Idaho-1981a, Washington-1980a, Washington-1981a, and Washington-1981b constituted the first group at the level of highest susceptibility.

At the next level, the Arizona-1981 and New Mexico-1981 populations composed the group of second to the highest susceptibility. The next level was occupied by one population sample, Idaho-1981b.

At the level of second most tolerance, responses of the Montana-1981a and Washington-1980b samples well equal to one another but not to those of the Idaho-1981b group. Finally, the Montana-1981b sample was most tolerant.

How can this kind of variation be explained? Estimates of natural variation within western spruce budworm populations suggest that 2-fold variation in responses is about as high as one might expect. The 18-fold difference we see, therefore, does not seem to be natural.

We have examined a number of variables among the treatment sites, and have concluded that the previous spray history of the areas has resulted in the population responses we observed. The treatment histories are shown in Table 9. The phenomena we believe account for differential responses are resistance, or genetic selection as the result of the use of one chemical repeatedly, and cross resistance, by which exposure to one chemical confers increased tolerance to a totally different chemical.

Table 9.--Relationship of response to carbaryl and previous treatment history at collection sites

Population (State-Year)	Insecticide used in area	LC_{50} (mg/ml)
Idaho-81a	None	2.2
Washington-81a	Fenitrothion 1975; Malathion 1976; Carbaryl 1977	2.7
Washington-80a	Fenitrothion 1975; Malathion 1967; Carbaryl 1977	3.5
Idaho-80	None	4.0
Washington-81b	None	5.8
New Mexico-81	DDT 1963; Malathion 1966	8.7
Arizona-81	DDT 1958	9.3
Idaho-81b	Carbaryl 1979	10.0
Montana-81a	DDT 1957; Carbaryl 1975	15.0
Washington-80b	Malathion 1967; Carbaryl	19.4
Montana-81b	DDT 1957	39.4

With one exception, all of the population samples which were significantly more tolerant than the most susceptible group were collected from areas previously sprayed with DDT. Overlaid on this general pattern is the use of other chemicals on some of the sites. None of the Idaho samples originated from an area sprayed with DDT. Idaho insects from an area sprayed with carbaryl in 1979 were almost five times more tolerant than the sample collected in an unsprayed area in 1981 and 2.5 times more tolerant than a sample collected from the same unsprayed area in 1980. Among the Washington samples, which were also from sites not sprayed with DDT, the sample collected from an area treated in successive years with three different chemicals and the sample from an untreated site varied by 2.2-fold. However, the sample from the Washington site sprayed with malathion and carbaryl was 3.3 times more tolerant than the sample from the untreated site, and 7.2 and 5.5 times more tolerant than the sample from the triple treatment site that was sampled in 1980 and 1981, respectively. Based on these differences, one can hypothesize that the high level of tolerance in the Idaho 1981b population is related to the previous use of carbaryl in that area. The response of the apparently resistant Washington population sample from the double treatment site might reflect cross-resistance between malathion and carbaryl, a phenomenon which was negated at the triple treatment sites by the prior use of fenitrothion.

The general pattern of greater tolerance in samples from DDT-treated sites may also be a result of cross-resistance. Cross-resistance between DDT and carbaryl has been described in the housefly (e.g., Plapp et al. 1979). The gene responsible for cross-resistance confers high levels of microsomal mixed function oxidase activity to resistant individuals (Plapp 1976). These enzymes are known to be primarily responsible for carbaryl metabolism. In other words, the resistant individuals have more enzyme by which to detoxify the insecticide. We postulate that a similar genetic mechanism occurs in the western spruce budworm. If this is the case, the tolerance level of the New Mexico and Arizona populations represents an intermediate shift between the natural, untreated, population responses and the more extreme tolerance levels attained by the Montana population. The difference in response of the two Montana populations is slightly greater than we would expect from natural variation alone. In addition, the greater tolerance of the group collected in an area only sprayed with DDT compared to the group from an area sprayed both with DDT and carbaryl is somewhat puzzling. However, the two collection sites are quite close to one another and interbreeding may have been extensive. Our hypothesis is that exposure to both DDT and carbaryl has shifted the population response as a whole into a higher tolerance level than that of the Arizona and New Mexico populations.

CONCLUSION

More research is needed in this area, not just with the western spruce budworm but with the spruce budworm, Gypsy moth, and Douglas-fir tussock moth. Carbaryl has been applied year after year in Maine, for example, and to our knowledge no one is monitoring the extent to which spruce budworm population responses might be changing as a result.

Finally, the insecticide registration process could be improved by incorporating consideration of the range of responses of insect populations to a chemical and not simply by making a generalization for an entire species.

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NUCLEOPOLYHEDROSIS VIRUS TRANSMISSION IN THE GYPSY MOTH, *LYMANTRIA DISPAR* (LEP: LYMANTRIIDAE)[1]

Kathleen S. Shields[2]

Abstract.--The gypsy moth (*Lymantria dispar* L.), the most important defoliating insect of hardwood trees in the eastern United States, is susceptible to a naturally occurring nucleopolyhedrosis virus (NPV). The Forest Service registered the NPV product GYPCHEK for use as a biological control agent against the gypsy moth, but effective use of GYPCHEK in pest management depends on a better understanding of the many factors involved in NPV infection, transmission, and initiation of epizootics. Recent research in these areas is discussed.

If you have not already met, I would like to introduce you to the gypsy moth, *Lymantria dispar* L. The insect's life cycle starts with hatching of the egg masses in late April or early May. Male larvae go through five stages, females go through six, and then pupate. The moths emerge about the middle of July and mate; then the female lays an egg mass contining up to 1,000 eggs. The eggs embryonate and 1st -stage larvae overwinter in a diapause state within the egg. There is only one generation each year.

The gypsy moth is not a native species. It was imported into the United States from France by Professor Leopold Trouvelot, an astronomer and naturalist who envisioned utilizing the insect for silk production (Medford Mercury Press 1906). In 1869, some larvae escaped from a window of Trouvelot's laboratory in Medford, Massachusetts (Forbush and Fernald 1896), and 10 years later an established gypsy moth population was completely stripping the leaves from large shade trees in residential areas surrounding the release site (Medford Mercury Press 1906). The gypsy moth is now considered the most important defoliating insect of hardwood trees in the eastern United States (McManus et al. 1979). In 1981, nearly 13 million acres of woodland were defoliated by the gyspy moth, compared with 5 million acres defoliated in 1980, and the infestation is still spreading south and west (McManus and Riddle 1982).

In addition to being a forest pest, the gypsy moth is also a public nuisance. The larvae are endowed with an abundance of setae that are a type of pruritic dermatitis in exposed individuals (Shama et al. 1982), and in heavily infested areas it is difficult to avoid exposure to gypsy moth larvae. Young larvae hang from thin silk threads and are dispersed by the wind; older larvae and their droppings make backyards, parks and recreational areas inhospitable.

Since the first major gypsy moth outbreak in 1889 (Forbush and Fernald 1896), attempts have been made to eradicate the insect with various pesticides. But many problems resulted from the use of synthetic pesticides, and after the 1972 Environmental Protection Agency (EPA) ban on the use of DDT in the United States, more emphasis was placed on control of the gypsy moth through the use of natural agents.

The gypsy moth is susceptible to a number of natural disease agents (Lewis and Etter 1978), including a specific nucleopolyhedrosis virus (NPV). The virus disease was first reported as "wilt disease" by Reiff in 1911 and by Glaser in 1915, but the causative agent was not demonstrated until 1947 (Bergold 1947). Since that time, extensive world-wide research has been directed toward using this virus as a biological control agent for the gypsy moth.

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Gypsy moth NPV is in the genus *Baculovirus*, family Baculoviridae (Wildy 1971). The host range of NPVs is restricted to invertebrates, and principally to the insects (Tinsley 1979). Most NPVs have been isolated from species of Lepidoptera, but some have been isolated from Orthoptera, Neuroptera, Trichoptera, Coleoptera, Hymenoptera, and Diptera (David 1975) and an NPV has been found in the pink shrimp, *Penaeus duorarum* (Couch 1974). NPV host specificity within the Lepidoptera varies. For example, the NPV originally isolated from the alfalfa looper, *Autographa californica*, is one of the least host-specific NPVs and is known to infect many species of Lepidoptera (Vail et al. 1971), while gypsy moth NPV seems to be selective for only the gypsy moth (Lewis 1981). The NPVs found in the Lepidoptera do not seem to infect other orders, and vice versa (Tinsley 1979).

The physical and biochemical characteristics of NPVs are quite different from those of viruses that infect vertebrates and plants (Tinsley 1979). The term nucleopolyhedrosis refers to the replication of these viruses in host cell nuclei, and the formation there of large numbers of characteristic polyhedral inclusion bodies. The inclusion bodies of gypsy moth NPV are irregular in shape and range from 1 to 10 µm in diameter. They contain many rod-shaped, enveloped viral particles (virions) surrounded by a paracrystalline matrix of protein. The genome is a large, circular, double-stranded DNA (Mazzone and McCarthy 1981). The polyhedral inclusion body protects the infectivity of the virions and purified inclusion body preparations can be stored, over a wide temperature range, either as dry powders or as suspensions (Lewis and Rollinson 1978). However, the inclusion body paracrystalline matrix protein can be readily dissolved in alkaline solutions, and virions released (Bergold 1963).

The characteristics of baculoviruses in general, and of this NPV in particular, suggest several reasons why gypsy moth NPV could be considered a suitable biological control agent: (1) it has an extremely limited host range and is unrelated to viruses that infect vertebrates and plants; (2) it occurs naturally and has been implicated as a cause of epizootics; (3) its polyhedral inclusion bodies can be produced in large quantities, stored for long periods, and easily formulated for aerial or ground application.

In 1974, the U.S. Department of Agriculture established an accelerated gypsy moth research, development, and application program. Within this program the Forest Service selected gypsy moth NPV for development as a viral pesticide, and in 1978 obtained EPA registration of the NPV product Gypchek. It was the first NPV product registered by the EPA for use on deciduous hardwood trees in the Northeast--the most heavily populated area of the United States.

Gypchek has many positive attributes but further development and improvement of formulations and application methods are necessary to optimize their effects. And ultimately the effective use of Gypchek in gypsy moth control depends on an understanding of the epizootiology of the virus disease, both natural and artificiaally induced (Lewis 1981). Information on the many factors involved in the course of NPV infection and in NPV transmission within and between generations of the gypsy moth is needed to construct an epizootiological model to predict population fluctuations and to better assess the role of natural NPV and of applied Gypchek in integrated pest management schemes.

Any epizootiological model has to start with infection of the host. Although viruses can be acquired transovarially, through parasitism, or as a result of injury, oral infection of larvae seems to be the most common route of entry of an NPV into an insect host (Granados 1980). When gypsy moth larvae consume NPV-contaminated foliage, the polyhedral inclusion bodies slowly dissolve in their alkaline digestive fluids, liberating virions in the digestive tract. The dissolution process is believed to be initiated by pH and possibly by some enzymatic degradation (Tinsley 1979). The liberated virions then presumably pass through the peritrophic membrane, which lines the midgut, and come into contact with the midgut epithelium. Passage of virions through gypsy moth midgut has not been documented, but since virions have been detected in the hemocoele within 2 hours of NPV ingestion (Shields 1983), it seems likely that they either traverse the intercellular spaces or enter the hemocoele by direct passage through epithelial cell cytoplasm.

Once within the hemocoele, virions enter hemocytes and replicate. Five hemocyte types are present in gypsy moth larvae: prohemocytes, plasmatocytes, coagulocytes, spherulocytes, and granulocytes; only the first three types seem susceptible to NPV infection. Virions apparently gain entry into hemocytes by viropexis, an engulfment process similar to phagocytosis. How the viral particles are released from phagocytic vesicles into the cytoplasm has not been determined, but it may be through simultaneous lysis or rupture of vesicle membrane and viral envelope.

Viral particles have often been found closely associated with cytoplasmic microtubles, which may be involved in their vectorial movement to the cell nucleus where the virus replicates. After the viral genome is uncoated, there is an eclipse period during which no viral units can be detected. During the eclipse period, the virogenic stroma (an accumulation of electron-dense chromatin-like material) appears and progeny viral particles are assembled in this region.

Once assembled, viral particles seem to acquire envelopes by a variety of means. Some are enveloped in the cell nucleus by newly synthesized viral envelope material. These virions are apparently restricted to the cell nucleus and seem destined for occlusion within polyhedral inclusion bodies. These virions probably have no role in secondary infections within the host. Other viral particles bud from the nucleus in long tubules of nuclear membrane which extend to the plasma membrane of the cell. Still other viral particles bud through the nuclear membrane into the cytoplasm, enclosed in a vesicle of outer nuclear membrane. Release of viral particles from these vesicles has not been observed, but it has been suggested that they may escape through breaks in the membranes (Granados 1978, 1980). The released viral particles bud through the plasma membrane into the hemocoele. The part of the plasma membrane initially contacted by the viral particle develops a peplomer morphology (surface spikes of viral glycoproteins) which is retained on that end of the newly acquired plasma membrane-derived viral envelope. Peplomers have not been observed on viral envelopes in host cell nuclei or on nuclear membrane-derived envelopes of viral particles in vesicles in the cytoplasm (Adams et al. 1977). It has been suggested that virions exhibiting a peplomer structure on the viral envelope are responsible for secondary and succeeding infections within the hemocoele (Adams et al.1977, Granados 1980, Granados and Lawler 1981).

Although polyhedral inclusion bodies are produced in the nuclei of gypsy moth hemocytes, they are produced in much greater numbers in the nuclei of cells of the fat body, tracheae, and epidermis, with the fat body probably producing the greatest numbers. Viral particles produced in these tissues apparently are routinely enveloped in the nucleus and occluded. Non-enveloped viral particles do not seem to be occluded by polymerizing protein, even though they maybe present in the nucleus when inclusion bodies are forming. Polymerizing protein with a regular crystalline lattice structure is deposited around and between virions. Increasing numbers of virions become occluded, and the ultimate size of the polyhedral inclusion bodies may be determined by depletion of virus polyhedral protein monomer (Harrap 1972, Tinsley 1976).

In late stages of infection, cell nuclei of susceptible tissues become greatly enlarged and are filled with polyhedral inclusion bodies. The nuclear membrane and plasma membrane may rupture, liberating inclusion bodies and not-yet-occluded virions into the hemocoele. Eventually, all susceptible tissues are infected. The lethal infection period for NPV in the gypsy moth is 10 to 14 days, but infected larvae often show no symptoms of the disease for much of this period. In very late stages of infection, larvae will stop feeding and become sluggish, and their integument often takes on an oily appearance. At death, larvae often hang by a proleg in an inverted position. As a result of cell lysis, the body contents are now liquified and are contained only by the very fragile integument, which easily ruptures, liberating masses of polyhedral inclusion bodies.

The body fluids of the host insect seem to provide some degree of protection to the virus against inactivation by solar radiation (Tinsley 1979). Gypsy moth NPV remains infectious at high levels for at least 1 year on environmental environmental surfaces (Doane 1975, Podgwaite et al. 1979). But exactly how the disease is spread among individuals and how NPV epizootics occur are not well understood.

Obviously, larvae can become infected by ingesting NPV-contaminated foliage, and this presumably happens in natural populations. Laboratory studies indicate that gypsy moth larvae can transport NPV from contaminated environmental surfaces to a food source (Podgwaite et al. 1981). Parasites and predators may also have a role in NPV transmission. Some entomophagous parasites can transmit NPV from infected to healthy gypsy larvae (Raimo et al. 1977), and positive correlations have been found between NPV mortality and the prevalence of various entomophagous parasites (Reardon and Podgwaite 1976; Godwin and Shields 1983). Several species of birds and mammals that are predators of the gypsy moth have been shown to pass and disperse active gypsy moth NPV within the environment (Lautenschlager and Podgwaite 1979). Much evidence suggests that this NPV can be transmitted from generation to generation of the gypsy moth by surface contamination of egg masses (Doane 1969, 1970), but it is not known whether NPV is deposited on the eggs by the female during oviposition or whether NPV in the environment is transported by wind or rain onto egg masses to infect emerging larvae. Although all of these types of NPV transmission undoubtedly occur in natural gypsy moth populations, to what extent they occur and their relative significance in NPV epizootiology remain to be determined. Much of this work is ongoing.

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THE SHORT- AND LONG-TERM EFFECTS OF INSECT ATTACKS ON TREES[1]

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Abstract.--Many people view all insects, except perhaps for honeybees and butterflies, as harmful pests. This view extends to those insects occurring and feeding on trees. It is true, however, only if one considers the short-term effects of insect attacks. Nevertheless, the effects on the forest as a whole must be considered over the long as well as the short term. An example is presented of the effects of ambrosia beetle attack on black walnut trees in which the long-term biological and economic effects are minimal.

About 75% of all the different kinds of animals alive today are insects: approximately 1 million species of insects have been described with an equal or larger number yet to be described. One estimate of the total number of insect species alive in the world is 30 million (Erwin 1982), although most estimates are between 1.5 and 3 million. Compare this figure to the 9,000 species of birds or 4,200 species of mammals. Insects are an important part of the environment in which we live because of sheer numbers and because of the economic impact they have on human society. The economic or destructive aspects of insects' presence in our society receive major emphasis because of the staggering dollar values attributed to insect-caused losses. The total annual value of insect damage to food and household products and to insect-transmitted diseases was estimated at $3.5 billion in 1957 (latest available figures) in the U.S. alone (Metcalf et al. 1962). The damage to forest trees and forest products was estimated at $2.5 billion in 1957 dollars (Metcalf et al. 1962).

Beneficial insects receive less attention and, therefore, their contributions to society usually remain unquantified. One exception is insect pollinators. Their value for producing fruit and seed crops was estimated at $4.5 billion in 1958 (Metcalf et al. 1962).

The number of destructive insects is small compared to the total number of species. Baker (1972) reported that 154 different insect pests reached outbreak status in eastern forests during a 10-year period. In southern Illinois, at least 300 species of insects occur on the black walnut *(Juglans nigra L.)* trees but only about 10% occur commonly (Nixon and McPherson 1977). These common species may or may not be potential pests, however. That they occur commonly and may feed on the trees does not necessarily mean they are harmful insects.

This paper is divided into two parts. The first briefly describes the short- and long-term effects of insect attacks on trees in general. The second gives a specific, although hypothetical, example concerning an insect pest of black walnut trees and the economic and biological effects of attack.

INSECT ATTACK ON TREES

Short-term effects

Insects that use trees as a food source or for habitat cause both direct and indirect short-term effects. Immediate and direct effects of insect attacks on trees occur because of chewing, boring, or sucking activities of the insects. These result in loss of tree biomass in the form of leaves, sap, seed, or wood; reduced height or diameter growth; reduced resistance to diseases or other insect pests; or death. Indirect effects of insect attacks occur because the forest environment

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and those organisms using the forest are affected. The immediate indirect effects include reduced recreational and esthetic values, increased fire hazards, altered habitat for wildlife, altered forest management goals and costs, degrade of forest products, and stress and anxiety in humans.

Immediate, direct effects of insect attacks on trees are the most easily and commonly studied by entomologists and by foresters and, therefore, receive the most emphasis. The short-term direct effects are often used by entomologists and pest control decision-makers to justify the need for control of forest pests causing recurring or widespread damage. The indirect effects, however, are acknowledged by researchers and forest managers but much less commonly studied because of lesser interest and because of greater difficulties involved in studying them. Therefore, little data are available on the importance of the indirect effects.

Long-term effects

The long-term effects of insect attacks on trees are less easily classified as direct or indirect because both individual trees and the entire forest are affected. These effects may include increased tree biomass, increased height and diameter growth, reduced competition, improved nutrient cycling, altered stand composition and plant diversity, and altered management goals.

Long-term effects of insect attacks also have received little inquiry, primarily because of the long time that must be devoted to studies of this type. Evidence is available, however, that some apparently destructive insects are actually beneficial to trees in the long term as opposed to the evidence that insects are harmful to trees in the short term. For example, insects such as the Douglas-fir tussock moth or the forest tent caterpillar are leaf-feeders that defoliate thousands of acres of trees when in outbreak status. Yet researchers have found that a few years after defoliation trees actually showed greater height and diameter growth than they did before defoliation (e.g., Brookes et al. 1978). This has been shown to be a result of increased nutrient cycling due to high concentrations of nutrients in dead insects, insect frass, and unused food parts (Mattson and Addy 1975). Another reason for improved tree growth is that defoliation causes an increase in the amount of light entering the forest stand and apparently causes new leaves to be larger; these new leaves have greater photosynthetic areas and a corresponding greater efficiency in the photosynthetic process.

Both short- and long-term effects of insect attacks must be considered in the process of deciding how serious a potential pest may be. Other considerations include the age of the trees (how near to harvesting and how much time the trees have to recover before harvesting) and the long-term management goal for the trees.

Following is a hypothetical example of an insect problem on black walnut trees growing in managed plantations and the implications of this insect over both the short and long terms.

AN EXAMPLE FROM BLACK WALNUT

The trees: Black walnut is the most valuable hardwood species in the U.S. because of its color, durability, and excellent workability for furniture-making. It occurs throughout most of the eastern U.S. except for the extreme northern and southern parts. Because of its popularity and desirability as a furniture wood, not many high quality trees remain in natural forest stands. Therefore, many persons are planting black walnut in managed plantations for investment purposes and to maintain a lasting supply of this beautiful wood.

A walnut grower must invest considerable time and money into establishing his or her plantation. Establishing a plantation includes preparing a site for planting, buying and planting the trees, and caring for the trees for at least the first 3 years after planting. These costs do not include the cost of the land itself, taxes on the land, or any other expenses incidental to the plantation (i.e., purchasing a tractor or other equipment for site preparation).

Assume a walnut grower wants to establish a 5-acre black walnut plantation with nursery-run seedlings planted at a 10- x 10-foot spacing, equivalent to 436 trees per acre. The total cost for planting 5 acres or 2,180 walnut trees is $1,301.75 (Table 1). The investment of $1,301.75 is one that must be carried until harvest time or until some income can be realized from the trees. For black walnut the time period to harvest is estimated to be from 60 to 80 years.

The management goal for the plantation is to grow trees to about 20 inches in diameter and harvest at about age 60. Based on the expected future value of black walnut at present-day prices, the income from the plantation is expected to be about $2,600 after 48 years and $30,500 at the end of 60 years (Table 2).

Table 1.--Costs of establishing a 5-acre black walnut plantation during the first 3 years[a,b]

Cost of trees: $0.28/tree x 2,180 trees	$ 610.40
Site preparation costs: $27.06/acre x 5 acres	$ 135.30
Planting costs: $45.48/acre x 5 acres	$ 227.40
Weed control costs: $21.91/acre/year x 5 acres x 3 years	$ 328.65
TOTAL	$1,301.75

[a]Assuming that standard nursery stock was planted at a 10- x 10-ft. spacing, which is equivalent to 436 trees per acre or 2,180 trees on 5 acres.

[b]Costs are taken from Marty and Kurtz (1981) and are the average costs in each category.

Table 2.--Expected income from a 5-acre black walnut plantation[a]

Age	No. trees removed	Expected income[b]
15	1,090	-
30	359	-
40	531	-
48	65	$ 2,600
60	135	$30,510

[a]Assuming the trees are allowed to grow to 20 inches in diameter before final harvest at age 60, and the plantation is thinned at ages 15, 30, 40, and 48 (after Marty and Kurtz 1981).

[b]Expected income figures represent 1981 stumpage price estimates projected forward at a 1.5% annual inflation rate (the inflation rate of walnut lumber prices is higher than the general inflation rate).

The insect problem: Now consider an insect problem that affects the trees at age 4. The ambrosia beetle *Xylosandrus germanus* appears in May and June of the 4th year after planting. In this hypothetical example, assume the beetle attacks 20% of the trees, causing dieback and apparent death of the trees.

X. germanus is an ambrosia beetle that attacks many species of trees, including black walnut. It attacks dying trees, recently cut tree stumps, and young trees that are apparently healthy. In this latter situation, it attacks plantation trees between the ages of 3 and 8. *X. germanus* attacks trees in this age group because it seems to prefer trees between about 1 and 2 m tall. The beetles attack at the base of the tree in mid-spring, causing rapid wilting and dieback (Weber 1982).

An important point is that the tops of trees die back but the roots are usually still alive. Attacked trees often sprout back from below the attacked points and seldom do whole trees die. In southern Illinois, none of almost 400 trees had died 3 years after attack by the beetle although most of them appeared to be dead immediately after attack (Weber 1982). Because of the dieback, attacked trees showed significantly reduced height and diameter growth in the year of attack. Two years later, however, new sprouts from the root systems of the attacked trees were actually growing faster than unattacked trees. The attacked trees recovered well, with the sprouts replacing the original trees (Weber and McPherson, in press).

Furthermore, *X. germanus* does not usually attack sprout trees and, although it may be present in a plantation for several years, it is a serious problem for only 1 or 2 years.

An initial estimate of the losses the beetle caused in this hypothetical example is about $6,400 (Table 3). The $275 immediate loss is based on the assumption that the trees must be replanted. But generally the trees do not die and thus do not need to be replanted. Therefore, the loss of $275 is not real. One potential cost, however, is the necessary pruning to remove excess sprouts from the attacked trees. This cost is about $15 for 436 trees (after Marty and Kurtz 1981).

The loss of $6,102 represents the assumed loss of merchantable trees at harvest time (Table 3). Again, the trees were not actually lost. Moreover, looking more closely at the final harvest figures, only 135 out of 2,180 (or 6%) trees planted will actually be harvested at age 60. This means that 94% of the trees will be removed earlier in various thinnings because they are too small, too poor quality for prime walnut grades, or too close to a more desirable tree nearby. The point is

Table 3.--Losses due to ambrosia beetle attack on black walnut trees at age 4[a,b]

Replacement costs for 436 trees	$ 275.36
20% of expected income at harvest time	$6,102.00
Total losses due to beetle attack	$6,377.36

[a] Assuming a 20% attack rate in a 5-acre plantation.

[b] Based on average management costs obtained by Marty and Kurtz (1981).

that only a few trees are selected as final crop trees and many are culled out along the way. Because of the rapid recovery potential of most black walnut trees after beetle attack, they probably will have the same chance as those not attacked to become final crop trees. If the recovery potential is lower, the selection opportunities will be reduced somewhat. The loss, however, will be much less than initially estimated.

CONCLUSION

From the evidence, therefore, I conclude that the long-term effects of ambrosia attack on black walnut trees are minimal, both biologically and economically. This is so because the ambrosia beetle attacks trees when they are young and have time to recover.

Insects do cause problems on trees and some insects on some species of trees may have serious effects. However, researchers and tree growers must balance the short-term effects and losses against the less serious long-term ones before recommending potentially expensive control measures.

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PANEL QUESTIONS

FIRST SESSION: Biological Aspects of Forest Pest Control

QUESTION (P.M. Hanson): Under optimal spraying conditions there are points when relatively low dosages caused high mortality depending on the compound you used or the insect age. I was wondering what practical or laboratory work has been done to investigate use of the model when joint applications of pesticides are a possibility. In other words, would the model be at all helpful or sophisticated enough to give a compromise?

RESPONSE (M.W. Stock): What do you mean by joint application:

QUESTION (P.M. Hanson): Two chemicals.

RESPONSE (M.W. Stock): Yes, we could do it. We've just completed six years of testing on mixtures of chemicals; we now have a data base that we could use. It's just that some more work needs to be done to see if using mixtures would actually have an economic benefit. We are doubtful that it would be useful. But basically with the model, all you need is the right data base.

QUESTION (P.M. Hanson): You didn't mention it today, but in your paper you said that the accuracy of the model was 73-95%, and I was wondering if you have any suspicions of what might have caused the variations from 100%. In other words, where would you look to find additional variables to make the model stronger?

RESPONSE (J.L. Robertson): Let me start. First of all I'd say the field test data was wrong - obviously. Mollie can take it.

(M.W. Stock): In any model like ours, you start with very simplistic assumptions and you put in only certain things to see how accurate it is. Then you say maybe if we add something it will be more accurate. This is just a beginning.

QUESTION (P.M. Hanson): What sort of variables do you think you might add?

RESPONSE (M.W. Stock): Some examples are better information about rainfall, the amount of cover protection of the foliage. We don't have these. I mention them as possible variables. Canopy cover is something to be considered, but we don't have any information on that in the model. There are all kinds of variables related to the spraying technology itself. So there are many more things that could be put into this to make it more accurate. So what we have right now is very rudimentary sort of model. But that is the way you start these things. If you put everything in to start with and it wasn't accurate you wouldn't even know where to start looking for the problem.

QUESTION (P.M. Hanson): I was wondering if either of you have been interested in expanding the model to account for subsequent changes the following years?

RESPONSE (M.W. Stock): It's something we can do eventually, but we don't have the data yet to be able to put the parts together. In other words when you spray, some of the insects are killed but some of them live, and you need to look at the F-1s and what happens to them; and we haven't been able to collect that kind of data yet. Also the very understanding that the populations vary at all and that the spraying might affect them from generation to generation is relatively new for forest insects, although, it certainly isn't for agricultural insects. But forest insects -- a lot of the things that are old hat in agriculture are just beginning to be recognized as true possibly for forest insects.

QUESTION (J.M. Herbers): I'd like to ask first a couple of very general questions, for those of us who are not up on insect toxicology. Can you tell us a little bit about the compound carbaryl itself -- how does it work, is it a neurotoxin, is it a clorinated methane derivitive or ?

RESPONSE (J.L. Robertson): It is one of the carbamates. It is a neurotoxin.

QUESTION (J.M. Herbers): Then why isn't it toxic to vertebrates? If it is a neruotoxin, those are generally broad spectrum.

RESPONSE (J.L. Robertson): Well, it is, but you have to ...

QUESTION (J.M. Herbers): Relative to DDT it's not?

RESPONSE (J.L. Robertson): Well relative to DDT it is toxic to mammals. Relative to other chemicals available it is not. Its got a methol group in it which somehow or another makes it safer.

QUESTION (J.M. Herbers): Is much known about how the insects actually do detoxify it?

RESPONSE (J.L. Robertson): A lot is known about some insects, like houseflys.

QUESTION (J.M. Herbers): But experience shows that insects in different orders and in different families can have very different mechanisms.

RESPONSE (J.L. Robertson): Right and nobody has looked at the detoxification, for example, in the budworm.

QUESTION (J.M. Herbers): If you don't mind, I would like to ask you quite a few questions about the genetics because I am a population geneticist myself. You've shown quite clearly that there is an enormous amount of variation among spruce budworm species, especially in the western part of the country; and also variation between species with respect to LD50s for carbaryl, and I was wondering if you've yet got enough data to start to partition the variance into between species, within species, between populations, within populations, and so forth. Because that I think is a really critical question -- where is the variance? Is most of it between populations, is most of it within populations and so forth.

RESPONSE (J.L. Robertson): I think we have a good basis to say most of it is within populations.

QUESTION (J.M. Herbers): But the point of your talk is that there is a lot of variance between population, as well.

RESPONSE (J.L. Robertson): Right, we think most of the variance occurs within a population.

QUESTION (J.M. Herbers): Doesn't that present problems, though, for your implication that resistence is related to previous spraying with something like DDT? If most of the variance is within populations, presumably individuals within a population have had similar histories, genomes have had similar histories, and so most of the variance should therefore be between populations rather than within. If the pesticide cross linkage is really important.

RESPONSE (M.W. Stock): Very good questions. All I can say is there is a lot we don't know yet. And the other thing is what constitutes a population. It is very ill-defined. Also, how much do these insects move from one place to another? Dispersal is a whole topic that is being researched for budworms and tussock moths and we don't really know how far they move. So even talking about what is a population is very nebulous right now. We've done... one of my graduate students ... comparative genetic study of all the species of *Choristoneura* and they are extremely homogenious, genetically at least, by isozyme work. They vary a lot in their response to chemicals, but in their general genetic relationship they are all very similar.

QUESTION (J.M. Herbers): Well along the same line, you mention in your paper that you've done quite a bit of lab work as well, which I think is really important as well as the field work -- and these bugs are reasonably easy to culture, is that right?

RESPONSE (J.L. Robertson): No, we're just good. They are not easy to culture.

QUESTION (J.M. Herbers): That blows the next question. I was just going to ask if you have yet started to perform selection experiments in the laboratory.

RESPONSE (J.L. Robertson): Okay, what we have done ... I should give a rundown on the lab colonies that we have. In 1967 we established a huge western spruce budworm colony in Berkeley that we were able to raise without diapause, which meant that it was available year-long, instead of having to put them in the refrigerator for four months. We have them available continuously. We have that as basically the baseline culture. Last year we established four other colonies form some of the population sites that i was discussing; and what we are planning to do when we get the colonies to sufficient size is to work on these problems more. Unfortunately, it takes about a year and a half to two years to get the colony built up to that level. Because we are not talking about tests that use 10-15 animals, we're talking about 500-1000 for each experiment.

QUESTION (H.M. Herbers): I can appreciate the difficulty because I work with an organism that has to go through a six month diapause and it is really a drag. Okay, well I'd like just one more question about the genetics, if you don't mind. It seems to me really critical in understanding resistance in natural populations, to understand whether that resistance comes about as an evolutionary response to a selection pressure, or whether that resistance is a result of some genes being turned on in the population. My understanding is that so far the available literature just cannot differentiate between those two. Can you suggest any way to approach this issue, obviously you have to do selection experiments in the laboratory and estimate heritability and so forth; but the whole issue of the physiological basis of resistance is that big black box still for many, many species.

RESPONSE (J.L. Robertson): I don't know yet, I have to wait and see what we get from the selection experiments. This whole thing has just been a step by step process.

(M.W. Stock): Interesting that you should bring that subject up. Last week I talked on bark beetles at a meeting in Banff and what we found is that when you stress the population, you get greater genetic diversity. There if a certain amount of theory that says if you stress a population you get less genetic diversity. We very clearly get more genetic diversity. It was a very interesting discussion, everybody got talking about why this would be so. We may try to test the bark beetles by stressing them and trying to differentiate in that way. Trying to figure out why, when you select and you kill off lots of them, when you put them under great stress you get greater diversity because the remainder hasn't much of a greater chance to diversify. It was a very big revelation, at first I thought it must be an artifact of collection. We did it wrong -- that's your first reaction, but then you realize that it is so consistent that you can't just say, because it doesn't fit with what you thought, that you did it wrong. So that is a thing we are testing now.

QUESTION (J.M. Herbers): Well that work is really very interesting and I applaud you for doing the hard work, I know it is hard work. My final question relates more to policy issues. Your work clearly shows that since there is variation within populations and between populations, that EPA registration procedures are just plain wrong. Now, can you suggest what the real implications are going to be for registering pesticides and testing them from your work?

RESPONSE (J.L. Robertson): You get caught between the bureaucracy you work for and science. I don't know what we're going to do besides diligently publishing our information. We present it whenever we can, and I guess basically we are trying to make enough people pay attention to what we are saying so that, hopefully, eventually the message will get through to people making the policies.

QUESTION (J.M. Herbers): Presumably your work is being funded by those same people who make policies.

RESPONSE (J.L. Robertson): No. I might relate a little story that sort of explains this. In 1971, I had spent I guess 5 years testing 25-30 chemicals against Douglas fir tussock moth as alternatives to DDT. When it came down to the issue of the emergency, the alleged emergency in Oregon, that year -- our project suggested five alternatives to DDT. Guess which chemical got sprayed? DDT! All you can do is present your data.

QUESTION (J.M. Herbers): Well, good luck to you. Thank you.

QUESTION (B.S. Burns): Your slides make me glad I haven't seen a gypsy moth caterpillar in a couple of years -- turns out they are even uglier when you look at them under a microscope, have to meet them face to face. So, I'm glad about that, but a couple of years ago, like everyone else in Vermont, we did have a real gypsy moth problem and I guess about half the oak stands in this state were defoliated. One thing that always struck me that about this virus is that when we got to an area where the moth population was collapsing and all the foliage had been chewed, the bugs were halfway through their development and the larvae that were left all had the wilt disease. I would report that they died from starvation and wilt. My question is, which are they dying from? Perhaps it is the same thing -- the starvation leads to wilt disease. But is there a way to say the caterpillars are dying from one or dying from the other?

RESPONSE (K.S. Shields): Well, a few years ago we did a study analyzing the causes of collapse in natural populations and the important disease agents in natural populations. Essentially we did necropsies on the insects and we determined that the nucleopolyhedrosis virus was the most important microbiological agent operating in various kinds of gypsy moth populations, sparse and dense. But, of course, that doesn't account for factors like starvation. There really isn't any way to determine when there are many factors involved, which one is the most important after the insect is dead. This all goes into the whole disease complex and the epizootiology model and population prediction. As Mollie mentioned, models start out with very simplistic kinds of schemes and then you test them. Well, we're really in the very, very infancy of testing ours. We really don't even have a model. We are in the process of assembling one, and starvation could be one factor.

QUESTION (B.S. Burns): If you are going to be using virus though it seems as if it would be helpful to know if you should apply it early in the build up of the insect -- like BT (the bacterial insecticide). Is it best to use it before the insects are too numerous, or is it better to use it later when the insect is already stressed by the starvation? When would virus be most effective in terms of the population build up if it were applied as an insecticide?

RESPONSE (K.S. Shields): Well, it depends on how you are going to introduce it into the population. If you are talking about aerial spray, the recommended application now is two doses, and you spray first when they are second instars. The reason for that is, if you spray too early when the insects are first hatching, they are not up in the canopy, they don't eat enough, so even though you can cover the foliage with inclusion bodies the odds of one very small first instar larvae ingesting a lethal dose of inclusion body are not great enough to justify spraying. If you wait too long, the virus still kills them, but the dosage goes up with the insect's body weight. The larger the insect the more it takes to kill it. So it's a compromise -- second instars are probably the best stage to hit in an aerial application, but in alternate application methods that is a whole different story.

QUESTION (B.S. Burns): Another question -- we always say a virus would be a great pesticide if it affected only gypsy moths and not the other insects, not the other creatures around; but I have a feeling if we ever got to doing this operation, if we were spraying it over houses, people would get concerned and think it was going to mutate, and what about the next andromeda strain, and all this. Are we really sure this thing can't mutate and become a bug that is a little more infective?

RESPONSE (K.S. Shields): No, of course not. You are never really sure. GYPCHEK was in safety testing for many years before EPA registered it. It has been tested against many, many species of invertebrates and vertebrates; it has been injected into brains of mammals, it has been through all sorts of extensive testing. But the most that we can say is that all evidence indicates that it is environmentally safe, that it is not infectious in any other species, and it is monitored. But that is something that will have to be looked at over the years as the organism is produced, if a commercial producer is making it. It will be important to monitor any microorganism to make sure that it has not mutated. This really isn't being done now.

QUESTION (B.S. Burns): Are the registration regulations more strict for microbials than chemicals because of this possibility of mutation:

RESPONSE (K.S. Shields): I really can't answer that because I am not familiar with the procedures for chemicals. Perhaps Jackie could -

(J.L. Robertson): I think that they are about the same.

(M.W. Stock): I would like to make just one point -- and that is, from a genetic point of view and from just a biological point of view, insects cycle naturally and deciding what is killing them is very difficult as we have been discussing here. At some point in time, the populations will decline naturally; Douglas fir tussock moth is very predictable in that way. So, if you spray at the right time you get very high mortality, whether it is caused by the spray or whether they were going to die anyway. So, causal relationships are very difficult to identify.

QUESTION (B.S. Burns): If we have to give communities and landowners, and so forth, advice on whether to spray and make that rather substantial investment on a piece of real estate, it would be nice not to ask people to spray if their population is going to collapse this year.

RESPONSE (M.W. Stock): Right. On the ohter hand if you tell them to spray then they say you gave them such wonderful advice because they all died. That is the politics of it, you see.

QUESTION (B.S. Burns): Okay, this is just a curiosity more than anything. I haven't been keeping up with my Mother Earth News or whatever it is, but I know they probably all say that you can macerate gypsy moth larvae and spray them on the trees and you can make your own virus insecticide yourself. Would that work: I mean if a homeowner asked me can I take a bunch of dead gypsy moth caterpillars and mash them up and spray them on the trees?

RESPONSE (K.S. Shields): Well, I hate to tell you what GYPCHEK is made of. That is what it is. Now, viruses of course have to be grown on living cells and there are two ways of producing baculoviruses, and the best way is to produce them in vitro, in cell culture. This has been attempted with gypsy moth virus, but it has not been economically feasible. There haven't been any gypsy moth cell lines that have been productive enough to justify the investment in them. So, some time ago the decision was made to produce it in vivo. So, we infect insects and shortly before they die - when they have maximum number of inclusion bodies - they are frozen and lyophilized. They are put through a mill which breaks off most of the setae which cause the allergenic reactions; and then they are ground up. And that is GYPCHEK. It is insect body parts and polyhedral inclusion bodies. Now this material is tested for presence of pathogenic microorganisms and this is the major problem with growing viruses in vivo. You have allergenic material from the insect parts and you have contaminated microorganisms. We further purify it for laboratory use, the pictures that I showed you of the inclusion bodies were highly purified; but it is much too expensive to do that for a spray operation. So GYPCHEK was registered as ground up insects. So, yes, it would work.

QUESTION (K.Carter): Barbara, I can see a lot of eager people out there who want to ask their own questions, so I'm not going to take too long. But there are a couple of things that came to mind while you were speaking that I just can't pass up the opportunity to talk about. I think that your study with the black walnut and the ambrosia beetles was an excellent example of the need to study the biological system, both of the insect and of the host over a long period of time in order to be sure that you have got all the implications before formulating a strategy. I just wonder if you feel that the biology of the trees has been followed sufficiently long to be able to predict whether these sprouts from the stumps will be of the same quality as the seedlings; because I know frequently it is the case, especially with sprouts from older stumps, that you expect poorer form or more suseptibility to heart rot, etc., from stump sprouts as opposed to seedlings.

RESPONSE (B.C. Weber): The same is true for black walnut trees. In my study we haven't followed the trees long enough to know if quality is affected in the future for these trees. I also don't know if that very fast growth rate is going to continue over the life of the trees; they may slow down again later on and in fact maybe go back to the slower growth rate or become susceptible again. But for a short period of time, within a few years after attack, the trees are better and the sprouts that do come up are usually very straight and very fast growing -- so they look good initially.

QUESTION (K. Carter): When you speak about them being faster growing -- that would be an annual growth rate. They do eventually catch up to where they would have been had they not been killed back to the ground at some point?

RESPONSE (B.C. Weber): I would say it would depend on the age at which the trees were attacked. If the trees are at age 4 in the example that I gave, I would say that the sprouts would catch up, because the sprouts are growing at the rate of maybe 5 feet a year and the trees would maybe be 7 feet tall for the average of the plantation. So, within 2-3 years the sprouts are going to be as tall or maybe even a little bit taller than the average tree.

QUESTION (K. Carter): I can tell there are a lot of geneticists on the panel this morning, because I am one too. I just have to give you or maybe one of the other speakers, too, would like to comment on the very long term effects of interactions between insects and forest trees on the genetics of the tree populations - and maybe talk a little bit about long-term co-evolution of the insects and their hosts. Would you like to do that?

RESPONSE (B.C. Weber): I am not a geneticist, so I am going to beg off a little bit on that one; except to way that with my study on the ambrosia beetle, the black walnut trees that I studied were from different seed sources - which means they had different genetic backgrounds. So I looked at this particular factor to see if the ambrosia beetles were affecting particular trees and then looked at the long term response of the trees after attack. What I found was that yes, there were differences among the different seed sources in which trees were attacked. I also found that the seed sources which were most heavily attacked were also the seed sources that recovered the best. Now, another thing, and this may be a coincidence, but the seed sources that were most heavily attacked and that recovered the best were also seed sources in areas where the ambrosia beetle occurs now. The seed sources that were attacked but did not recover very well are in places where the beetle is not presently found. This insect is an introduced insect into the country. It was introduced in the early 1930's. Now I don't think the insect has been around long enough to put any kind of evolutionary pressure on the trees to affect the fact that some trees are resistant and not resistant. I think it may be just an artifact of the population, but some of the differences were significant. If somebody else wants to talk about the co-evolutionary aspects, I defer to them.

RESPONSE (M.W. Stock): At this meeting that I recently attended, another thing they found was that if you take - say- Douglas fir and you put spruce budworms from the same area on it there is less damage than if you mix them from different areas say, from 100 miles apart. So that the adaptation certainly goes both ways. You get most damage if you take a population of budworm and a population of Douglas fir from two different areas. So, there are really very high levels of co-evolution. That was the whole subject of that meeting -- it was quite fascinating. The other thing is that in bark beetles, some of the controversy -- there is a fair amount of controversy about how to manage bark beetles, you can't spray very effectively since they whip out of one tree and whip into another one so fast they aren't exposed -- but one of the management techniques involves cutting down vigorous trees that the beetles might be likely to attack. This is, over a period of time, not really terrific for the stand. That is a very interesting subject for discussion, and as I say we recently spent two days on it and just barely scratched the surface of some of these questions. Mostly we raised questions -- like here. You don't answer a whole lot but you recognize the questions exist.

QUESTIONS FROM THE AUDIENCE:

COMMENT (A.E.Carey): Because E.P.A.'s Office of Pesticide Programs payed my way here, I feel I should mention a couple of things in terms of how pesticides are registered under the Federal Insecticide, Fungicide, and Rodenticide Act, and how this is administered by E.P. A. You have to keep in mind that E.P. A. is required to register a whole spectrum of pesticides. In order to do that, we had to set up a series of registration guidelines you can hand out to any potential manufacturer -- of anti-fouling paints, slimicides for paper mills, saniflush, and baculoviruses -- so the guidelines don't seem to be very specific to this particular use of a chemical or a microbial agent. The guidelines had to be written "generically". Secondly, you have to keep in mind that forestry uses of pesticides are considered by E.P.A. to be a minor use compared to the agricultural uses. The Forest Service has done a very good service by conducting the additional work to allow this particular kind of agent to be registered for forestry uses because it is really not worth it for a chemical company who must answer to stockholders to go ahead with the research that is required. It is not cost-effective for them. The Forest Service has done this and thus certain agents have been registered for forestry uses. We have to keep this in mind when speaking of impact on E.P.A. registration standards. It's not that simple.

QUESTION (S.V.Kossuth): I have a question for Mollie. What I would like to know is have you looked at the stages of development of the insect in relation to when they are most susceptable to the various strains?

RESPONSE (M.W. Stock): That's a question that was brought up during coffee break. The instars, the different larval stages, vary in their susceptibility to different chemicals and not just a linear fashion. There are no gross changes in the esterases during larval development. We've seen changes, great switches, between, say, when pupation occurs. That is certainly something that would be worth looking at. We have not compared the instars in great detail. But with the instars that we have compared, say second, third, fourth and fifth instars, there are no changes. No obvious changes in frequency at least, but there are other things that need to be looked at. That is a good possibility especially with acephate, which is directly related; the esterases are directly related to metabolism of acetate.

QUESTION (C.J. Wang): Do microbials associated with insects affect their response to chemicals?

RESPONSE (J.L. Robertson): Certainly a possibility but, unfortunately, when you run a bioassay for a chemical all you have got are your controls, and the question is did they live or did they die? So, we don't know.

RESPONSE (M.W. Stock): Back to bark beetles. When a bark beetle attacks, there is a very close relationship between the fungus, the various fungi, that are carried by a bark beetle, and whether or not it kills the tree. There is a very close relationship which is essential in understanding the tree mortality and the relationships between them. I think that's a very good question -- something we don't know a whole lot about, but more is being learned all the time. I think we know more about it -- maybe I'm wrong, but I think we know more about it in the bark beetle-tree relationship, than we do in budworms and the defoliators.

QUESTION (R.S. Kelley): A question for Kathy. Is there any evidence to suggest a direct carry-over of a sub-lethal dose of virus within the insect from one generation to the next?

RESPONSE (K.S. Shields): There is no evidence at present. Some of this work is being done now -- working with sublethal doses, looking for chronic infections - evidence of chronic infections, transiviral transmission -- all this area. To my knowledge no one has produced any positive evidence of this occurring. There is a lot of negative evidence, but the fact that you can't find it doesn't mean its not there. There is another whole area that really hasn't been investigated and that is the area of viral latency. For many, many years a lot of people have suspected that gypsy moth virus may be operating in some kind of a latent form that could be triggered by different stress agents, but we really don't know about that. It is not an easy area to study. It's not an inexpensive area to study either. So we really don't know that, but all evidence so far on low dose levels that I am aware of is negative. One theory that is being proposed now for many of the baculoviruses is sort of the single bullet theory -- that it takes one viral particle to infect an insect and if that one viral particle invades the cell and replicates that insect is a dead insect. The dose response is just the odds of getting that one viral particle in an infectious form into a cell. Now this is just a theory, but evidence is being accumulated that supports this theory.

QUESTION (R.S. Kelley): My second question related to the break-down of virus by ultraviolet radiation. What do you know about survivability of the virus on the egg mass?

RESPONSE (K.S. Shields): Well, the testing programs that are being done now would spray egg masses shortly before hatch. If this is going to be used as a home owner kind of technique, people would be advised to go out in the middle of April and spray their egg masses, just shortly before the insects are due to hatch so that it wouldn't be exposed for that long a period of time. Also, there is difference in virus preparations. The virus that is liberated from a dead insect is incorporated with all of the insect body parts -- all this proteinaceous matter -- and this virus seems to be more protected from ultraviolet radiation than purified preparations. We did virus persistence studies as part of the E.P.A. registration package. We went out into natural populations that had never been treated with virus, but that had had natural virus incidence in the past years. We went out in the spring before the insects hatched and collected bark samples, soil samples, litter samples and some lethal doses of virus in these samples, as tested by bioassay. So when it's protected from UV either by a formulation or by the insect body fluids, or the fact that it is just not exposed to light because it is down in the crevices of the bark, it is quite resistant. Egg masses are covered with many, many layers of setae that the female deposits on the eggs. If you take an egg mass to a laboratory and just squirt it with virus - just plaster it and put it under the scanning scope, the first time I did that I was positively horrified because I put it under there and I couldn't find any virus. Yet I knew I had just loaded this thing up with it. Well, it soaks down in to the layers of the setae, and when you spray an egg mass you can find inclusion bodies right on the surface of the eggs, below many, many layers of the setae. So they probably would be more protected in that fashion and may go from one generation to the next.

QUESTION (R.S. Kelley): Where do you find your greatest number of lethal doses?

RESPONSE (K.S.Shields): There were differences in samples -- I really can't remember the specifics of the data. The bark was very variable and we assumed that it probably depended on whether an insect had died on that particular piece of bark or not. We had one little sample that was half the size of a dime, scraped off the crotch of a maple tree, from one plot that had never been sprayed with virus; this was supposed to be the pre-spray sample. It wiped out every insect. You know, LD100 on everything. We couldn't dilute it down enough. There were probably a half a dozen larvae that died right in that little spot. So that was really high, other samples were minimum or none at all.

QUESTION (M.Morselli): Is there any indication of the virus having an effect on the tree?

RESPONSE (K.S. Shields): No, we have no indication of that. In the environment, if viral particles are present they will not be viable for very long. Viral particles are wiped out very, very readily by ultraviolet light - or by desication, or many other things. They are not very stable at all. The inclusion body is much more stable, but the inclusion body has to be dissolved in order for virus to gain entry into any tissue. The inclusion bodies are very, very stable; except at high pH; the reason that inclusion bodies dissolve in lepidoptera larvae is primarily because of the gut pH. Once the inclusion bodies dissolve, then the viral particles have to enter cells. We really don't know very much about what determines the host range of a virus. This virus won't replicate in anything except gypsy moth. We really don't know what determines the host range of a virus; we strongly suspect it may be something like these protein structures on the viral envelope that could act as sort of a lock and key mechanism to gain entry into a cell. You can dissolve the inclusion bodies, but that doesn't mean anything. The virus has to gain entry into a cell. it has to gain entry into the nucleus, it has to be able to uncoat its DNA and start its replication process. So the fact is that baculoviruses have the most restricted host range of any of the viruses. They are the only virus group that has no counterpart at all in either plants or vertebrates. It is very, very unlikely that a baculovirus could have any mode of action in something as different from a gypsy moth as an oak tree is.

QUESTION: I would like to ask Barbara how the Xylosandrus is killing the tree and if there are preventative measures.

RESPONSE (B.C. Weber): Xylosandrus germanus is an ambrosia beetle; that means it is related to bark beetles and therefore it carries a fungus that it uses as its nourishment when it is growing inside the tree. My hypothesis is that it is carrying other fungi into the tree that cause the wilting and the dieback of the tree. So it is an interaction between the beetle, some fungus or fungi or other microorganism, and the tree itself that actually causing the dieback. To speculate on some preventive measure -- that one is difficult because you would have to figure out which of the three agents is the more important cause and then work on that one to prevent it. Right now we don't know enough about them all to speculate very far; so I'm going to hedge on that one.

QUESTION: Is it a bark infection in the lower part of the tree?

RESPONSE (B.C. Weber): It occurs in the lower part of the tree and the beetle tunnels all the way into the wood, sometimes all the way into the pith; so its not just in the bark area.

QUESTION (B.C. Weber): I have a question for Kathy. My question is -- she talked about the larvae that were parasitized by the fly; and then later being affected by the virus also. My question has to do with the long term affects on the fly populations. Aren't the parasites being killed in the virus-infected larvae?

RESPONSE (K.S. Shields: Yes, that's exactly true. We're looking at it more from the aspect of population prediction. It is true that if you were going to use Blepharipa as a vector of virus, the virus mortality will increase and the Blepharipa population will decrease. So that depends on whether you are interested in parasites or gypsy moths; and most people just want gypsy moths dead, they don't really care how it gets killed. But, the aspect that is interesting about it is if you are trying to assess populations from one year to the next -- if Blepharipa is operating in the gypsy moth population , its a pretty good bet that gypsy moth population is going to have Blepharipa. We are not sure of that but the laboratory evidence exists.

DISPLACEMENT: ONE CONSEQUENCE OF NOT MEETING PEOPLE'S NEEDS[1]

Dorothy H. Anderson[2]

Abstract.--Defines displacement from a recreation researcher's viewpoint and illustrates it with findings from a study of use within the Boundary Waters Canoe Area Wilderness. Findings show that displacement is likely to be caused by litter, noise, overuse, and encounters with others. In many cases, the causes of displacement can be managerially controlled.

Forest managers seek to manage recreation resources to provide people with opportunities to meet their recreation needs. But because recreation use continues to change, some people's needs are not met. Failure, for whatever reasons, to meet people's needs often increases visitor conflicts, visitor displacement, and visitor dissatisfaction.

The purpose of this paper is to help nonrecreation natural resource professionals understand what happens when some people fail to have their recreation needs met. The paper will focus on visitor displacement, one consequence of failing to meet recreation users' needs. Specific intents of the paper are to define and briefly discuss displacement and to provide a context for examining the displacement phenomenon in recreation environments. Selected findings and management implications from a study of recreation displacement are presented to illustrate the phenomenon.

DEFINING DISPLACEMENT

In the social sciences, geographers and sociologists often refer to displacement as free-compelled or forced migration brought about by political forces or government actions (Burdge and Ludtke 1973, Muller 1976). Displacement, then, refers to involuntary movement from one place to another and generally precludes a return to the original location (Shields, M. 1975). To illustrate this meaning, suppose an individual lives in the path of a proposed roadway. If plans for the roadway are approved, the individual is forced to move but is free to choose where to move.

In recreation research we have taken the geographer's and sociologist's definition of displacement and have extended it to include the social psychologist's viewpoint. Adding this viewpoint allows us to examine movement as specific kinds of changes in an individual's behavior. We recreation researchers define displacement as the outcome of a decision to change behavior--an outcome caused by adverse changes in the recreation environment. In addition, displacement can be either on-site or off-site and it can refer to either spatial or temporal changes people make in their recreation behavior (Anderson 1980). On-site displacement is the outcome of a decision to change behavior within a recreation area; off-site displacement is the outcome of a decision to leave a recreation area altogether. Off-site displacement always reflects a spatial change

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in behavior, but on-site displacement may reflect a spatial as well as temporal change in an individual's behavior. For example, people who have been displaced on-site may hike different trails, camp at different sites, and enter a recreation area through different access points. Any of these behaviors reflect spatial changes. An example of a temporal change could be people who decide to enter a recreation area through the same access point but at a different time of the day, week, month, or year. Once in the area they use the area in the same way as they have in the past.

According to our definition, displacement is caused by adverse changes in the recreation environment. An adverse change is simply a change the recreation user does not like. These changes are classified as social, environmental, or managerial. An example of an adverse social change might be an increase in the number and kind of users to a recreation area. Increases in use often lead to greater pressures and competition for space among recreation users (Lucas 1964, Knopp and Tyger 1973, Schreyer and Nielson 1978).

Environmental changes can be vegetation or landscape changes brought about by natural or human forces. Fires, floods, insect infestations, and mining and timber practices can alter the landscape significantly and sometimes make it less desirable for recreation use. For example, in some parts of Pennsylvania, recreation use has decreased as populations of gypsy moths have increased. Many recreation users, not desiring to recreate in areas heavily infested with these insects, have been forced to recreate in other areas where gypsy moths have not yet invaded (Shields, K. 1983).

Displacement can also result from managerial changes stemming from new directives, policies, and legislation. For instance, increases in the number of users to some federal lands have prompted land managers to allocate use through various rationing schemes. Some recreation users are displaced from these areas because they do not want the bother of applying for admittance to the area. Other users are more directly displaced when their applications for admittance are denied because entry quotas are filled.

MODELING DISPLACEMENT

Because displacement is defined as a change in an individual's behavior, it can be modeled in an attitude-behavior context. An individual's intent to behave a particular way depends on the individual's attitude toward behaving that way. Symbolically we can show that attitudes are composed of beliefs and evaluations of beliefs (Fishbein and Ajzen 1975):

$$A_B = \sum_{i=1}^{n} b_i e_i$$

where, A_B is an attitude toward performing a behavior,

b is a belief about the consequences of performing a behavior, and

e is an evaluation of the favorableness or unfavorableness of performing a behavior.

Combined, beliefs and evaluations measure an individual's attitude toward performing a behavior. Thus two people in the same environment may behave differently because their beliefs differ, their evaluations differ, or their beliefs and evaluations differ.

The following example uses this model to illustrate displacement in a recreation context. Two anglers who have fished a particular river in the past are considering fishing it again. Since the time of their last fishing trip on the river, a canoe rental business has begun operating about a mile upstream of their favorite fishing spot. The first angler believes that the canoe traffic generated by the rental business will markedly decrease the opportunity to catch fish. Because catching fish is this angler's most important reason for using the river, not catching fish will strongly diminish the first angler's recreation experience. Based on this belief and evaluation, the first angler decides not to return to the river and fish. Catching fish is also the second angler's most important reason for using the river and not catching fish would strongly diminish this angler's recreation experience. However, unlike the first angler, the second angler does not believe that the canoe traffic will decrease the chance to catch fish and decides to return to the river to fish. Although both anglers share the same evaluation for catching fish, their beliefs differ. Therefore, their attitudes and consequently their intentions differ toward fishing from that particular place along the river. The first angler has been displaced because the decision to fish elsewhere (ie. change behavior) was made in response to an adverse change in the recreation environment (ie., canoe traffic). In contrast the second angler has not been displaced.

SELECTED FINDINGS FROM A STUDY OF DISPLACEMENT[3]

We conducted a study in the Boundary Waters Canoe Area Wilderness of northeastern Minnesota's Superior National Forest to find out if evidence of displacement exists, and if so, to identify the likely causes of displacement. The Boundary Waters, encompassing more than one million acres of land and water, is the only lake-land wilderness in the United States.

Methods

Every group entering the Boundary Waters is required to have a permit, and copies of the permits are retained at the Supervisor's Office of the Superior National Forest. We drew a sample of 1,016 names from permits issued between Memorial Day and Labor Day in 1978 and in 1979. A questionnaire was mailed to each permittee included in the sample. Nearly 85 percent of the users surveyed returned the questionnaires.

Because we were interested only in on-site displacement within the Boundary Waters, we needed to look at people who had used the Boundary Waters several times. Therefore, people who had made fewer than five trips to the area were excluded from our study. After eliminating these people, 619 questionnaires remained.

We measured changes in behavior with the following questions:

a) On your recent visits to the Boundary Waters did you enter through different entry points than you did on your early visits?

b) On your recent visits to the Boundary Waters did you select campsites differently than you did on your early visits? and,

c) On your recent visits to the Boundary Waters did you enter on a different day of the week than you did on early visits?

We defined early visits as the first half of the total number of visits made to the Boundary Waters and recent visits as the last half of the total number of visits made. Respondents could answer either "yes, at least some of the time" or "no, never" to each question. For those answering yes, we measured their attitudes toward selected outcomes of the use changes.[4]

Beliefs about the outcomes of each use change were measured by asking respondents how likely each outcome would be if they did not change behavior. For example, those users who changed entry points were asked to:

> Think back to your early visits to the Boundary Waters. Pick an entry point that you used on early visits but not on recent visits. Write the name of that entry point in the space provided. If you were to use that entry point now, how likely do you think each of the following would be?

Users who selected campsites differently or entered on a different day were asked similar appropriately worded questions. A 7-point Likert scale, ranging from "not at all likely" (scale value = 0) to "very likely" (scale value = 6), was used to measure the strength of the users' beliefs about each outcome. Evaluations of outcomes were measured by asking users how much each outcome, associated with a use change, added to or detracted from the users' recreation experience. A 7-point Likert scale, ranging from strongly detracts (scale value = -3) to strongly adds (scale value = +3), was used to assess the strength of user evaluations. Belief scores and evaluation scores for each outcome were multiplied to develop attitude scores.

By our definition, displacement occurs when users change their behavior in response to adverse changes in the recreation setting. Users' perceptions of adverse social changes were identified through negative attitude scores. For example, a user may no longer use an entry point that was used frequently in the past because the user believes that if this entry point were used, contacts with noisy people would be 'very likely'. Moreover, these contacts 'strongly detract' from the user's recreation experience. This user's belief score would be 6 and the evaluation score would be -3, yielding an attitude score of -18.

Behavior changes

More than 70 percent of the 619 respondents surveyed changed their use of the

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[3] Much of the material in this section has been excerpted from an earlier paper. See Anderson, D. H. and Brown, P. J. forthcoming issue of Journal of Leisure Research.

[4] Attitude measurements were not made for those answering "no, never."

TABLE 1

Belief and Evaluation Scores for Selected Outcomes

Outcomes Related to Changing Entry Points	Belief[a] Scores	Eval.[b] Scores	Outcomes Related to Changing Campsites	Belief[a] Scores	Eval.[b] Scores	Outcomes Related to Changing Entry Days	Belief[a] Scores	Eval.[b] Scores
See litter along portages	4.04	-2.70	Find litter in the campsite area	3.30	-2.63	Come into contact with noisy people	4.04	-2.64
Come in contact with noisy people	4.00	-2.62	See peeled birch trees	3.16	-2.62	Camp within hearing distance of others' campsites	3.71	-2.32
See litter along the shore	3.47	-2.70	Camp at heavily used campsites	2.73	-2.12	See large groups	4.33	-1.91
See worn-out campsites	4.14	-2.08	Camp within hearing distance of others' campsites	2.25	-2.34	Camp at heavily used campsites	3.83	-2.11
See large groups	4.50	-1.92	Camp at sites easily seen from others' campsites	2.71	-2.02	See motorboats	3.86	-1.96
See motorboats	3.70	-1.97	See tents of others from your campsite	2.82	-1.98	Camp at sites easily seen from others' campsites	3.82	-1.93
See worn-out portages	3.98	-1.79	See watercraft pass by my campsite	3.76	-1.42	See organizational groups	4.40	-1.57
See organizational groups	4.34	-1.59	Camp close to hiking trails	1.78	-1.02	See other people at entry points	4.84	-1.18
See other people at entry points	5.20	-1.17				See other people on portages	4.66	-1.15
See people on portages	4.74	-1.18				See canoes	5.00	-0.73
See canoes	5.27	-0.68						

[a] Belief scores were obtained by averaging scores across all respondents. Beliefs could range from 0.00 (not at all likely) to 6.00 (very likely).

[b] Evaluation scores were obtained by averaging scores across all respondents. Evaluations could range from -3.00 (strongly disagree) to +3.00 (strongly agree).

Boundary Waters over time. Eighty-four percent (n=513) of these people used different entry points on recent trips compared to early trips. Seventy-five percent (n=454) of the respondents selected campsites differently and 73 percent (n=438) entered the Boundary Waters on a different day of the week.

Beliefs and evaluations of beliefs

Belief and evaluation scores are shown in Table 1 for outcomes associated with selecting entry points, campsites, and a day to enter the Boundary Waters. The scores were averaged across respondents. Belief scores greater than 3.00 are evidence that respondents believed the outcomes associated with one of the three changes were likely. Scores less than 3.00 indicate that outcomes associated with a behavior change were unlikely to occur. Evaluation scores greater than zero represent outcomes that are perceived as adding to the respondents' recreation experiences. And, outcomes perceived as detracting from experiences have score values of less than zero. None of the outcomes we report here added to the users' experience.

Changes that respondents made in entry points and entry day show that respondents believed that if they behaved as in the past, then the outcomes listed were likely and would detract from their experiences. According to means for outcomes related to campsite selection, respondents believed that if early behaviors were followed most of these outcomes would be somewhat unlikely but any one of these outcomes would detract from their recreation experiences.

Attitudes

We combined belief and evaluation scores to determine respondents' attitudes toward each outcome associated with a behavior change (Table 2). Individual attitude scores were averaged across respondents to produce aggregate attitude scores.

Litter, noise, and overuse (i.e., seeing worn-out campsites and portages, camping at heavily used sites) were perceived more negatively than seeing other people. This finding was true for all three kinds of behavior changes considered. Also, fewer users perceived visual encounters with others as negative outcomes, than those who perceived litter, noise, and overuse as negative outcomes. The most striking implication of these findings is that displacement is likely to be caused by more than visual encounters with others. An additional implication is that encounters with others may not be as important in displacing users as other reasons.

MANAGEMENT IMPLICATIONS

We believe that the outcomes we identified as related to displacement can be managerially manipulated. Our study documents that change, and possibly displacement, is taking place within the Boundary Waters and that this change is at least partly due to adverse environmental and social conditions. Being aware of the conditions and the resulting changes in use patterns is useful in planning and can lead to specific management objectives and practices. For example, stronger messages could be issued to inform the recreating public that litter, noise, and resource vandalism are not acceptable. Clean-up patrols could be directed to spend more time in areas where litter is a problem. Managers could close worn-out campsites and portages to allow these areas time to recover. Campsites in good condition could be monitored and corrective actions taken before overuse causes deterioration.

During 1983 Boundary Waters resource administrators will develop a new multi-year management plan. Their management strategy will be based on guidelines outlined in the Recreation Opportunity Spectrum (ROS) system. For management purposes the Boundary Waters has been divided into three of the six zones included under ROS: primitive, semi-primitive nonmotorized, and semi-primitive motorized. Managers there seek to provide different kinds and levels of recreation opportunities for each zone. Information from our study about resource conditions that might influence displacement is one input these administrators will use as they develop carrying capacities for these zones (Sober 1983). For example, campsites might be spaced farther apart in primitive zones than in semi-primitive zones. This action, while controlling the total number of users allowed in primitive zones, would also decrease the chance of hearing or seeing other users from a campsite. Although the study data have limitations, we are encouraged by the response of the resource administrators in the Boundary Waters and what we might learn as they implement new management actions.

Our findings also have implications beyond the Boundary Waters. Other recreation areas across the country have experienced use increases similar to the Boundary Waters, and some people using these areas are probably also being displaced within these areas. In addition off-site displacement is probably also occurring. That is, people are being displaced from one resource area to another.

TABLE 2

Mean Attitude Scores Toward Selected Outcomes

Outcomes Related to Changing Entry Points	N[a]	Score[b]	Outcomes Related to Changing Campsites	N[a]	Score[b]	Outcomes Related to Changing Entry Days	N[a]	Score[b]
See litter along portages	484	-11.05	Find litter in the campsite area	443	-8.83	Come into contact with noisy people	389	-10.88
Come in contact with noisy people	468	-10.82	See peeled birch trees	440	-8.30	Camp within hearing distance of others' campsites	370	-8.75
See litter along the shore	476	-9.46	Camp at heavily used campsites	391	-5.52	See large groups	291	-8.73
See worn-out campsites	427	-9.43	Camp within hearing distance of others' campsites	413	-5.17	Camp at heavily used campsites		
See large groups	347	-9.23	Camp at sites easily seen from others' campsites	371	-5.15	See motorboats	302	-8.01
See motorboats	376	-8.41	See tents of others from your campsite	333	-4.95	Camp at sites easily seen from others' campsites	333	-7.51
See worn-out portages	360	-7.84	See watercraft pass by my campsite	286	-4.86	See organizational groups	258	-7.40
See organizational groups	310	-7.12	Camp close to hiking trails	310	-1.43	See other people at entry points	198	-5.89
See other people at entry points	247	-6.34				See other people on portages	237	-5.65
See people on portages	292	-5.90				See canoes	193	-3.77
See canoes	245	-3.59						

[a] The number of respondents indicating they held both a belief and evaluation about an outcome.

[b] Scores were obtained by multiplying belief scale values (range = 0 to 6) by evaluation scale values (range = -3 to +3).

For planning and managing purposes, resource administrators need to look at recreation areas within a region and understand how change in one area affects another area. For example, does change in an area signal that new users are coming into the area? If so, should management objectives be written to promote or discourage this kind of change? If objectives are developed to promote succession or new users coming into an area, what happens to the users who were there before? Are they displaced? If they are displaced, where do they go and how do they impact other recreation resources in the region? For those people who are displaced, what kinds of recreation areas and recreation activities do they substitute for the ones they have lost? The answers to these and other similar questions are not known. To answer these kinds of questions, resource administrators at all levels need to know people's preferences for different recreation environments. Equipped with this kind of information administrators can identify recreation areas that are suitable for and capable of sustaining different kinds of users and a variety of uses and, thus, lessen the likelihood of visitor displacement.

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THE HANDICAPPED USER IN OUTDOOR RECREATION RESOURCE ENVIRONMENTS: IMPLICATIONS FOR RESOURCE PLANNERS[1]

Lou G. Powell, Ph.D.[2]

Abstract.--In recent years recreation and resource planners have given increased attention to the provision of outdoor recreation opportunities for individuals with handicapping conditions. Planners are faced with the challenge of designing accessible environments which meet the needs and interests of all users while maintaining the integrity of surrounding natural resources. Current literature provides the planner with valuable information that can guide environmental design and program decisions concerning the handicapped users. This paper presents principles for planning outdoor recreation experiences that are compatible with the expressed needs and interests of many handicapped individuals. It is important that further study be conducted so that planners will have access to a greater knowledge base from which to derive decisions. Recommendations for future research are provided.

INTRODUCTION

Handicapped Americans are increasingly voicing a need for independence, dignity, risk, and adventure. In response to this need, outdoor recreation and resource planners must focus upon the design of environments that are suited to the needs and interests of all users. In recent years, engineers have embraced the study of ergonomics to construct living and work spaces that are highly compatible with the potential users. The application of this science requires a strong technical knowledge of the needs of the consumer, the characteristics or qualities of the environment, and the dynamics of the relationship between the consumer and his or her surroundings. Similarly, the outdoor recreation and resource planner who wishes to design an ergonomic environment which meets the needs and interests of all users while maintaining the integrity of the surrounding natural resources, must have access to technical knowledge concerning the needs of potential users as well as the recreation resource environment. Only then can design principles evolve which offer the greatest compatibility.

This paper presents the planner with information which can have application to decisions effecting environmental design for handicapped users. Questions to be addressed through future research efforts are also posed. The literature currently available to recreation resource planners focuses primarily upon information concerning the outdoor recreation interests and physical accessibility needs of handicapped people. While further research must be conducted in order that planners have an adequate knowledge base from which to base decisions, current literature does reveal some guidelines for planning. A discussion of selected principles follows.

PRINCIPLES FOR PLANNING

Integrated recreational settings

Handicapped individuals have strongly articulated the need for, and an interest in, recreation facilities and activities, especially in informal, integrated, outdoor recreational settings (Peterson et al. 1977). In the early 1960s the U.S. Forest Service began

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[1] Paper presented at the Symposium on Research in Forest Productivity, Use and Pest Control: Contributions by Women Scientists, September 16-17, 1983, Burlington, Vermont.

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developing highly specialized recreational facilities for handicapped persons, such as the Roaring Fork Braille Trail in Colorado, Mammoth Lakes Campground in California, and Trout Pond in Florida. User feedback indicated that many handicapped individuals were specifically avoiding these segregated areas, preferring to struggle in the inaccessible facilities so they could be with their families and/or the majority of other users. Thus it was learned that some handicapped individuals wished to be included in the mainstream of life, without an inordinate amount of special or separate facilities and programs (Carroll 1973; AAHPER 1977; Fay et al. 1976). Consequently the Forest Service has revised its service philosophy for handicapped individuals. Current practice within the Forest Service is to discontinue development of segregated recreational areas and instead focus upon the elimination of physical barriers which prevent the use and enjoyment of existing forest lands and recreational areas (USDA 1983; Fay et al. 1976).

While this apparent responsiveness of the Forest Service is a positive sign, and will better address the needs of many handicapped individuals, there are still important and relevant questions which go unanswered and may have implications for the current planning approach. Are there sub-groups of potential handicapped users that would prefer and/or need special facilities (e.g. multiply handicapped or severely handicapped individuals)? If so, are there sufficient numbers of potential users within these sub-groups and/or federal legislative mandates which would support at least some highly specialized areas?

Tangential to this planning principle is the concern of handicapped individuals that planners might generalize the findings of a sample of individuals who have one disability to represent or imply the preference of individuals with different disabilities. As there are a myriad of interests and abilities among the nonhandicapped population, so are there among handicapped individuals.

Normalized outdoor environments and activities

Handicapped individuals indicate a preference for activity opportunities and facilities much like those preferred by nonhandicapped peers. Beechel (1975) found that while some special accommodations are necessary to facilitate pursuit of certain outdoor recreation opportunities, handicapped individuals prefer outdoor environments that are as close to normal as possible. In addition, Carroll (1973) found that the types of outdoor recreation preferred by a sample of handicapped individuals were hiking, water sports, picnicing and camping; experiences that are commonly enjoyed by nonhandicapped peers.

Threshold for adaptation

There is evidence that a threshold level of adaptation appears to exist, beyond which further design changes are likely to be perceived as stigmatizing (West 1981). There are several case study examples in which planners, designers, and programmers have invested dollars, time, and sincere concern in projects that have altered outdoor areas and facilities for the presumed benefit of the handicapped user. Yet, in spite of this investment in improved service capability, it was found that there was no subsequent increase in use of these areas and facilities by handicapped consumers. Contrary to this no increase in use pattern, handicapped consumers, consumer advocates, federal legislative mandates, as well as numerous descriptive research studies validate that design and accessibility improvements in outdoor recreation facilities and programs continues to be a major desire expressed by the potential handicapped user. Thus to what can we attribute this inconsistency between use patterns and interests?

There is some evidence that a threshold level of adaptation appears to exist, beyond which further design changes are likely to be perceived as stigmatizing and as a result, discourage use. A personal experience which occurred during a research study of the accessibility features of New Hampshire State Parks (Powell 1982) tends to further support this claim. Throughout the New Hampshire study, it was noted that most accessible campsites were designated by large, two- by three-foot blue signs displaying the international access symbol. These signs were clearly visible to all passersby. During an interview of a handicapped user who had selected an inaccessible site, the following comments were recorded:

"I come here to get away from the pressures of my job and my handicap. Those signs are like a flashing red light. A man stopped by my campsite today and didn't realize one of my legs was missing until thirty minutes later when he asked me if I would help him put his boat in the water. I reached for my crutches under the picnic table and stood up. He gasped. I don't think he would have ever stopped by if I had camped at a site that had one of those signs. As it happened, I was able to help him relax around me and we're off on a fishing trip in the morning." Viable alternatives to this more stigamtizing practice of obtrusively posting access signs might include dissemination of information on accessible campsites at time of check-in and/or identification of such sites on camp maps and other literature.

This handicapped user's story suggests additional unanswered questions, e.g. Is this handicapped individual's feelings characteristic of many other individuals? Are there particular types of adaptations that handicapped individuals find especially stigmatizing? Are there alternative means to facilitate use that are less stigmatizing?

Continuum of opportunities

Not all persons with handicapping conditions desire the same level of outdoor adventure experiences. As with the general population, adventure is a personally defined experience. "Just as some able-bodied persons prefer more challenging primitive wilderness areas while others want campgrounds with all the comforts of home, some individuals with handicapping conditions want longer and more difficult hiking trails than other handicapped persons." (AAHPER 1977, p.67). Implications for planning that may be derived from this principle are numerous. For example, it becomes important to offer a continuum of outdoor recreation opportunities and settings for handicapped individuals due to the consequent diversity of needs and preferences which must be met -- a planning principle which is already applied to the nonhandicapped population.

Trail design and information.--Consistent with this thinking is the practice of placing signs at the entrance of outdoor trails that inform potential users of the trail length, the level of difficulty (using a national rating scale much like those used for ski slopes) and a map indicating the location of rest stops and accessible toilet facilities. This information will allow each potential user (whether handicapped, nonhandicapped, elderly, or small child) to make personal choices about taking the trail based upon individual ability. Other alternatives that should be considered for hiking trail accessibility are the all-terrain vehicle, snowmobiles, gondolas, or horseback riding, all of which can be realistic means of mobility over natural terrain for many handicapped individuals. Provision of trails with varied gradations and 3/8ths minus crushed rock can also offer opportunity for all users without being costly or aesthetically damaging (Helbig 1978). The cries and concerns of some resource planners that all natural areas will soon be covered with blacktop in order to accommodate the handicapped can be alleviated.

Trails for blind individuals.--The trails enjoyed most by blind persons are those that have been left in as natural a state as possible (as long as they are safe). Such a state affords a more challenging experience (Beechel 1975; Fay et al. 1976; AFB 1972). Research by the U.S. Forest Service and the National Park Service indicates, "while braille trails are popular with sighted visitors, they are usually useless to the blind individual" (Fay et al. 1976). This conclusion is based upon the following facts: 1) less than ten percent of blind individuals can read braille; in addition, there are several 'languages' of braille; and 2) braille signs are highly subject to vandalism. Alternative solutions to accessibility have included the use of audio interpretive devices such as tape recorders in lieu of signs, use of 'differential' trail surfaces which by feel and/or sound distinguishes the trail from its surroundings making trails safe from obstacles, and making trails interesting to all the senses (Beechel 1975; AAHPER 1977; Fay et al. 1976). An example of such a trail is in the New Jersey Pine Barrens which stresses pond ecology, forest management, and plant and animal relationships.

Benefits to all users

Physically handicapped individuals are not the only persons who benefit from barrier-free access designs. Reports have shown that there are fewer tripping and falling hazards and therefore fewer public liability claims and worker related accidents in barrier-free settings. Ramps and wider door construction meet with the highest fire prevention standards, so buildings with barrier-free design generally have lower insurance rates (Harris et al. 1977). A survey at the University of Kansas concerning new curb cuts installed on campus found that people interpreted the reasons for the improvement in terms of their own life situation, not as improvements for the handicapped. Ninety percent of the respondents felt the curb cuts were made to help bicycle riders, and those respondents who were service employees felt the curb cuts were made to facilitate deliveries (Harris et al. 1977).

Cost of accessibility

Finally, it should be noted that while plans to make new and existing facilities and areas accessible may incur additional costs, surveys conducted by the General Accounting Department of HEW indicate that "in new construction, the additional cost for accessibility is less than one-half of one percent and renovating existing facilities, no more than three percent" (AAHPER 1977). In addition there are 'low cost' or 'no cost' approaches to establishing accessible environments that are frequently overlooked. Examples include: placing cup dispensers beside water fountains for wheelchair users; tilting bathroom mirrors when they cannot be lowered; providing an accessible unisex bathroom so that companions can assist their handicapped partner; asking the telephone company to lower a telephone; using taped messages when possible; and changing door weights so they may be opened with less effort.

DIRECTIONS FOR FUTURE RESEARCH

A review of existing outdoor recreation research literature indicates the following:

1) There is little evidence of empirical studies that have specifically examined the handicapped user.

2) Few existing studies pertaining to nonhandicapped user characteristics and behavior have been validated with reference to the handicapped user. Research theory that has been applied to nonhandicapped user behavior patterns and preferences may indicate approaches for expanding the relevant knowledge base of planners. For example, the Opportunity Theory has been tested using a population of different socioeconomic groups, but the literature appears to be void of such hypothesis testing with handicapped individuals. The fact that handicapped people in the U.S. have on the average significantly lower earnings than the nonhandicapped suggests the potential relevance of study in this area.

Recreation researchers have also investigated the causes of conflict among users of outdoor recreation with regard to the concept of goal interference. "Lifestyle tolerance", the tendency of accept or reject lifestyles different from one's own, was derived by Jacop and Schreyer (1980) as one of the major classes of factors which produce conflict in outdoor recreation. The nature and extent of user interaction among handicapped and nonhandicapped individuals may have serious implications regarding the success with which handicapped individuals are integrated and accepted into traditionally nonhandicapped environments. This author could not identify any existing research which supports or refutes user conflict/goal interference using the independent variable of noticeable handicapping conditions.

3) Much of the research to date with respect to outdoor recreation participation of handicapped individuals has focused upon physical design barriers. It has been hypothesized that physical removal of architectural barriers will result in a significant increase in participation of handicapped individuals. While there is little argument that barrier-free design presents increased opportunity there is evidence that removal of barriers in and of itself will not guarantee use. Researchers have only just begun 'to scratch the surface' in terms of studies which focus upon intervening variables that may have an impact upon the use of physically accessible facilities.

4) Most of the research that has examined the benefits of outdoor recreation for handicapped individuals has taken place in segregated camp settings. More research is needed in areas that are used by the general public such as national and state parks, national forests, nature centers, and backcountry and wilderness areas.

Further, it appears that existing research which has potential application to the handicapped user in the resource environment appears to be dichotomous in nature. There is a body of descriptive research which focuses upon the expressed outdoor recreation needs and interests of handicapped persons. This research has been conducted primarily by professionals in Therapeutic Recreation and the allied health fields. Another body of empirical and descriptive research exists which explores the behavior of the nonhandicapped user as well as the environmental impact of these users. This research has resulted in recreation resource planning and management.

A greater convergence of these research efforts is needed. Our research knowledge base concerning the handicapped recreation resource consumer can be greatly enhanced if our investigations are expanded to include study of use patterns, participant behavior and environmental impacts of these users. Further study of variables that potentially inhibit or facilitate use of resource environments by handicapped users is imperative. The author encourages researchers who investigate recreation resource user behavior to include the handicapped user as a variable when feasible. Collaboration of those researchers who are knowledgeable about issues concerning handicapped persons with researchers who have expertise in recreation resource planning can potentially result in new planning principles which will lead us toward a more ergonomic environment for all natural resource users.

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DEER DENSITIES AND FOREST REGENERATION[1]

by Nancy G. Tilghman[2]

Abstract.--Preliminary results of a study of the effects of five deer densities and three cutting treatments on development of tree seedling reproduction on the Allegheny Plateau of northwestern Pennsylvania show that higher deer densities reduce the height growth made by seedlings in clearcut and thinned stands. Moreover, there are fewer tree seedling species, less _Rubus_, and more fern at higher deer densities.

INTRODUCTION

The Allegheny hardwood forest type covers nearly 12 million acres in Pennsylvania, New York, Maryland, and West Virginia (Fig. 1). The major tree species of these forests are black cherry (_Prunus serotina_ Ehrh.), red maple (_Acer rubrum_ L.), sugar maple (_Acer saccharum_ Marsh), and white ash (_Fraxinus americana_ L.). Most of the world's supply of cherry lumber and veneer for furniture and paneling comes from these forests. The maples are used for furniture, flooring, and specialty products, and the white ash are used for baseball bats and tool handles (Marquis 1975). The overall value of timber in the cherry-maple forests of northwestern Pennsylvania averages about $2500 per acre. Timber receipts on the Allegheny National Forest alone run between $4 million and $6 million per year.[3]

The Allegheny hardwood forests of northwestern Pennsylvania are valuable for other reasons as well. Over 100 million people live within a day's drive of these forests and many of them take advantage of the recreational opportunities for camping, hiking, and boating there (U.S. Forest Service 1975). The beautiful scenery, especially the spectacular fall foliage, attracts many city-dwellers to the cherry-maple forests. These forests are the home of numerous species of wildlife. Many visitors to these forests enjoy the chance to observe animals in the wild; others come to hunt deer, turkey, grouse, and bear. Over 1.25 million people buy hunting licenses in Pennsylvania, more than in any other state in the nation.

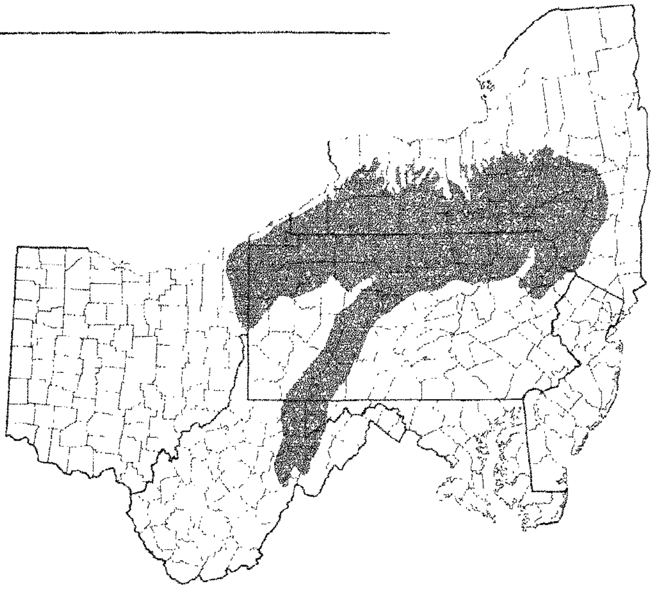

Figure 1.--Distribution of the Allegheny hardwood forest type.

But the future of these forests is in jeopardy because there are not enough young tree seedlings to replace the overstory trees after harvest. Although there are several interrelated reasons for this, browsing of seedlings by white-tailed deer (_Odocoileus virginianus_) is a major one.

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[1] Paper presented at the Symposium on Research in Forest Productivity, Use, and Pest Control: Contributions by Women Scientists, Burlington, Vermont, September 16-17, 1983.

[2] Research Wildlife Biologist, USDA Forest Service, Northeastern Forest Experiment Station, P.O. Box 928, Warren, Pennsylvania 16365.

[3] Personal communication from J. Hockinson, Timber Staff Officer, Allegheny National Forest, USDA Forest Service, Warren, Pennsylvania, 1983.

BACKGROUND

A look at the future of these forests must begin with a brief look at the past. Before it was settled by white men, white pine-hemlock-hardwood forests covered much of this area. Clearcut logging of these forests between 1890 and 1930 resulted in today's cherry-maple forests (Marquis 1975). Thus, these second-growth forests are essentially even-aged and most are between 50 and 110 years old (Fig. 2). Nearly three-quarters of these stands will be ready to harvest in the next few decades, but because regeneration is inadequate their owners hesitate to harvest them.

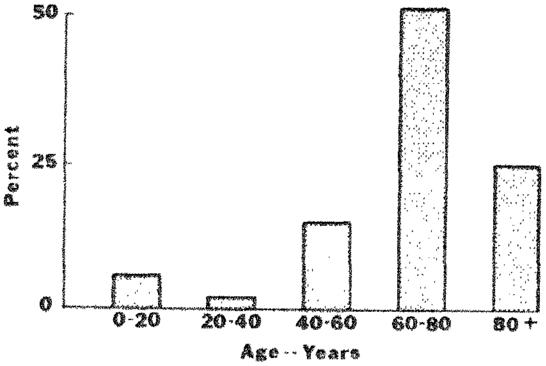

Figure 2.--Age-class distribution of Allegheny hardwood forests in northwestern Pennsylvania.

Although it is difficult to separate the history of white-tailed deer populations in northwestern Pennsylvania from that of the rest of the state, a statewide review of deer population trends suggests what happened in the Allegheny hardwood forests. In the late 1800s, white-tailed deer populations were subject to intense hunting pressure. Deer were hunted for market and sold to the many logging camps around the state. There were no laws restricting the number or sex of deer that could be taken or the season when they could be hunted. Dogs and baits were commonly used in the pursuit of deer. By the turn of the century, deer had nearly been eliminated from Pennsylvania (Forbes et al. 1971). Then several steps were taken to protect the remaining deer, including the institution of a "bucks only" hunting season. Deer were brought in from other states and introduced to areas from which they had been extirpated. At the same time, extensive clearcutting provided an abundant food source for the deer. The combination of protection from overhunting, abundant food, and the lack of natural predators allowed the deer population to increase dramatically (Fig. 3) (Forbes et al. 1971).

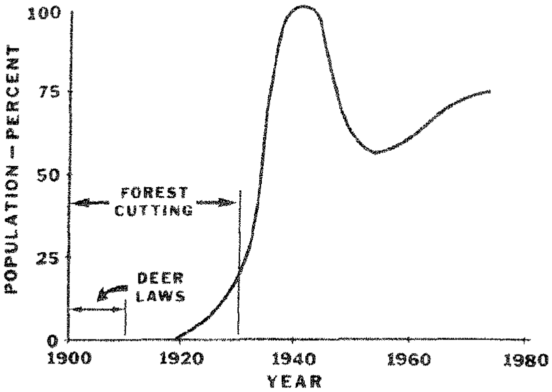

Figure 3.--Deer population trends in Pennsylvania. After Marquis (1975), adapted from Leopold (1943), Bennett (1957), and records of Pennsylvania deer harvests.

By the early 1920s, deer damage to forest reproduction was evident (Frontz 1930). As the new forests grew out of the reach of the deer, deer food became scarce. The loss of previously abundant food resources and lack of overstory cover caused widespread winter starvation by the late 1920s. In 1928, the taking of does was legalized throughout Pennsylvania in an attempt to curb population growth. Nevertheless, deer numbers in Pennsylvania probably reached a peak of about a million deer by the late 1930s (Forbes et al. 1971). But the doe seasons, increases in the total harvest, and large winter losses reduced the deer herd to about half its peak by 1950 (Bennett 1957). Since that time, statewide deer populations have gradually increased to about 750,000 deer (Fig. 3).[4]

The problem of high deer populations browsing on tree seedlings to the point of greatly altering or even eliminating the new generation is not unique to northwestern Pennsylvania. Foresters and biologists have noted this conflict between forest and wildlife resources in other areas of the

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[4] Comparison of population estimates of the statewide deer herd is confounded by changes that have occurred in the method of estimating deer populations. While the actual numbers may not have been accurate in past years, the general population trends indicated by these estimates are useful.

country (e.g. Washington, Oregon, Wisconsin, Michigan, New York) and at various times since the beginning of forest management.

ALTERNATIVES

Over the years, several techniques have been developed to alleviate the overbrowsing of tree seedlings. On the Allegheny plateau, numerous repellents have been tested, from those that taste terrible to those that smell rotten. None of these have proven effective in reducing browsing at high deer densities. At low deer densities, some repellents have been effective, but they require frequent and expensive reapplication.[5] Aerial application of nitrogen and phosphorous fertilizers to induce rapid height growth of existing seedlings beyond the reach of the deer has been tried, but this, too, is expensive (Auchmoody 1982). Fencing regeneration cuts has also proven effective, but again a sizable expense must be borne by the landowner. Electric fences can cost from $17 to $160 per acre (Brenneman 1982), while 8-foot woven wire fences cost from $100 to $350 per acre.[6]

Although these techniques may provide short-term protection of small areas from deer browsing, they are only bandaid solutions. Those who manage the deer herd and its habitat have been working together to come up with a long-term compromise that will ameliorate the economic and ecologic impact of high deer populations on forest resources. The first step in the process is to bring the deer herd down to level at which the forests can be regenerated.

MANAGING THE DEER HERD

The Pennsylvania Game Commission (PGC) manages the state deer herd on a county-by-county basis. They have developed deer population estimates for each county. For example, their overwintering deer density estimates for the four counties in which the Allegheny National Forest is located range from 15 to 30 deer per square mile.[7] Using forest age-class information, the PGC has also developed deer population goals for each county based on the overwinter carrying capacity of forests of various ages. In three of the counties mentioned above, the PGC has set goals that call for a decrease in the county-wide deer population, while in the fourth they want to maintain the population at nearly the same level.[7] Although these goals are based on the best information presently available, they come primarily from studies of deer condition and survival. They are not goals for deer population levels that will allow adequate tree reproduction. We need better information on which to base our management strategies. Just what is the optimum deer density that will allow hikers and hunters to enjoy deer in the forest, but still allow enough tree seedlings to survive to perpetuate the forest?

ENCLOSURE STUDY

The U. S. Forest Service's Northeastern Forest Experiment Station at Warren, Pennsylvania, has initiated a 10-year study of the effects of several deer densities on tree regeneration in Allegheny hardwood forests. A second objective of this study is to examine the preferences of deer for browse among the numerous species of woody and nonwoody understory plants.

Methods

Four 160-acre enclosures have been established in Allegheny hardwood stands of northwestern Pennsylvania. Two of these sites are located on the Allegheny National Forest, one is located on State Game Land 30, and one on Elk State Forest and National Fuel Gas forest land (Fig. 4). Each of these enclosures has been constructed of 8-foot woven wire fencing and has been subdivided into four subenclosures. Different deer densities have been established in each of the subenclosures with one deer in 64 acres and one, two, and four deer in each of the 32-acre areas, simulating 10, 20, 40, and 80 deer per square mile (Fig. 5). Small exclosures (1/250 acre) were randomly placed in each subenclosure to represent zero deer per square mile. Each subenclosure was also subjected to three different cutting treatments-- 10 percent was clearcut, 30 percent was thinned, and the rest was left uncut.

A system of permanent milacre sampling plots was established in each subenclosure, with 25 plots in the clearcut, 15 plots in the thinning, and 20 in the uncut portion. The height and number of each species of tree seedlings on these plots were tallied before deer were installed; they will be remeasured every other year over the 10-year period.

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[5] Office report (Study 98) by R. Ernst, USDA Forest Service, Northeastern Forest Experiment Station, Warren, Pennsylvania, 1980.

[6] Personal communication from J. Hockinson, Timber Staff Officer, Allegheny National Forest, USDA Forest Service, Warren, Pennsylvania, 1981.

[7] Personal communication from W. Shope, Wildlife Biologist, Pennsylvania Game Commission, Millerstown, Pennsylvania, 1983.

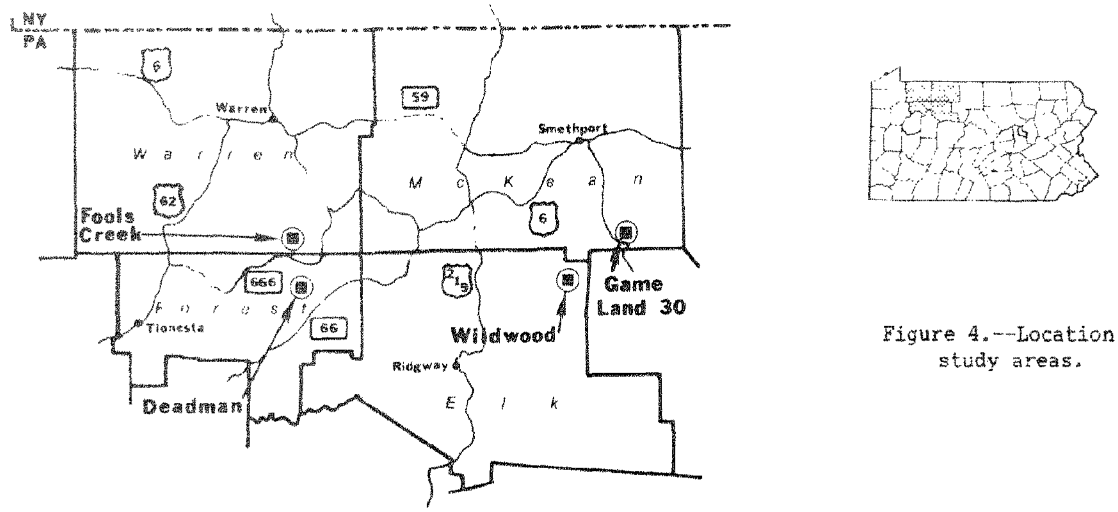

Figure 4.--Location of study areas.

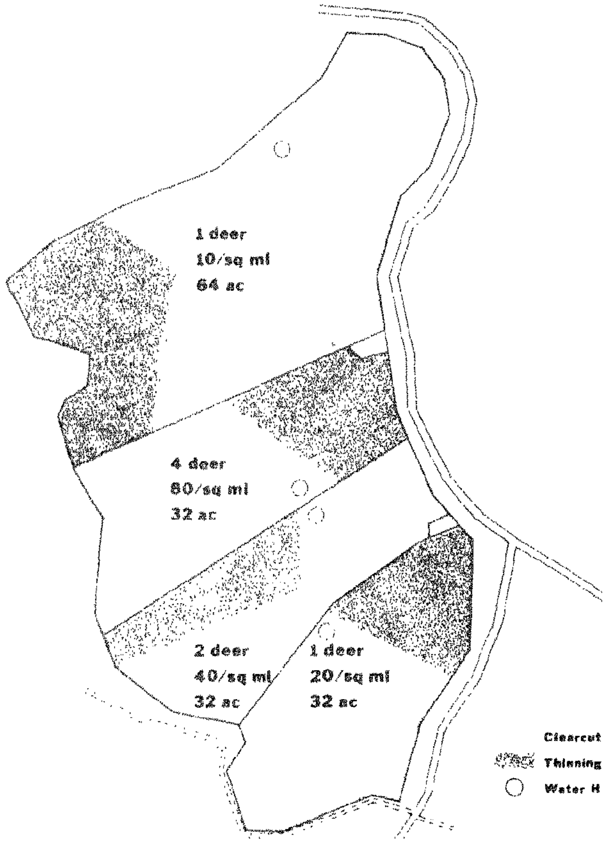

Figure 5.--An example of the layout of one of four deer enclosures.

The percentage cover of various herbaceous plant species has also been recorded and will be monitored throughout the study.

Preliminary results

This past summer we took the first remeasurements of vegetation on two of the four study areas and already we can see differences in the vegetation. Some differences are the result of cutting treatments, but others can be attributed to the density of deer. In the clearcuts, differences in the height of tree seedlings are readily visible. For example, in the 10-deer/square-mile clearcut, the average height of the tallest tree seedlings is nearly 7 feet (Fig. 6a). In the 80-deer/square-mile clearcut, however, the dominant seedlings are not yet 4 feet tall (Fig. 6b). Most of the tallest seedlings in the high-deer-density enclosures were located in slash piles where they escaped browsing. The average height of seedlings outside the slash piles in the 80-deer/square-mile clearcut was less than 2 feet.

Unprotected seedlings in our highest deer density enclosures were significantly shorter than seedlings in any of the other densities, protected or unprotected (Table 1). The protection offered by slash in the two highest deer density treatments allowed seedlings to grow as tall as those found in unprotected areas of the lower deer density enclosures. At low deer densities, seedlings located in slash piles were as tall as those found in our control areas inside the exclosures. Thus, slash left on the ground after a clearcut can provide protection for the new seedlings and result in a shorter rotation for the new stand.

Figure 6a. Height growth of tree seedlings in the 10-deer/square-mile clearcut.

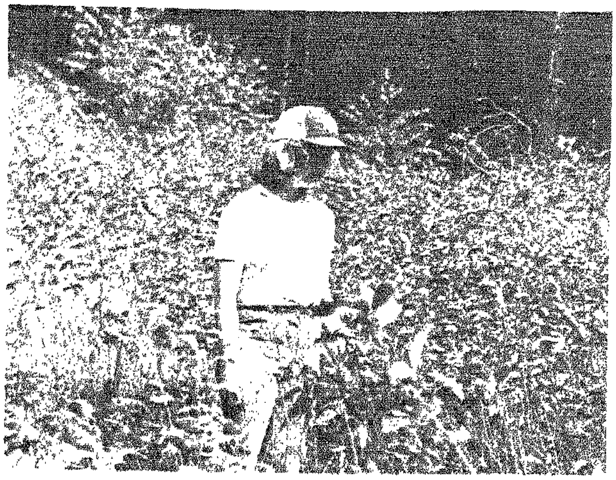

Figure 6b. Height growth of tree seedlings in the 80-deer/square-mile treatment.

Table 1.--Comparison of effects of slash on the height of tree seedlings in different deer densities.

Height of dominant stems		
< 2'	3' - 5'	> 7'
80 deer[a] - no slash	80 deer - slash	0 deer - no slash
	40 deer - no slash	0 deer - slash
	40 deer - slash	10 deer - slash
	20 deer - no slash	20 deer - slash
	10 deer - no slash	

[a] deer = deer per square mile.

We are also beginning to see evidence of changes in the species composition of the regeneration from different deer densities. In the 10-deer/square-mile treatment, a wide variety of tree seedling species can be found--black cherry, red maple, sugar maple, white ash, yellow-poplar (*Liriodendron tulipifera* L.), American beech (*Fagus grandifolia* Ehrh.), sweet birch (*Betula lenta* L.), yellow birch (*Betula alleghaniensis* Britton), aspen (*Populus* spp.), cucumbertree (*Magnolia acuminata* L.), pin cherry (*Prunus pensylvanica* L.), striped maple (*Acer spicatum* Lam.), serviceberry (*Amelanchier* spp.), devils-walkingstick (*Aralia spinosa* L.), and staghorn sumac (*Rhus typhina* L.). Black cherry and pin cherry seem to dominate. In the clearcut, many of these young black cherries are stump sprouts. The diversities of tree seedling species in the 80-deer/square-mile treatments at the two study areas were different. At one site where the regeneration potential was high, the number of tree seedling species was nearly the same as that found in the low-deer-density subenclosures (Table 2). The abundance of seedlings and more rapid height growth on this good site allowed a wider variety of tree seedlings to grow out of the reach of deer. At the other study area, however, there were significantly fewer tree seedling species in all cutting treatments of the high-deer-density subenclosures (Table 2). Because they are preferred browse, species such as pin cherry are significantly less common in the 80-deer/square-mile treatment. Only the less palatable species are left, and there is a tendency for black cherry to dominate. Although black cherry is our most valuable timber species, this shift toward a monoculture of black cherry is considered undesirable from both timber and wildlife management viewpoints. A monotypic forest runs the risk of complete destruction by insects or disease and decreases the diversity of wildlife habitats available.

Table 2.--Number of seedling tree species by deer density and cutting treatment for two study areas, one of high reproductive potential and one of lower reproductive potential.

Cutting treatment	Reproductive potential	Number of deer per square mile				
		0	10	20	40	80
Uncut	High	9	8	8	7	8
	Low	11	12	8	10	7
Thinning	High	10	8	10	10	8
	Low	13	12	13	9	9
Clearcut	High	10	10	11	11	10
	Low	12	12	10	11	10

Changes are also apparent in the relative abundance of certain herbaceous species. Ferns cover nearly four times as much area in the high deer density clearcuts as they do in the lower deer densities (Table 3). These ferns, primarily hayscented fern (*Dennstaedtia punctilobula* (Michx.) Moore) and New York fern (*Brachyelytrum erectum* Schreb.), produce chemicals that interfere with the germination, growth, and survival of young black cherry seedlings. Blackberries (*Rubus* spp.) are also affected by high deer densities. In the high deer density thinnings, deer have reduced the amount of blackberry cover by 50 to 75 percent as compared with the low deer density thinnings (Table 3). Blackberries, a favorite food of deer, are not abundant where deer browsing is heavy. Just as ferns have been shown to interfere with tree seedlings, so blackberries have been shown to interfere with ferns and grasses. Thus deer browsing not only has a direct effect on the growth and survival of tree seedlings, but can indirectly affect them as well by eliminating the blackberries that would ordinarily limit the spread of ferns and grasses.

Table 3.--Percent ground cover by ferns and *Rubus* at different deer densities.

Ground cover	Cutting treatment	Number deer per square mile				
		0	10	20	40	80
Fern	Clearcut	6	3	10	24	15
Rubus	Thinning	70	64	70	50	10

RECOMMENDATIONS ?

With only two of the four areas remeasured, our results are in no way conclusive. It is still too early to come up with any recommendations for desired deer densities to benefit both wildlife and forestry resources. But even after 2 years, we are witnessing changes in the vegetation, changes that affect not only the future forests of the region, but habitat for other wildlife species as well. When deer populations are too high, the natural understory of the forest may be eliminated. In some instances, deer may compete directly for food items with other wildlife, such as snowshoe hare (*Lepus americana*) and wild turkey (*Meleagris gallopavo*). Cover, roosting, or nesting sites may be eliminated for other wildlife species such as ruffed grouse (*Bonasa umbellus*) and low-nesting songbirds (Passeriformes). These changes in the forest happen gradually as the deer herd builds up, so it is often difficult to attribute changes in the abundance of other wildlife species to the deer. For those species whose territories or home ranges are small enough, we will be looking for population differences among the various deer-density treatments. To date, a study of songbird diversity and abundances has been initiated in these enclosures. High deer populations can also have an effect on the deer themselves. Several studies have shown that deer raised on poor nutrition will generally be in poorer physical condition. Bucks tend to have smaller racks, and does tend to produce twins less often. Thus, reducing deer densities to levels compatible with existing range conditions can improve the outlook for both forests and wildlife.

As efforts are being made to bring the deer herd more in line with the habitat available, other efforts are underway to provide better deer habitat. The Allegheny National Forest has developed a cooperative agreement with the Pennsylvania Game Commission which not only calls for a reduction in the local deer herd, but requires that the National Forest make regeneration cuts totalling at least 2000 acres per year and at least 7000 acres of thinnings or initial shelterwood cuts. These measures are designed to provide additional food for deer and to spread the deer out over a wider area. These efforts to manage both the deer and its habitat will benefit the entire forest ecosystem including the deer, other wildlife species, and the new forest regeneration.

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PATTERNS OF WOLF PREDATION
AND EFFECTS ON MOOSE FEEDING HABITATS[1]

Joan Edwards[2]

Abstract.--Observations of moose (*Alces alces andersoni*) were made at the northeastern end of Isle Royale Wilderness National Park, Michigan, to determine the food preferences, distributions and diets of moose. Moose show strong food preferences which correlate with nutrient content. Adult bulls, solitary cows and yearlings shift distribution so that they track these high preference, high nutrient food items. In May and June, they feed on the ridges of the main island where high nutrient food items are first available; only in July and August do they move to the small outer islands where high quality foods are available later. Cows with calves deviate significantly from this pattern by going to the small islands in May prior to the leafing of high nutrient foods and remaining there throughout the growing season.

These distributions of moose suggest that wolf predation may significantly alter the feeding patterns of cows with calves, the age class most vulnerable to wolf predation. Cows may protect their calves from wolves by remaining on the wolf-free outer islands and avoiding the main islands where wolves are present. These data suggest that wolves not only affect moose population dynamics directly through kills but also indirectly by altering the diet of reproductive cows, those individuals that most directly contribute to population growth.

INTRODUCTION

The wolf (*Canis lupus*) and moose (*Alces alces andersoni*) populations on Isle Royale, Michigan have been carefully monitored since 1959 and historical records as well as intermittent studies are available for 1904-1958 (Mech 1966, Peterson 1977). The population trends suggest a classic example of a predator stabilizing the population dynamics of their major prey species. Prior to the wolves' arrival on Isle Royale, the moose showed oscillating population size; after the wolves' arrival, moose population size wa relatively stable.

Although the wolf and moose population dynamics on Isle Royale are among the most well documented for a large mammal predator-prey system (Frenzel 1974), the moose-plant interaction on Isle Royale is less well unde stood. The purpose of this paper is to repo behavioral evidence that the moose-plant int action is, in part, mediated by wolves. Thi study suggests that wolves not only affect the moose population directly through kills but also indirectly by altering the diet of cows with calves, those individuals that are most important in contributing to population growth. First I use behavioral evidence to establish the location and types of high qua ity foods. Then I examine whether the prese of wolves deters moose from feeding on the h quality plants and in the best feeding areas

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STUDY SYSTEM

General Information

This study was carried out on Isle Royale National Park in Lake Superior, Keweenaw Co., Michigan (48° 10' N, 88° 30' W) from May through September 1974-1976. The land area of the park covers 210 square miles and consists of a main island (72km long and 14km wide at its widest point) and approximately 200 smaller islands. The closest shore to Isle Royale is the Canadian north shore which is 21km to the northwest. The study site is located at the northeastern tip of Isle Royale and includes the northeastern tip of the main island and 44 peripheral islands. The topography is characterized by parallel ridges and valleys (elevation on the main island sites in the study area vary from 183m at Lake Superior level to 329km at Mt. Franklin; the small islands are all fairly low-lying with none exceeding 24m above lake level). The primary forest type at the northeastern end of Isle Royale is boreal White spruce (*Picea glauca*)-- balsam fir (*Abies balsamea*)-- paper birch (*Betula papyrifera*) forest (Cooper 1913, Brown 1937, Linn 1957).

Isle Royale is a particularly good natural laboratory for several reasons. First it is an isolated and bounded system. Since There is little interaction between animal populations on Isle Royale and those in Canada (Mech 1966, Peterson 1977), emmigration and immigration do not have to be monitored. Second, it is a wilderness national park and therefore no hunting is allowed. This is particularly important for behavioral studies of moose since it is easier to get good observations of moose in non-hunted populations (Geist 1971, Goddard 1970). Finally, Isle Royale has a relatively simple food web. Islands traditionally have fewer species than mainland sites (MacArthur and Wilson 1967). For example, bears, white-tailed deer and coyotes which are all found on the Canadian north shore are absent from Isle Royale. Therefore there is one dominant food chain, wolves which[3] eat moose which, in turn, eat plants.

Population dynamics of moose and wolves

The population trends of both moose and wolves, based on data from Mech (1966) and Peterson (1977), are summarized below and in Figure 1.

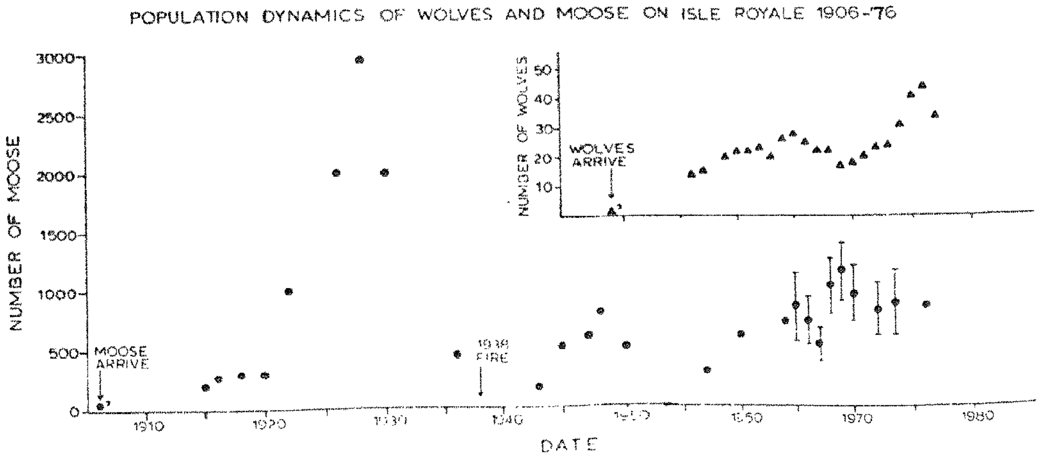

Figure 1.--Population trends of moose (●) and wolves (▲) on Isle Royale from 1906-1976. Data are from Mech (1966) and Peterson(1977). The early moose estimates, those without bars, are based on ground counts or strip aerial surveys. The error for these estimates is potentially high (e.g., the estimate of moose population size in 1930 was 1,000 -3,000; for such cases, the mean of the two extremes is represented on the figure). The later estimates, those with bars, are based on stratified aerial surveying. The bars represent 95% confidence intervals.

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[3] There is some variation in this food chain. For example, wolves also include beaver, hare, birds and plants in their diet. See Peterson (1977) for a detailed analysis of wolf diets on Isle Royale.

Moose.-- Moose probably arrived on Isle Royale by swimming from the Canadian north shore. Although the exact date of their arrival is uncertain, early observations by Adams and Hickie (Mech 1966) indicate moose arrived on Isle Royale about 1905. The moose population initially showed an exponential or "J-shaped" growth pattern increasing from about 200 moose in 1915 to an estimated 2,000 moose by 1925 (Mech 1966). The moose then presumably began to deplete their food supply and the population crashed to less than 200 by 1943. Regrowth of the vegetation due to both low moose population levels and to a fire that burned approximately 1/3rd of the island in 1938, allowed the moose population to grow until the arrival of wolves. Then there was a drop in the moose population in the 1950's, a gradual rise during the 1960's, and a slight decline during the 1970's (Mech 1966, Peterson 1977).

Wolves.-- Wolves probably arrived on Isle Royale during the late 1940's by walking across the ice from Canada, although there are some reports that wolves were present earlier (Mech 1966). In general, with the exception of a slight decline during the 1960's, the wolf population has been increasing. The Isle Royale population is famous for being the densest known wolf population (Jordan et al. 1967).

Effects of wolves on moose population dynamic.-- Although it is difficult to determine the effect of wolves on the moose population based on comparative data alone, the population trends suggest that the wolf population has stabilized the moose population by preventing wide oscillations in moose population size. The assumption is that the wolves are keeping the moose population at a level where the direct effects of food supply are not the primary limiting factor. However, evidence of nutritional stress and malnutrition are still evident in the moose population. Peterson (1977) reports depleted fat in the bone marrow, decreased twinning rates, and decreased calving rates, all of which indicate poor nutrition. In addition not all moose deaths can be accounted for by predation. Wolves at most only account for about 2/3rds of the mortality in the moose population (Peterson 1977); the remainder may be related to malnutrition.

Effects of wolves on moose-plant interactions.-- The evidence of malnutrition suggests that the moose-plant interaction contributes to mortality in the moose population. In this paper, I report behavioral evidence that wolves mediate the moose-plant interaction by limiting cows with calves to wolf-free areas that are poor feeding sites.

MATERIALS AND METHODS

To determine the food preferences, distribution and diets of moose, I used two methods, direct observations and vegetation sampling.

Observations

To find moose, I followed regular routes, either on foot or in non-motorized boats. When moose were sighted, they were observed for as long as possible. For each observation the date, location and class of moose (adult bulls, cows without calves, cows with calves, and yearlings) were recorded. Then I recorded their diet in terms of the number of bites of each plant species (June-August). During May, I was only able to record the number of bites of three categories of food (winter foods, herbs and shrubs) since the leaves of deciduous herbs and woody plants were too small to be easily identified. Plants were identifed while the moose were feeding or immediately after the animal had left the feeding site. Binoculars (8x24) were used as visual aids. Shannon-Weiner indices of diversity (H') and eveness (J') (see Pielou, 1974, for discussions of H' and J') were calculated for each detailed feeding observation (from the beginning of the observation to the beginning of rumination).

Vegetation sampling

Temporal availability of food items.-- To determine the temporal availability of food items, plant leafing patterns were determined from a 790m long permanent transect perpendicular to the main ridge of the main island extending from the south shore at the base of Tobins Harbor (elevation 183m) to the top of the Greenstone ridge (elevation 262m). Permanent sampling sites were marked at 20m intervals. At each site, the number and type of plant species within a meter distance of the sampling point were noted. At time intervals of 4 (1974) or 10 (1975 and 1976) days, each site was checked, and for each plant species present, initial bud break was noted and the length of the longest leaf was measured.

Food preferences.-- To determine food preferences among herb species, I sampled Minong Island (3.6ha) for eaten and uneaten herbs. There were 19 parallel transects at 1-50m intervals perpendicular to the ridge of the island. Along each transect 1-m^2 quadrats were censused at 1-10m intervals (Fig.2). A total of 262 quadrats were censused by recording all herbaceous shoots and scoring them as eaten or uneaten. Preference rankings were based on both the proportion of shoots eaten (number of eaten shoots sampled of species A/total shoots sampled of species A) and on pairwise comparisons. For each pairwise comparison only quadrats which 1) had a minimum of one eaten shoot (indicating that a moose had been to the site) and 2) were comprised of at least 80% of the two species being compared were used in the analysis.

The food preferences among species of de-

Figure 2.--Sampling sites on Minong Island. Each line of dots represents a transect; each dot a sampling site where a 1-m^2 quadrat was censused for eaten and uneaten herbs.

ciduous trees and shrubs are based on studies by Belovsky and Jordan (1978) and Edwards (1978).

RESULTS

Food preferences of moose

Moose show clear preferences in food choice. Their seasonal shifts in diet delineate three broad categories (Fig.3). During the winter when no other foods are available, they feed exclusively on winter foods (woody twigs, evergreen needles and lichens). However, as soon as new leafy vegetation is available, moose switch to eating herbs, the first plants to leaf in the spring. Finally when leaves from deciduous trees and shrubs are available, moose switch to eating them and continue to eat them almost exclusively for the remainder of the growing season. Thus three categories of foods can be listed in order of preference from the most preferred to least preferred: leaves from deciduous trees and shrubs, leaves from herbs and winter foods.

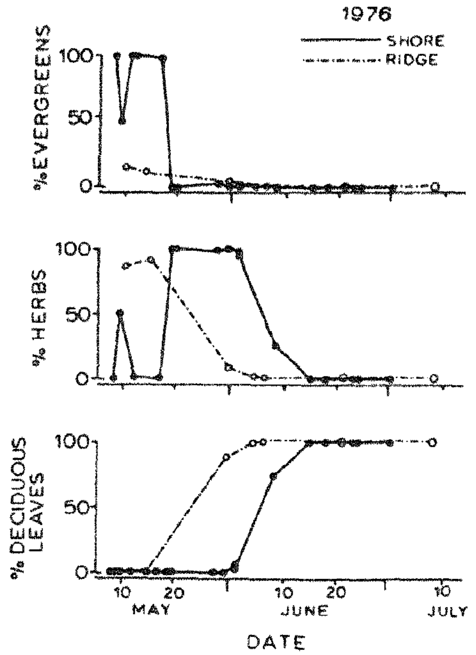

Figure 3.--Comparisons of diets of moose at shoreline and ridgetop sites, 1976. Each symbol represents one feeding observation.

The herbs can be further subdivided into high preference and low preference herbs. First, the herbs can be ordered by the proportion of the total population eaten (Fig.4). Second, in most cases, these preferences can be confirmed by pairwise comparisons. Table 1 summarizes the results of the pairwise tests, an example of which is shown in Figure 5. There were 8 pairwise tests where the two species being compared co-occured and therefore a valid comparison could be made. In all 7 cases where the moose showed a clear preference between two species, the pairwise comparisons correspond with the ordering based on the proportion of the total population eaten. For the last case, the comparison between Clintonia borealis and Geocaulon lividum, the pairwise test indicates no preference (i.e., for those quadrats analyzed, the plants are eaten in proportion to their relative abundance). However, the proportion method indicates G. lividum (10% eaten) should be preferred to C. borealis (4% eaten). However both are low preference food items and the low proportion of C. borealis eaten is probably be-

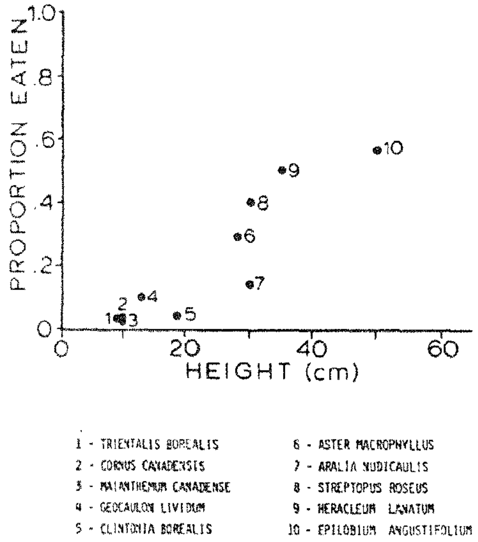

Figure 4.--Relationship between height and the proportion eaten for 10 herb species on Minong Island.

cause *C. borealis* is more common and is concentrated on the northwestern side of the island, an area not frequented by moose (Edwards 1978).

Table 1.--Summary of preferences between pairs of herb species. A + indicates that moose prefer the plant in the column to the one in the row. A - indicates that insufficient data were available to determine preferences between the two species. A = indicates that no clear preference was shown.

	A. macrophyllus	*A. nudicaulis*	*C. borealis*	*G. lividum*	*M. canadense*	*T. borealis*	*C. canadensis*
Aster macrophyllus							
Aralia nudicaulis	-						
Clintonia borealis	-	+					
Geocaulon lividum	+	-	=				
Maianthemum canadense	-	+	+	-			
Trientalis borealis	-	-	-	-	-		
Cornus canadensis	+	+	-	+	-	-	

Based on both ranking methods, *Aster macrophyllus*, *Aralia nudicaulis*, *Streptopus roseus*, *Heracleum lanatum* and *Epilobium angustifolium* were considered high preference herbs (herbs 1) and *Trientalis borealis*, *Cornus canadensis*, *Maianthemum canadense*, *Geocaulon lividum* and *Clintonia borealis* were considered low preference herbs (herbs 2). Similarly, based on previous studies, the shrubs were divided into high preference (shrubs 1) and low preference (shrubs 2).

The choice of food items by moose reflects differences in the nutrient quality of the food. Young leaves of herbs and deciduous trees and shrubs have the highest nutrient values and are easier to digest than woody tissues or old leaves (see Edwards 1983 for a detailed list of references). The winter diets of moose are essentially maintenance diets (LeResche and Davis 1973); most malnutrition occuring in late winter (Peterson 1977). In addition, moose appear to maximize bite size. They prefer tall herbs to short herbs (Fig.4) and prefer shrubs to herbs. Moose can eat shrubs more efficiently since they can strip the leaves from entire branches; for herbs, only a few shoots can be eaten in one bite.

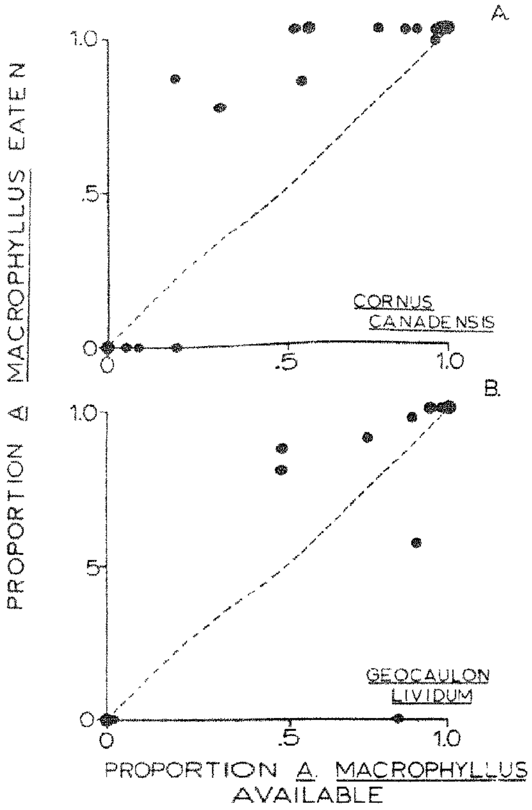

Figure 5.--Examples of pairwise comparisons showing preference relationships between *Aster macrophyllus* and *Cornus canadensis* (A) and between *A. macrophyllus* and *Geocaulon lividum* (B). See Table 1 for a summary of the results from the pairwise comparisons. Proportion of *A. macrophyllus* available = number of *A. macrophyllus* shoots in the quadrat/number of shoots of both species being compared. Proportion of *A. macrophyllus* eaten = number of eaten *A. macrophyllus* shoots/number of eaten shoots of both species.

Availability of plant foods

Foods are available at different times of the year depending on the location. Data from the permanent transect indicate that plants leaf first on the ridges of the main island and last along the shoreline and on the small islands (Fig.6).

Predicted feeding pattern

The food preferences of moose and the availability of plant foods can be used to predict the feeding patterns of moose. Since moose have strong food preferences and young deciduous foliage has the highest nutrient value (Edwards 1983), moose should feed on the ridges in the early spring and then as plants leaf at lower elevations, they should move to the shoreline and island sites.

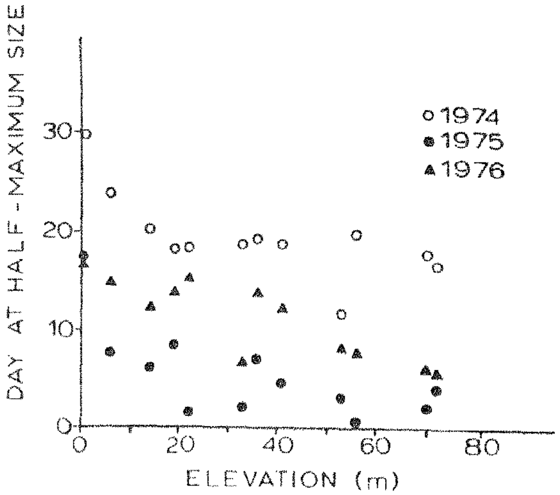

Figure 6.--Relationship between elevation and the day a leaf reaches half the maximum size for Viburnum edule. For all years there are significant correlations between elevation and the day a leaf reaches half the maximum size (1974, $R = 0.71$, $P<0.01$; 1975, $R = 0.67$, $P<0.02$; 1976, $R = 0.85$, $P<0.001$).

Observed distributions and diets

Distributions.-- Solitary cows and adult bulls followed the predicted feeding pattern. They were on the ridges of the main island in May and June and moved to shoreline and island sites in July-September (Fig.7A and B). Yearlings also followed the predicted feeding pattern but tended to stay on the ridges of the main island which are near the shore rather than at higher elevations. The distributions of cows with calves deviated sharply from the predicted pattern. In May, prior to the leafing of most herbs and shrubs, they swam to the small islands to calve (Edwards 1983) and remained on the small islands throughout the growing season (Fig.7C and D).

Diets.-- In May, bulls, solitary cows and yearlings switched to eating non-winter foods earlier than cows with calves (Fig.3). The earliest observations of bulls, solitary cows or yearlings eating non-winter foods was 10 May compared to 18 May for cows with calves. During May, there were significantly more observations of cows with calves eating only winter foods (10 out of 15 observations of cows with calves

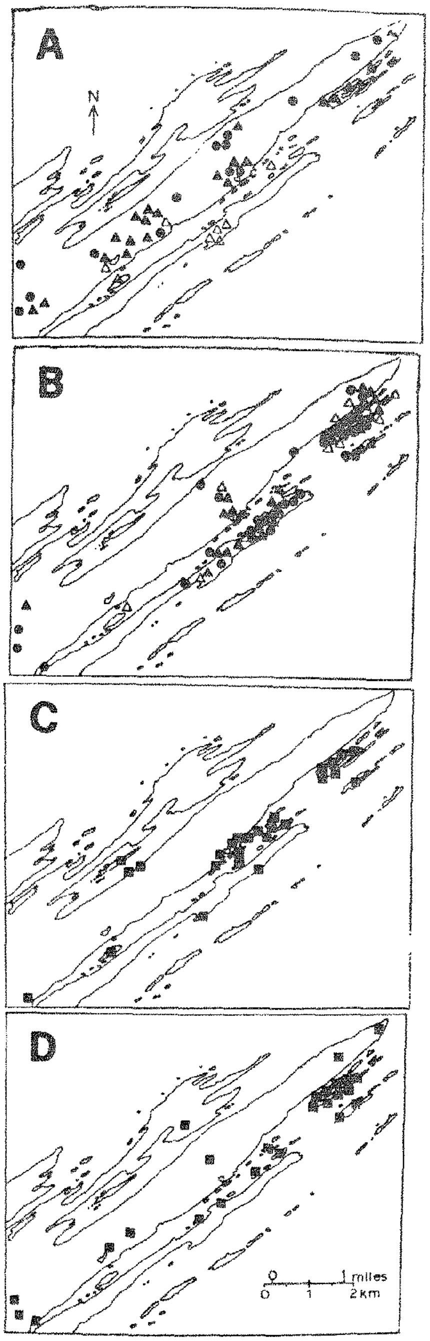

Figure 7.--Distribution of adult bulls (●), solitary adult cows (▲), yearlings (Δ), and cows with calves (■) at the northeastern end of Isle Royale National Park, Michigan from May-June (A and C) or July-August (B and D). Each symbol represents one observation (from Edwards 1983).

compared to 1 out of 12 observations of other moose, 2 x 2 contingency table $X^2 = 9.3$, $P < 0.005$). Cows with calves also continued to eat winter foods as late as 18 June; the latest date for other moose was 30 May.

The diets of moose from June-August are summarized in Table 2. Bulls, solitary cows, and yearlings predominantly ate high preference shrubs (86%) with lesser amounts of low preference shrubs (10%) and preferred herbs (4%). There were no observations of these moose eating low preference herbs or winter foods during this period. In contrast, cows with calves ate a significantly lower quality diet. They ate significantly more herbs than other moose. In addition, they continued to eat some winter foods during this period.

Table 2.--Analyses of feeding observations for cows with calves and other moose (solitary adults and yearlings) during June-August. See text for explanation of food categories. Data are means ± standard errors. P-values are based on Mann-Whitney tests. n.s. indicates no significance at $P < 0.05$. (from Edwards 1983).

	Cows with calves	Other Moose	P-value
Number of Plant species	6.0±0.46	4.3±0.28	<0.01
H' (diversity)	0.55±0.04	0.34±0.03	<0.01
J' (evenness)	0.71±0.04	0.55±0.03	<0.01
Proportion of shrub 1	0.55±0.07	0.86±0.04	<0.01
Proportion of shrub 2	0.17±0.06	0.10±0.03	n.s.
Proportion of herb 1	0.15±0.04	0.04±0.03	<0.01
Proportion of herb 2	0.13±0.04	0.00±0.00	<0.01
Proportion of winter foods	0.01±0.00	0.00±0.00	n.s.

DISCUSSION

Moose clearly show strong food preferences that correlate with the nutritional value of the food item. Although solitary cows, adult bulls and yearlings track the locations of the high preference food items, cows with calves, which are probably under the greatest nutritional stress due to pregnancy and lactation, deviate from the expected feeding pattern by remaining on the small islands throughout the growing season. As a consequence, cows with calves have a poorer diet than other moose.

Cows with calves appear to sacrifice a good diet to protect their offspring from predation by wolves. The distribution of cows with calves correlates with the predation patterns and the distribution of wolves on Isle Royale. Wolves prey most heavily on calves (Cowan 1947; Burkholder 1959; Mech 1966, Peterson 1977); healthy older moose are relatively invulnerable to wolves (Mech 1966). However, since wolves are almost exclusively limited to the main island during the growing season, the small islands are virtually wolf-free (Edwards 1983) and cows with calves avoid contact with wolves by remaining on the small islands.

Cows with calves may not only sacrifice the food quality of terrestrial food items, but remaining on islands may also limit their access to aquatic macrophytes, an important source of sodium for moose (Botkin et al. 1973, Belovsky 1978). The main locations for aquatic macrophytes are in the inland lakes and shallow bays of the main island. Yet cows with calves which require additional sodium intake for reproduction and lactation (Belovsky 1978), remain on the small islands where the shorelines are wave-washed and unsuitable for the establishment of aquatic vascular plants.

Although the effect of the lower quality diet of cows with calves has not been quantified, field observations suggest that the diet of cows with calves does create nutritional stress. Cows with calves develop new coats later than solitary cows or adult bulls and, in general, cows with calves appear thinner, especially in May and June. A poor diet, in turn, may increase mortality or lower reproductive success (Edwards 1983).

The results from this study indicate that for the wolf-moose-plant system on Isle Royale, wolves not only affect moose population numbers directly through kills but also indirectly by mediating the moose-plant interaction. In this case, the pattern of wolf predation is causing a shift in the distribution of cows with calves to wolf-free areas. This predator avoidance by reproductive cows is, in turn, causing a shift in their diets. Thus the increase in malnutrition observed in the moose population during the last 20 years may be due to the wolf-moose interaction rather than to a simple interaction between the moose and the vegetation. These data also suggest that the mechanics of control in the moose population involve complex interactions among all three trophic levels of the wolf-moose-plant system.

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WATER TRANSPORT IN SOIL AND ROOTS: INFLUENCE OF ROOT PROPERTIES ON WATER UPTAKE[1]

Susan J. Riha and Mary Ann Levan[2]

Abstract.-- An analog is used to predict the effects of changing root density and root resistance on the ability of stands of trees to maintain potential transpiration rates as the soil dries. Increasing root density and decreasing root resistance can increase water uptake, especially when the soil is moist. However, in these simulations, after an extended period of no rainfall, there was little difference in transpiration rate between high and low root density or root resistance stands.

Water moves in response to a potential gradient from the soil into plant roots, through the vascular system of the plant and then, in the vapor phase, through stomates into the air. An analog model, first proposed by Van den Honert (1948), in which soil and plant resistances are considered in series, has generally been used to describe this movement of water. Using this approach,

$$E = \frac{\psi_s - \psi_1}{R_s + R_r + R_x + R_1} \qquad (1)$$

where E is the rate of water flow from the soil to the plant leaf (kg m^{-2} s^{-1}); ψ_s and ψ_1 are the water potentials of the bulk soil and the leaf, respectively, (J kg^{-1}); and R is the resistance to water flow (m^4 kg^{-1} s^{-2}) in the soil-plant continuum. This overall resistance is the series combination of soil (R_s), root (R_r), xylem (R_x), and leaf mesophyll (R_1) resistances to water flow.

When the rate of water flow into the plant equals the rate of water moving in the vapor phase through stomates into the atmosphere (transpiration rate), then the system is in steady state and actual transpiration is said to equal potential transpiration.

When the rate of water flow from the soil through the plant is less than the rate of water vapor moving out of the plant, then plant water content and hence potential must at least temporarily decrease. Decreases in plant water potential cause both direct and indirect decreases in plant growth.

Since the rate of water flow from soil through plants is considered to be controlled by a series combination of resistances, there has long been an interest in understanding these resistances, measuring them, and establishing their relative importance (Newman 1974). Soil resistance is considered the resistance to water flow from the bulk soil to the cortex of a cylindrical root. The equation used to calculate this resistance is derived from one by Gardner (1960);

$$\frac{q}{2\Pi r l} = -k \frac{d\psi}{dx} \qquad (2)$$

where q is the rate of water uptake (kg s^{-1}), r is the radius of the root (m), l is the length of the root (m), k is the hydraulic conductivity of the soil (kg s m^{-3}), ψ is the water potential of the bulk soil or root surface (J kg^{-1}), and x is half the mean inter-root distance (m), which depends on root density. Thus soil resistance is a function of both plant (root density and radius) and soil (the hydraulic conductivity) properties.

Root resistance is considered the resistance to water flow between the root cortex and xylem with the bulk of this resistance apparently located in the endodermis. In practice, root resistance (or its inverse, root conductance), is generally either calculated or measured as a property of the entire root system. Conductance is then considered directly proportional to root length, and partitioned through the profile according to the pattern of root density with depth.

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Water moves within the xylem after crossing the endodermis in the root and before entering the mesophyll in the leaf. This xylem resistance is usually considered small compared to the other resistances. The mesophyll resistance is the resistance to passage from the xylem into the mesophyll cells. Although this resistance is probably not as large as the root resistance, it may be of the same order of magnitude.

It has sometimes been assumed that some measure of drought adaptation can be achieved by increasing root density and/or decreasing root resistance, thereby increasing water uptake from the soil. Root system parameters considered important to the pattern of soil water withdrawal from the profile are total root length and its distribution within the profile. Theoretically, both soil and root resistance depend on root density. Soil resistance is directly proportional to the mean inter-root distance, increasing as root density decreases. The partitioning of root resistance within the profile directly depends on the distribution of root density with depth.

The total root length to be partitioned through the profile is generally expressed as L_A, root length per unit of ground surface area. The range in reported values of L_A for woody species, grasses, and other herbs is surprisingly small (Table 1), with considerable overlap between plant groups. (Reported values for woody species do not include mycorrhizae.)

Table 1.--Root length per unit of ground surface (L_A) for selected plant groups

Plant group	Number of species examined	L_A (cm/cm^2)	Reference
Woody species	*	23 - 480	See Table 3
Gramineae	15	100 - 4000	Newman 1969
Other herbaceous species	7	52 - 310	*Ibid.*

*Four individual species plus three mixed stands.

Although the L_A of woody species may vary by more than an order of magnitude, there are probably upper and lower limits not much outside this range which bracket all natural forests in which canopy closure has occurred. The data of Hopkins (Fig. 1) are typical of woody root systems, demonstrating the non-uniform density distribution with depth generally observed. Root density decreases rapidly, often exponentially, with depth, with most root length concentrated in the surface organic horizons.

Root system density is apparently controlled by both water and nutrient availability in the profile. Certain nutrients such as phosphorus move to roots by the relatively slow process of diffusion; uptake of such nutrients is greatly enhanced by increases in soil-root contact area. Uptake of nutrients such as calcium, which move to roots mainly by the relatively fast process of mass flow, is less affected by root-soil contact.

Table 2. Root length per unit of ground surface (L_A) for selected woody species

Stand Description	Age	Location	L_A	Reference
Spruce flat balsam fir, red spruce, red maple, yellow and white birch	mature	Adirondack Mts. USA	23	Hopkins, 1939
Good hardwood sugar maple, beech, yellow birch	mature	Adirondack Mts. USA	28	*Ibid.*
Poor hardwood red spruce, beech, sugar maple, yellow birch, red maple, hemlock	mature	Adirondack Mts. USA	43	*Ibid.*
Pear var. William Bon Chretian	20-40 y	Goulburn Valley Australia	26-69	Cockroft and Wallbrink, 1969
Douglas fir	36 y	Oxford England	77	Reynolds, 1970
Douglas fir	20 y	Vancouver Is. Canada	107	Nnyamah and Black, 1977
Scots pine	45 y	Thetford Chase England	126	Roberts, 1976
Jarrah (*Eucalyptus marginata*)	mature	Darling Range Australia	480	Carbon *et al.*, 1980

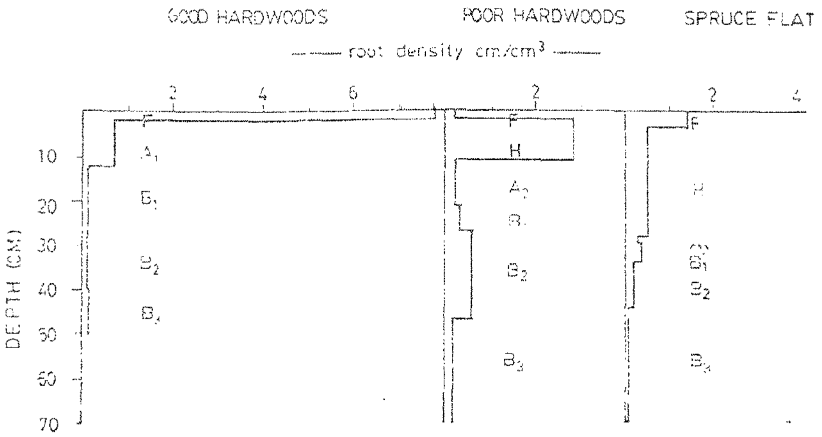

Figure 1. Pattern of root density with depth in three mature stands in the Adirondacks. Stand composition was as follows: good hardwoods - sugar maple, beech, yellow birch; poor hardwoods - red spruce, beech, sugar maple, yellow birch, red maple, hemlock; spruce flat - balsam fir, red spruce, red maple, yellow and white birch. After Hopkins 1939.

Possibly, high surface root density is a response to the almost exclusive occurrence of such nutrients as phosphorus in the organic layers, with much lower subsoil densities adequate for uptake of mass-flow nutrients and water. This scheme implies that only relatively low root densities are sufficient for water uptake.

Field observation such as that just described suggests that dense root systems are not, however, generally produced in the soil volume supplying the bulk of the water to a stand. In addition, the interdependence of the quantity (water content) and resistance terms of the equations describing water flow, together with the nonlinear form of their relationship make it impossible to imagine the effect on water flow of a change in one of the parameters. For this reason, an analog model of the soil-plant-atmosphere continuum must be used to predict the effect on water uptake of changes in such parameters as root density and root resistance. In this approach, a set of equations describing water flow is solved iteratively in short time steps, constantly modifying the interdependent factors in the equations, and arriving at solutions impossible to obtain mentally. This approach can also indicate which properties of the system (such as soil water content) are most responsive to changes in root parameters, and therefore are most easily measured.

The following is a brief description of the model. Initially, some potential daily transpiration is set (Table 3), and this is divided into hourly rates. The soil is divided into a number of layers (i), with different root densities assigned to each layer. Root systems with an L_A of 28 or 280, with density decreasing exponentially with depth were chosen for use in the model. The transpiration rate has to equal the sum of the water uptake rates for each of the soil layers:

Table 3. Values used in model

Description	Value	Dimension
Soil (silt loam)		
Initial water content	0.25	$m^3\ m^{-3}$
Bulk density	1.3	$Mg\ m^3$
Saturated hydraulic conductivity	0.0003	$kg\ s\ m^{-3}$
Air entry water potential	-2.1	$J\ kg^{-1}$
Empirical value from soil moisture release curve	4.2	-
Plant		
Total root length	280 or 28	$cm\ cm^{-2}$
Depth for 63% of roots	0.20	m
Root radius	0.001	m
Total root resistance	3×10^6 or 7.5×10^6	$m^4\ s^{-1}\ kg^{-1}$
Total leaf resistance	2×10^6	$m^4\ s^{-1}\ kg^{-1}$
Leaf water potential at which stomatal closure occurs	-1200	m
Atmosphere		
Potential transpiration rate	4	$mm\ day^{-1}$

$$E = \sum_i E_i = \sum_i \left(\frac{\Psi_{xi}-\Psi_{si}}{R_{si}+R_{ri}}\right) \qquad (3)$$

The xylem water potential is then calculated by rearranging equation 3 (Childs et al. 1977). If the xylem resistance is assumed to be negligible, the leaf water potential can be calculated using the equation:

$$\psi_1 = \psi_x - ER_1 \qquad (4)$$

The leaf water potential is calculated by combining equation 3 and 4 to obtain:

$$\psi_1 = \sum_i \frac{\psi_{si}/(R_{si} + R_{ri})}{\sum_i 1/R_{si} + R_{ri})} -$$

$$E\ [R_1 + \frac{1}{\sum_i 1/(R_{si} + R_{ri})}] \qquad (5)$$

The first term on the right of the equation can be considered a weighted mean soil water potential, $\bar{\psi}_s$ (G. S. Campbell, personal communication). As the leaf water potential becomes more negative, stomatal resistance increases, thereby decreasing the actual transpiration rate below the initially assigned transpiration rate.

E_i, the amount of water uptake by roots in each layer of soil, is a sink term in the Richard's equation, which is used to calculate soil water flow between soil layers. The equation used to describe the relationship between soil water potential and soil hydraulic conductivity are given by Campbell (1974). The values used in these equations are specific to a soil and, in this model, they are assumed to be constant with depth (Table 3).

Model results are presented by plotting the ratio of actual to potential transpiration (E/EP) against the weighted mean soil water potential (ψ_s) over time. Results of studies with Pinus contonta presented in this way (cf. Lopushinsky 1975) have shown that when the soil water potential becomes increasingly negative, transpiration decreases rapidly, reaching some constant low value. Model results follow this expected pattern (cf. Fig. 2 and 3). In this study, the model was used to compare stands of trees with comparatively low and high root densities, as well as root systems with low and high root resistances.

The model results presented in Figure 2 illustrate the effect of increasing rooting density an order of magnitude uniformly through the profile. For approximately the first 10 days, both higher and lower root density stands transpire at the maximum rate. In the next 10 days, actual transpiration falls below potential transpiration more quickly in the stand with lower root density. By 20 days, the stand with the higher density root system is transpiring slightly more than the stand with the lower root density. In addition, the soil of the higher root density stand has a lower mean soil water potential. At 40 days, actual transpiration is slightly higher for the stand with the lower root density, while the soil of the high root density stand still has a more negative soil water potential. Thus, increasing root density tenfold resulted in only slightly increased water uptake. The total amount of stored water this represents is 5 mm, or slightly more than the potential transpiration rate for a single day.

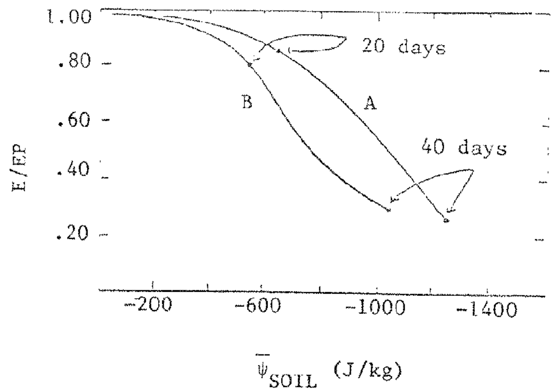

Figure 2. Effect of root density on the relationship between actual transpiration/potential transpiration and the weighted mean soil water potential over time. A - higher root density stand (280 cm cm^{-2}); B - lower root density stand (28 cm cm^{-2}).

The model results presented in Figure 3 illustrate the effect on water uptake of increasing root resistance by 250%. Increasing root resistance decreases the transpiration rate the stand achieves even under well-watered conditions. On the twentieth day after rain, the stand with the lower root resistance is transpiring closer to a maximum although the mean soil water potential for both stands is similar. By day 40, the transpiration rates of both stands are similar and less than 30% of maximum, while $\bar{\psi}_s$ of the stand with the higher root resistance is slightly less negative than that with the lower root resistance. These effects are predicted by the model mainly because, for a given transpiration rate, the stand with the higher root resistance attains more negative leaf water potentials than that with lower root resistance. If the relationship between leaf water potential and stomatal resistance remains the same for both stands, then in the stand with the higher root resistance, E/EP will decrease sooner due to increasing stomatal resistance. This remains the case until the weighted mean soil water potential approaches the critical leaf water potential.

Table 4 presents the model predictions of soil water potential and soil water content for 2 days and 3 depths at high and low root densities. Enhanced water uptake from the soil effected by changes in root density and distribution would be difficult to detect. According to model predictions, there would be no measurable differences at day 10 between the high and low root density

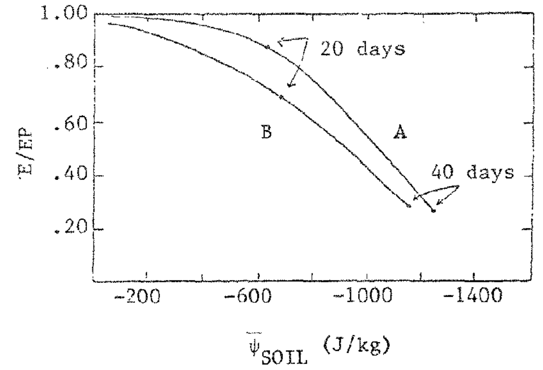

Figure 3. Effect of root resistance on the relationship between actual transpiration/potential transpiration and the weighted mean soil water potential over time. A - root system with lower resistance (3×10^6 m^4 s kg^{-1}); B - root system with higher resistance (7.5×10^6 m^4 s kg^{-1}).

soils and only slight differences in the surface 50 cm at day 30. The model predicts that there would be differences between the higher and lower root density stands in the predawn and midday leaf water potentials by day 30 (Table 5).

Table 4.--Comparison of predicted soil water potentials and soil water contents under low and high root density stands

		Low root density		High root density	
Day	Depth	ψ_{soil}	Soil water content	ψ_{soil}	Soil water content
	cm	J/kg	cm^3/cm^3	J/kg	cm^3/cm^3
10	0 - 27	-300	.16	-300	.16
	27 - 53	-150	.19	-150	.19
	53 - 80	-60	.23	-60	.23
30	0 - 27	-1080	.12	-1100	.11
	27 - 53	-940	.12	-1090	.12
	53 - 80	-430	.14	-680	.13

Table 5.--Comparison of predicted predawn and midday leaf water potentials of low and high root density stands

	Predawn ψ_{leaf}		Midday ψ_{leaf}	
Day	Low root density	High root density	Low root density	High root density
10	-210	-210	-730	-720
30	-850	-1000	-1590	-1310

Model simulations have shown that increasing root density and decreasing root resistance do lead to increases in stand water uptake. It is difficult to evaluate, however, whether changes in the quantity and pattern of water uptake lead to increased stand survival and productivity.

Increasing root density and decreasing root resistance result in maintenance of higher transpiration rates for a longer period. However, this increased depletion of soil water in turn causes soil water potential to be more negative. These stands then must establish lower leaf water potentials to maintain a gradient for flow.

In addition, production and maintenance of roots, decreases in leaf water potential, and increases in stomatal resistance all involve energy expenditures which must be balanced against the energy gains resultant from improved water status of the stand.

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IMPACT OF FUSIFORM RUST ON LOBLOLLY PINE PLANTATIONS[1]

Kathleen E. Moore[2]

Abstract.--An individual tree growth model (PTAEDA) developed at Virginia Polytechnic Institute was modified to reflect the effects of fusiform rust infection. The data base for rust effects was a heritability study in a high hazard area for rust. Mortality, growth loss, and product quality loss for individual trees are all strongly affected by the year after planting in which infection takes place.

INTRODUCTION

Fusiform rust is a serious disease of loblolly and slash pines under plantation management. The causal organism, *Cronartium quercuum* F. sp. *fusiforme*, produces galls on the branches and main stem of the pine host. Mortality, growth loss, and product degrade are the major categories of loss.

Construction of impact models for plant diseases has been left chiefly to plant disease epidemiologists. The importance of these models to the manager of a crop should be obvious: an objective means of evaluating management alternatives under different disease conditions is essential. The uses of impact models extend also to the evaluation of control measures and genetic selections. The aim should be to reduce impact, not just the amount of disease.

A dialogue between growth and yield modelers and forest pathologists is necessary in part because the quantification of gain from various management alternatives can sometimes be a different process than the quantification of loss. The difference is a function of the individual's purpose in constructing the model. Models designed to demonstrate gain do not give accurate results when they are used to model loss.

Prediction of disease loss requires the integration of models of disease development, stand development, and impact -- all of which share a complex set of relationships with time. Time is something the forest manager must understand well; the perception of time on the part of the forest manager distinguishes him/her from the managers of other crops. Study of the impact of fusiform rust illustrates these concepts; both the problems and benefits associated with impact modeling are demonstrated.

The objective of the research reported here was to develop a model of impact of fusiform rust on yields from loblolly pine plantations that could be used by forest managers to evaluate management alternatives, based on an early assessment of the disease. The approach taken was to modify a preexisting growth and yield model for loblolly pine, using data on rust and growth from a heritability study.

ANALYSIS OF THE DATA BASE

The data used were the first 10 years' measurements of 9600 trees in the loblolly pine heritability study. Some detailed data on individual galls were also taken at age 17. Details of the study are available in Stonecypher *et al* (1973). The study is located in a high rust-hazard area in South Georgia. There are six replications in the planting design, three at each of two locations. The two locations differed in the amount of rust that was present: one location experienced approximately 20% incidence of stem infection, while in the other as many as 65% of the trees in one rep had stem infections by age 5.

Mortality was the first category of impact explored. The relationship (regression) of rust-associated mortality (RAM) at age 10 with percent stem-infected at earlier ages revealed that there is a difference in the

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slope of the regression lines using the age 3 percent-infected as the predictor versus using the age 5 percent-infected. A higher proportion of trees infected at age 3 die by age 10 than those infected at age 5. This result confirms published results of Wells and Dinus (1978).

This led to the hypothesis that the probability of an individual tree dying of rust was strongly affected by the year in which it became infected. A non-linear relationship, in which probability of mortality declines steeply with age-at-infection, describes this trend (Fig. 1).

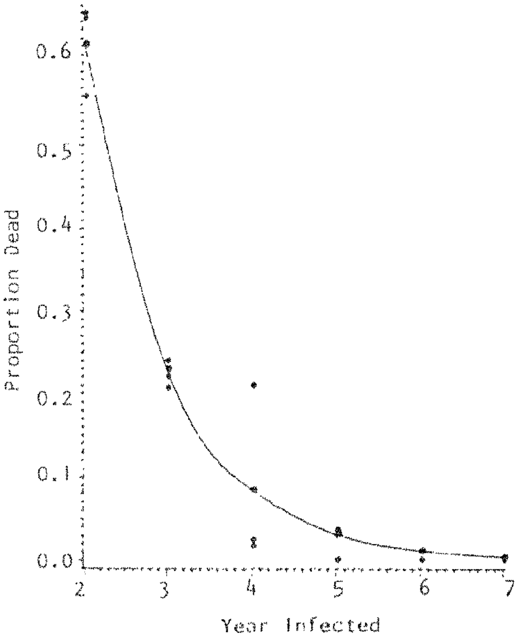

Figure 1.--Exponential decline model for relationship of proportion dead (rust-associated mortality) with year infected.

The second category of impact is individual-tree growth reduction. Here too, age-at-infection is a significant factor. Trees infected by age 3 are smaller at age 10 than those infected at age 5, but not age 3. Infected trees may have 15-20% less volume at age 10, if they were infected early.

The effects of rust, while dramatic for many trees, are apparently minimal for others, in terms of effects on mortality and growth. The result is that at age 10 in the heritability study, many infected trees occupied good competitive positions in the canopy, indicating that this population of loblolly pine has a substantial degree of tolerance to the disease. This also implies that many infected trees have a good chance of surviving to rotation when higher-value products, such as plywood (which are more severely affected by rust galls) are the expected return.

Height of the gall on the stem is also related to the year in which infection takes place, because the rust fungus infects the new shoots of the tree each year.

MODIFICATIONS TO THE MODEL

An individual tree growth model, "PTAEDA," which was developed by Richard Daniels and Harold Burkhart at V.P.I. (1975) was modified to reflect the effect of fusiform rust, based on an analysis of the heritability study data. This model, as it was originally constructed, "grows" a stand of trees to the end of the juvenile phase by using a series of regression equations describing how height and mortality are related to the input variables, i.e., site quality, planting density, site preparation, etc. Following the juvenile period, each tree is grown individually, year by year, based on an assessment of its competitive position. At any specified time in the life of the stand, stand summaries as well as a detailed "snapshot" of each tree can be produced by the model.

The model was modified in the following ways:

1. Fusiform rust is input as a disease progress curve -- the incremental amount of rust (percent stem-infected) in each year following planting, through age 8. Each tree is randomly assigned an infection-year on the basis of this input.
2. Mortality is assigned to each tree randomly based on the probability of mortality associated with the year in which the tree became infected.
3. A separate diameter distribution for trees infected by age 3 but which survive to age 10, is calculated.
4. Gall height and length at age 10 are determined for each surviving infected tree, again using year-infected as the predictor.
5. The option of selectively thinning rust-infected trees to achieve a specified basal area was added.
6. The degree of spatial aggregation of infected trees can be specified. This

was accomplished with a method similar to that described by Daniels *et al* (1979) in a seeded-stand simulator.

7. A measure of solid-wood products loss was obtained when a bucking and sawing program was interfaced to PTAEDA; logs are bucked above any rust gall on them.

RESULTS AND DISCUSSION

The individual tree model format of PTAEDA has made it a useful tool for exploring the impact of fusiform rust. This format has allowed the incorporation of mortality, growth loss, and product degrade information into the model, as well as ready modification for selective thinning and manipulation of the spatial pattern. The results beyond the juvenile stage, however, are not verified and therefore should be regarded as simulation.

The model, because it is dependent on a competition index calculated on inter-tree distances, is sensitive to reductions in stand density. Individual trees respond to the decrease in competition by growing faster. This aspect of PTAEDA would appear to exaggerate tree growth at the lowest stand densities.

Nonetheless, the following general results were obtained with simulations of a wide range of rust progress curves:

1. Over longer rotations (up to 35 years), losses in standing volume may be ameliorated through increased growth of individual trees. This is essentially a thinning effect, and requires verification.

2. Most volume losses are from thinnings, because of the above-mentioned amelioration in standing volume over time.

3. Because many infected trees are projected to rotation, most financial loss could be from product degrade, depending on the objectives of management. With the bucking and sawing scheme in this model, there is a loss of both lumber volume and grade.

4. In the first 15 years, volumes losses are 5-20% of the volume from uninfected stands, depending on the shape of the disease progress curve. Some results of rust-modified PTAEDA output are given in Table 1.

Comparisons of the projections to age 15 with published estimates from stand models (Nance *et al* 1981, 1982) indicate that these losses are comparable, given that slash pine appears to be more sensitive than loblolly to the disease.

Table 1.--Average height, diameter, and cubic-foot volumes resulting from simulations of thinned plantations under different rust progress curves. Simulated planting density, 680 stems/acre with a site index of 60.

	Rust Infection[a], %		
	0.0	34	54
Age 8:			
Height, ft	17.5	16.8	16.9
Diameter, in.	4.3	3.9	3.9
Volume, ft^3	753	488	415
Age 16:			
Height, ft	38.5	40.3	41.4
Diameter, in.	6.4	6.6	7.2
Volume, ft^3	1,790	1,576	1,532
Thinned Vol.[b], ft^3	841	728	632
Age 25:			
Height, ft	59.8	61.2	60.4
Diameter, in.	11.7	12.1	12.2
Total Vol.[c], ft^3	4,953	4,725	4,576

[a] Total percent stem infection through age 5, weighted by probability of mortality for each infection-year.

[b] Row thinning.

[c] Standing volume + thinned volume.

RELATIONSHIP BETWEEN LOSS AND DISEASE

There are several ways of expressing the relationship between an early assessment of disease and the final yield of crop. It is important to find the type of expression that reflects the particular dynamic of disease and host that is of interest.

In this case, it is clear that any prediction of yield loss in the future has to take account of the age-dependency of impact. The spatial pattern dependency may also have to be taken into account. Since mortality appears to be the largest factor in impact on total volume production, a measure of disease that is based on percent stem-infected at ages 1 through 5 weighted by the probability of mortality associated with each year, was constructed. A linear relationship resulted.

The relative magnitude of the various impacts that rust may have on yield depends upon the management of the stand and the products expected from that management regime. For instance, in shorter rotation pulpwood-only stands, rust impact on final standing

DATA AND METHODS

Tree cores were extracted from 15 to 19 red spruce trees from each of three sites located along the mountains of Maine (Table 1): Elephant Mt. in western Maine, Sugarloaf Mt. near Kingfield, and Traveler Mt. in Baxter State Park. All three sites are above 900 m elevation and are representative of the highest elevation stands of red spruce in this region. The cores were prepared and analyzed densitometrically at the Swiss Federal Institute of Forestry Research, Birmensdorf, Switzerland. They were first carefully sawn to 1.2 mm thickness, acclimated to constant hygroscopic conditions, and then they were x-rayed. A narrow beam of light was then passed through the developed x-ray film, ring by ring, and the brightness was recorded. The measured densities were calibrated to represent actual wood density. Total ring width and maximum latewood density for each yearly ring were recorded mechanically, as well as minimum earlywood density, earlywood width, and latewood width, which were used in other studies (Conkey 1982). Each parameter was carefully crossdated among all core series to assure exact dating (Stokes and Smiley 1968). Standard dendrochronological practice involves standardization of the core series to remove biological growth trends and age effects (Fritts 1976); this was done in preparation for the climatological analyses, which can be negatively influenced by growth trends. The original core series of ring widths and maximum densities were also individually averaged without standardization, for use in assessing non-climatic influences on growth.

Several tests of association were calculated among the width and density averaged series, including the Pearson product-moment correlation coefficient, correlation of first-differenced series, and the two-way chi square (χ^2) test of contingency tables (Nie et al. 1970; Gordon 1980; Conkey 1982). The first correlation coefficient indicates the degree of coherence integrated over all frequencies, measuring both the number of cases which agree between two series as well as the relative degree of correspondence. The coefficient is quite sensitive to long-term trends in one or both series. The effect of such trends may be eliminated by taking the first differences

Table 1.--Collection site descriptions and locations.

Site name, Chronology length and depth	Geographical location, map reference	Geological characteristics	Site description
Elephant Mt. 1667-1976 17 trees sampled, 12 cores used in final chronologies	44° 46' N 70° 46' W Franklin Co., Oquossoc quadrangle. Elevation 3000' - 3100' (915-945 m) ENE slope, 5°-10°	Granitic base, little soil development, largely humus. Within drainage of Swift - Androscoggin Rivers.	Relatively flat, hummocky area; spruce are tall, with medium to thick species density, foliage restricted to high branches. Other species include: *Betula* sp., *Oxalis montana*, *Abies balsamea*, ferns and mosses. Relatively open stand below canopy. *Picea rubens* clearly dominant.
Sugarloaf Mt. 1776-1976 19 trees sampled, 34 cores used in final chronologies	45° 02' 30" N 70° 19' W Franklin Co., Stratton quadrangle. Elevation 3600' (1097 m) NE slope, 35°	Igneous base, gabbro/diorite, with sandy solifluction deposits. Thick humus material, soil depth uncertain. Within drainage of Carrabassett - Kennebec Rivers.	Steep, exposed slope, partially cleared for ski trails, rest is densely wooded with much fallen dead wood. Proportion of spruce is low, most young growth is fir. Other species include: *Abies balsamea*, *Betula papyrifera*, *Oxalis montana*, mosses. *Abies* is dominant with the older *Picea*.
Traveler Mt. 1728-1976 15 trees sampled, 26 cores used in final chronologies	46° 04' 30" N 68° 51' W Piscataquis Co. Traveler Mt. quadrangle. Elevation 3050' - 3200' (930-975 m) NNW slope, 10°-20°	Traveler rhyolite base, hummocky humus cover, close to bedrock. Within drainage of the East Branch of the Penobscot River.	Moderate slope, close to summit of burned-over peak. Spruce density moderate, greatly interspersed with similar-size fir. Few very old specimens. Lots of downed trees, and open areas with dead standing snags. Other species include: *Abies balsamea*, *Betula* sp., thick ground cover of raspberry, ferns, clintonia, bunchberry, sorrel.

of both series ($X_i - X_{i-1}$), and recalculating the correlation. This first-differenced correlation coefficient thus emphasizes the high-frequency degree of correspondence between two series. Finally, the χ^2 contingency analysis is conducted in order to indicate the existence and strength of any non-linear relationship between two series, a relationship which might produce low values of correlation. Whereas the significance of the χ^2 statistic indicates the presence of the relationship, its nature (linear or curvilinear) is revealed only by examination of the contingency table itself. The application of such tests of association help define the similarities and differences from one tree-ring site to another as well as the degree of correspondence between wood quantity (width) and wood quality (density) at each site.

RESULTS AND DISCUSSION

Statistical tests of association

An important criterion for dendrochronological analysis of tree samples is that the visible ring patterns of growth be similar enough from one tree to another and one site to another to allow exact calendar years to be assigned to each ring; such correlation is due to regional environmental similarities, usually climate. Examination of test results among the ring-width variables from the three red spruce sites in Maine (Table 2, top) indicates that significant site-to-site correlation does indeed exist for this growth variable. High-frequency correlation ("r-1" on the table) is also significant, and is higher than the correlation at all frequencies ("r"), indicating the existence of long-term trends in each series that are site-specific, compared to the year-to-year variations of width. Standardization of the series would, theoretically, remove unreplicated trends in the data that are due to uneven ages represented here in the averaged series. Results of the χ^2 analysis support the existence of statistical coherence among widths from one site to another, and linearity is inferred for all except the Traveler/Elephant comparison, where the higher χ^2 value relative to the r value may imply a somewhat curvilinear pattern to the relationship.

Maximum density test results (Table 2, bottom) show increases in every test and every site comparison over the ring-width results. There is still an indication of dissimilar long-term trends from one site to another, seen in the increase of r-1 values over the r values, but strong coherence at all frequencies is suggested by the high values for all three tests. Clearly, the regional similarity of maximum density values is strong, and implies a strong macroclimatic control on latewood density.

Ring widths and maximum densities relate less well to each other at each site (Table 3) than they do among themselves from site

Table 2.--Tests of association[a] of the averaged series of maximum density and ring width among three sites in Maine.

Width	r	r-1	χ^2
SUG/TRV (201)	.346	.518	41.79
SUG/ELE (201)	.456	.602	86.28
TRV/ELE (249)	.230	.502	51.45
Density	**r**	**r-1**	**χ^2**
SUG/TRV (201)	.547	.748	115.88
SUG/ELE (201)	.573	.726	101.32
TRV/ELE (249)	.648	.776	137.26

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[a] Sample size in parentheses. SUG = Sugarloaf
TRV = Traveler ELE = Elephant
r = correlation
r-1 = correlation of first differences
χ^2 = 2-way chi square contingency table test
All test are significant at $p \leq 0.05$.

Table 3.--Tests of association[b] between maximum density and ring width averaged time series at each of three sites in Maine.

	r	r-1	χ^2
Sugarloaf (201)	.186	.240	22.49 NS
Traveler (249)	.195	.235	27.07
Elephant (310)	.307	.218	40.24

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[b] Tests and symbols as in Table 2.
NS indicates lack of significance, $p \leq 0.05$.
All other results are significant.

to site, indicating that the two growth parameters, while apparently influenced by macroclimate to varying degrees, do show differing responses to environmental stimuli. Large rings often exhibit lower overall specific gravity; thus wood quantity and wood quality are, generally, inversely related. The positive correlation between ring width and maximum latewood density seen here (Table 3) implies that the environmental stimuli affecting quantity and quality of wood may not be dissimilar, but that the actual physiological response may differ, perhaps in timing or duration.

Width and density averaged series

Macroclimatic influences on growth are evidenced both by the results of the tests of association, and by regression analyses in which the widths and densities were used to predict growing season temperature, producing explained variance values of up to 0.47 (Conkey 1982). There remains much in the width and density variation, however, that does not appear to be climate-related, but instead implies the influence of other more site-specific or non-climatic environmental phenomena.

Figure 1 is a composite plot of unstandardized values of ring widths, averaged year by year at each site. Total average ring width for each year is visually broken down into earlywood and latewood portions, indicating both the relatively small proportion of red spruce wood that is considered "latewood" (between each set of plotted lines), and the resulting very strong

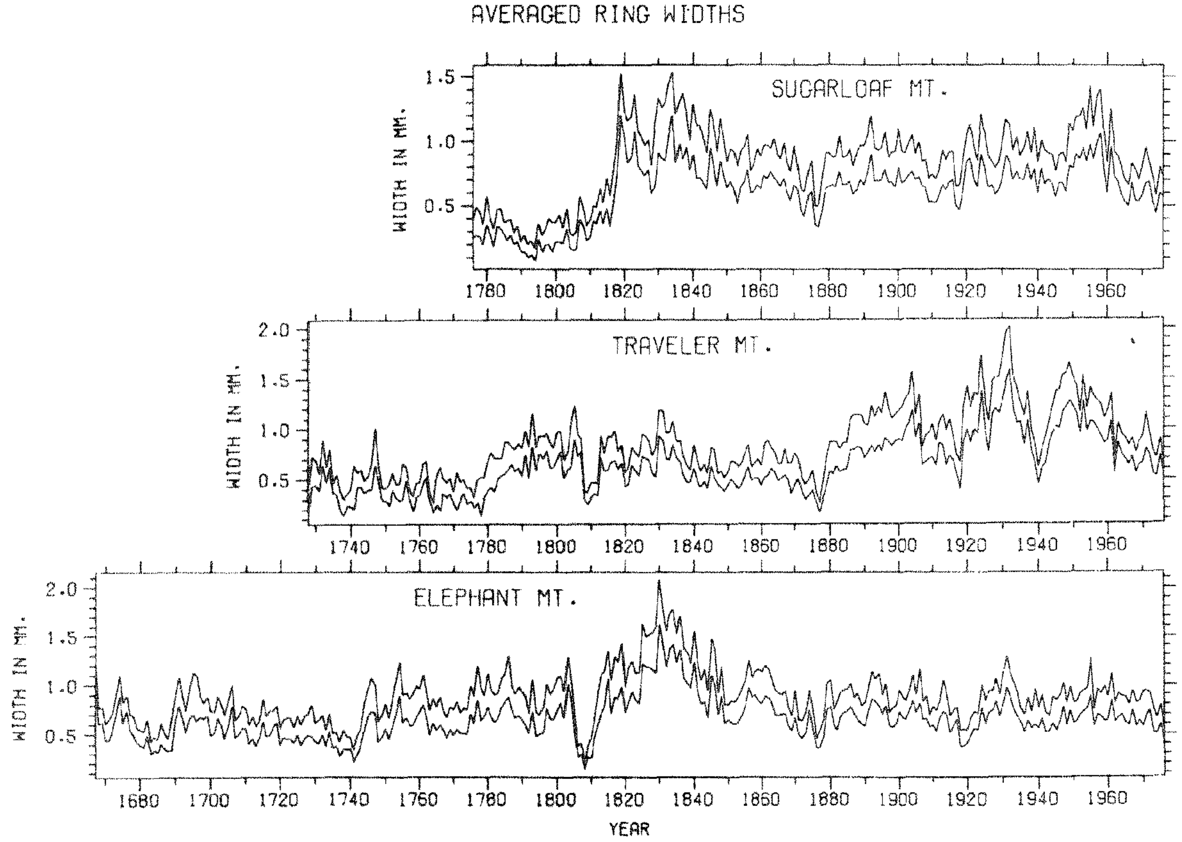

Figure 1.--Averaged ring widths (in millimeters) from three red spruce sample collection sites: Sugarloaf Mt. (top), Traveler Mt. (middle), and Elephant Mt. (bottom), Maine. Within each site plot are averaged total ring widths (upper line in each case) and averaged earlywood widths (lower lines); the distance between the two plotted lines is equal to the latewood width for each year.

similarity between earlywood and total ring widths. Patterns of growth suppression (narrow rings) and release (wide rings) are evident, both individually and in synchrony among the three sites, indicating regional and site-specific changes in forest productivity through time.

Those patterns in synchrony, both at high and low frequencies, include narrow rings in 1740, wide rings by 1830 with a gradual decrease until the late 1870s. All three sites show an abrupt growth decrease in 1917-18, and marked period of lower growth in the last two decades of record. Many of these patterns may be climatically controlled; the most recent growth decrease does appear, for instance, to follow a marked decline in spring temperatures at nearby climatic stations (Conkey 1982). A gradual warming during the last decades of the 19th century (Willett 1950) may also be reflected in the increase in ring widths after the late 1870s.

Maximum density variations can be seen in figure 2. The series in general show much less long-term trend than the ring-width series, as well as a greater variation on a year-to-year basis, in an oscillating fashion. Like the ring widths, however, many patterns of the densities can be traced from one site to another, indicating again the strong influence of regional climate on wood density. These are mostly of a high-frequency nature, with individual years standing out: 1740, again, with low density, and a jump from high to low in 1815-1816, high in 1831, 1841, 1846, 1870, and low in 1888, 1917, and 1954-56. Many of these relate to known events of a climatic nature, such as the cold spring and summer of 1816, and the cool-warm-cool pattern in 1954-56.

Some of the synchronous patterns, and, presumably, all of the non-synchronous ones, may be influenced by environmental events other than macroclimate. These may be best understood by examining both the width and

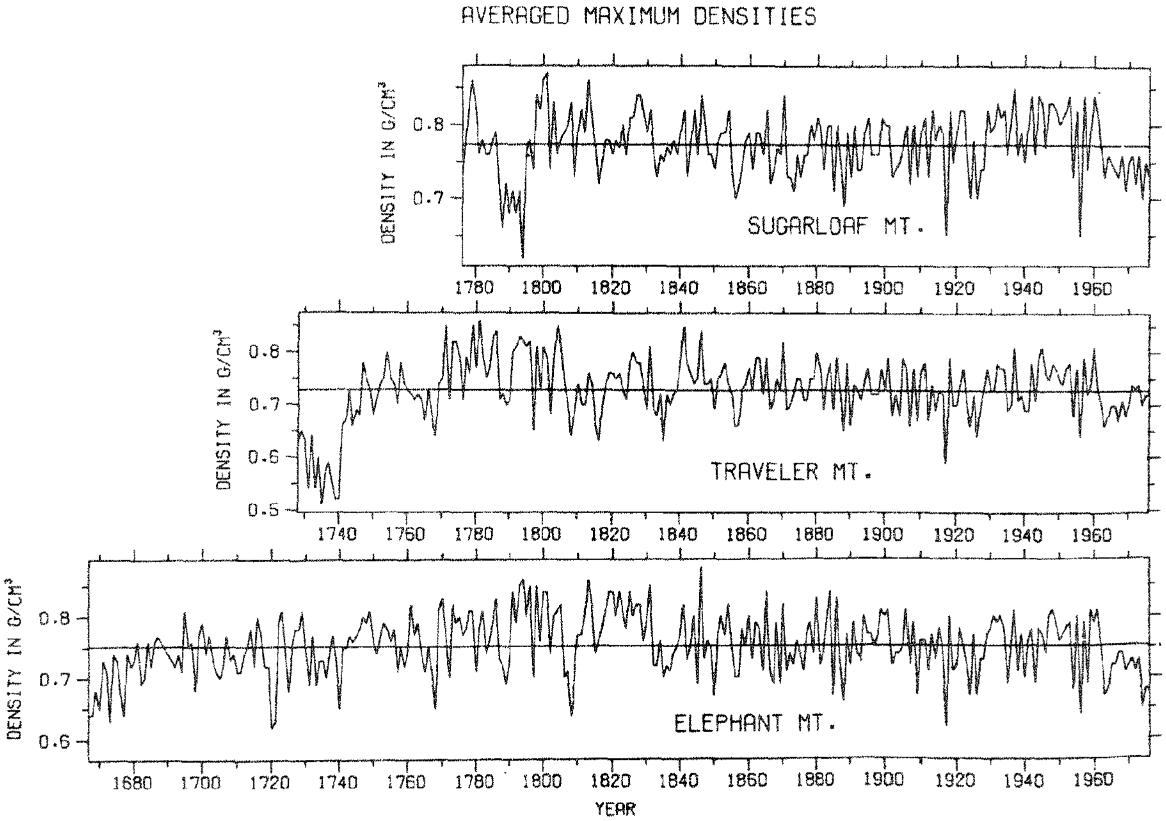

Figure 2.--Averaged maximum density values (in grams per cubic centimeter) from three red spruce sample collection sites: Sugarloaf Mt. (top), Traveler Mt. (middle), and Elephant Mt. (bottom), Maine. A horizontal line in each case represents the mean of each complete series.

density variations together. For instance, Traveler and Elephant show a marked ring-width decrease in 1808, with a one-year decrease in density as well. Ring widths at both sites, however, remain suppressed for several years. Such a pattern may indicate an insect infestation as seen from affected but surviving trees, with a ring-width suppression of several years duration, but a very quick return to mean density levels once the infestation peaks (Schweingruber 1979). The Sugarloaf site may not have been affected; or, conversely, it may have been cleared out of older individuals in that infestation, reducing the competition for light and nutrients for the young trees that grew underneath, and contributing to the surge in growth there after 1810. Many new trees enter the averaged series at this point at all three sites; this too may indicate canopy opening. Much of Maine was hit by a spruce budworm attack from 1912 to 1920, affecting spruce as well as fir; again there is a one-year low maximum density (1917), and a several-year ring-width decrease and slower return to mean values. At Traveler Mt. there is a marked increase in ring widths after this time, perhaps indicating an opening canopy. The only historically documented fire that I am aware of occurred near Traveler Mt. in 1903 (Anderson 1979); it is not clear from the width or density record that the sampled stand was directly affected by it.

The abrupt growth decrease at Traveler in 1940, however, is more elusive. It is not reflected in deteriorating climatic conditions (Conkey 1982), nor is the pattern repeated at either of the other two sites. Since damage from hurricane, fire, or wind throw would presumably result in growth increases for the surviving trees, without a sharp growth decrease, none of those influences are suspected as causes; the pattern looks similar to other known events of insect damage or disease.

Still other events appear to be coincident with climate in producing growth changes. According to climatic records, 1917 underwent a cool spring, perhaps stimulating the low maximum density for that year as well as contributing to the susceptibility of the mostly mature individuals to an insect attack. The recent decline in width and density at all three sites correlates well with decreases in spring temperatures (Conkey 1982), but the decrease may be enhanced by a changing chemical environment in the forests that has been suggested to affect tree growth elsewhere (Siccama 1982).

Finally, suspected non-climatic events may mask the expected response of growth to known climatic events. The "year without a summer", 1816 (Baron 1980), is apparently such a case: all three width series show a great increase in growth during that time, perhaps due to an increase in light and nutrient availability from the death of older diseased individuals prior to 1810. Density values had already returned to more nearly normal levels by 1816, and thus show the decrease in density that one would expect from the well-known cool growing season (Conkey 1982), but the widths may have been more strongly affected by the growth surge than by the cooler than normal temperatures.

CONCLUSION

Statistical and visual examination of dendrochronological series of ring widths and peak densities reveals spatial similarities over distances of up to 200 km, indicating a regional environmental control on growth that is probably climate, or climate-related. It is also clear that a one-to-one correspondence between climate and the growth patterns does not exist, even for the highly spatially coherent maximum densities. Instead, the patterns of changing ring widths and densities through the past 300 years and across the mountains of Maine show that the effects of growth are many and varying; there is a mosaic on each stand produced by age differences, canopy clearing due to wind throw, fire, and insect attacks, and regional climatic influences on the physiology of individual trees. This provides the great wealth of information on changing forest productivity which is thus represented by the spatial and temporal patterns of accurately dated ring-width and wood density series.

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MULTIPURPOSE SLASH PINE - GENETICS AND PHYSIOLOGY OF GUM NAVAL STORES PRODUCTION

by

SUSAN V. KOSSUTH

Abstract.--Genetic studies show that oleoresin or gum yield obtained by the bark chipping method is under strong genetic control in slash pine (Pinus elliottii Engelm). Selection and breeding for increased gum yields have made significant gains in both gum production and rapid growth because the two traits are positively correlated. Thus, a multipurpose strain of slash pine, good for high gum yields, pulpwood, poles sawtimber etc. is currently in an advanced generation breeding program.

Anatomical studies of resin canals in slash pine dating to 1922 showed that the vertical and radial resin canal systems are interconnected and that gum exuded from chipped faces originates from both systems. Early work also demonstrated that the number of traumatic resin canals begins to increase about 4 weeks after chipping commences.

The fourth generation of chemicals for increasing gum yield have just begun being tested. The first were non-growth regulating chemicals, including sulfuric acid which is widely used to stimulate gum flow. The second generation was herbicides, including 2-4-dichlorophenoxyacetic acid, which was as effective as sulfuric acid. However, it was not adopted commercially because at effective levels it was toxic to longleaf pine which is also chipped commercially and grows in mixed stands with slash pine.

Ethylene releasing compounds were the third generation of chemicals. Two-chloroethylphosphonic acid (CEPA) increased gum yields from slash pine by 37 percent when added to sulfuric acid, and the effect was additive. The best CEPA treatment without sulfuric acid gave gum yields 22 percent below the sulfuric acid commercial control. Hence, sulfuric acid is considered the critical component in increasing gum yields. The mode of action of the sulfuric acid is probably to prevent crystallization of resin acids and prevent tylosoid formation while the action of CEPA is probably to release ethylene, which induces gum synthesis and new resin canal differentiation.

The fourth generation of chemicals for increasing gum yields stimulates the plant to produce ethylene. Some of these include calcium plus cytokinins and auxin plus cytokinins. They are still being tested.

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INTRODUCTION

The techniques for collection of oleoresin or gum from living pine trees were brought to this country in 1606 when the naval stores industry was established in the Southeastern United States (Curry, 1943). Today, slash pine (<u>Pinus elliottii</u> Engelm.) and longleaf pine (<u>Pinus palustris</u> Mill.) are the only two species used for the production of gum naval stores, which are so-named because the gum was initially used for caulking ships. Oleoresin is composed of about 20 to 25 percent terpenes and 75 to 80 percent resin acids or rosin. Today gum is used for a variety of specialty products including paint thinners, varnishes, shoe and metal polishes, perfumes, flavorings, cleaners, disinfectants, tackifiers, plasticizers, adhesives, and recently as ethylene stock for plastics.

Clements (1974) described modern techniques for collecting gum from living trees. For 1/3 of the tree's circumference at breast height (1.37m above ground), rough outer bark is removed to prepare a smooth surface from near the ground to about breast height. This process is called rossing. A collection cup is then mounted close to the ground, and just above it, a gutter or apron that spans the rossed surface and is tightly nailed to the tree for channeling gum into the cup. In early spring, a 1 to 2 cm strip of bark, chipped down to the cambium, is removed across the smoothed surface just above the gutter. This is the first streak. Either a 50 percent liquid sulfuric acid solution is sprayed on the new wound or a 50 percent sulfuric acid paste is applied as a bead across the top of the wound adjacent to the intact bark. Every 2 weeks, if the liquid is used and every 4 weeks if the paste is used, a new streak is made by chipping off another 1 to 2 cm of bark down to cambium above the last wound and the new fresh cut surface is retreated. Chippers attempt to remove just enough bark to expose some xylem tissue that has not been killed by the upward penetration of the sulfuric acid.

In 1941, research was initiated to identify individual trees that yielded significantly more gum than the average (Mitchell, 1942; Dorman, 1945) so that these high-gum yielding selections could be used in a breeding program, propagated, and the progeny used in commercial plantations. Simultaneously, the anatomy and physiology of gum yield were being studied. After the first 12 trees were selected in 1941, rapid growth, good form, disease resistance, high specific gravity, etc. were added as selection criteria (Squillace and Dorman, 1961). Progeny of the resulting trees could then be used for several purposes, including gum yield, pulpwood, poles, sawlogs, etc., and the concept of a multipurpose strain became a reality after several years of work (Gansel, 1972). Slash pine is planted more often than longleaf pine and the program has emphasized this species.

The objectives of this paper are to summarize the past and current research on the genetics and physiology of gum yield in slash pine.

VARIATION & HERITABILITY OF GUM YIELD

Slash pines vary widely in gum yield and growth rate within and among stands throughout the natural range. No reports to date have shown that trees in a given part of the range of slash pine may be genetically superior for gum yield (Barrett and Bengston, 1964). However, early work has demonstrated that gum yield is a highly heritable character, and this finding has been verified (Squillace, 1962). Up to 3-fold differences in gum yield were documented as early as 1932 (Wyman, 1932), and within a stand of 363 20-year-old trees the best 5 and 10 percent of the trees had twice and 1.8 times as much gum as average trees (Squillace, 1965).

Using the micro-chipping technique of Ostrum and True (1946), Squillace (1962) analyzed wind and control pollinated progenies. Approximately 50 percent of the high-gum-yielding parent trees had high-gum-yielding progeny. Progeny of all the high-gum-yielding parents averaged 55 percent more gum than progeny from average yielding trees. Heritability for gum yield was 55 percent, indicating that 55 percent of the variation in gum yield among trees was due to genetic and not environmental effects. Other estimates of narrow-sense heritability for gum yield ranged from 45-90 percent, and broad sense estimates ranged from 67-90 percent (Mergen <u>et</u>. <u>al</u>. 1955; Squillace & Dorman, 1961; Goddard and Peters, 1965).

Today, less than 1 percent of the available slash pine are worked for naval stores. However, several clonal seed orchards of high-gum-yielding selections have been established because high gum yield is positively correlated with height growth (Squillace, 1965). This correlation means that high-gum-yielding trees tend to grow rapidly but not all fast growing trees are necessarily high gum yielders. Based on this information, the USDA Forest Service has continued an advanced generation breeding program for multipurpose slash pine to improve high-gum-yielding slash pine selections which have shown other desirable characteristics. Progeny of the current strain will produce 50-100 percent more gum, grow 12 percent faster, and give 12 percent more tall oil at the pulpmill than average slash pines. High-gum-yielding trees in a short-term progeny test were 24 percent taller than commercial check trees (Gansel, 1972). No correlation has been found between straightness or branch angle and gum yield (Gansel, 1965).

Physical factors that influence gum flow include the number and size of radial/vertical resin canals, flow rate, viscosity and exudation pressure of gum (Schopmeyer et al. 1954; Mergen et al. 1955; Bourdeau and Schopmeyer, 1957). Barrett and Bengston (1964) found that viscosity of gum could account for 12 percent of the variation in gum yield, but they did not find a positive correlation between gum exudation pressure and yield as did Bourdeau and Schopmeyer, (1957). The latter demonstrated that yield was inversely correlated with viscosity. Mergen et al. (1955) found that gum viscosity of progeny was about intermediate between those of their parents and therefore was under genetic control. Similarly, gum exudation pressure of progeny was correlated with that of the parents and also was considered a heritable character; however, gum exudation pressure and gum viscosity do not show the same inheritance pattern (Bourdeau and Schopmeyer, 1957). Thus, four characteristics of slash pines appear to be improvable in a genetics program: (1) obtain progeny that have high gum yields and rapid height growth, (2) low gum viscosity, (3) numbers of vertical and horizontal resin canals, initially or in response to wounding or chemical treatment, and (4) high gum exudation pressure. The last characteristic may help protect the tree from fungal spore invasion and insect pests.

PREDICTING GUM YIELD

Squillace and Dorman (1961) microchipped wind, and control-pollinated progeny from parents of high and average gum-yielding capacities. Wind-pollinated progeny from high-gum-yielding parents had less gum than control-pollinated progeny from high-gum-yielding trees from the same parents. However, a highly significant correlation coefficient of 0.89 was found between control and wind-pollinated progenies of the same parents. This means one can predict the yield of progeny from a controlled cross if progeny from the wind-pollinated parents have been evaluated.

Naval Stores producers may chip a given tree for 10 to 12 years. If it is a low-yielding tree, the time and labor expended may be uneconomical for the yield obtained. A correlation coefficient of 0.76 was found between yield of the first 4 streaks of trees and total yield over a 4 year period. Thus, early-season yields can be used to predict long-term production (Squillace et al. 1969).

Microchipping is also a valid means for evaluating individual trees, such as in a progeny test (Kraus, 1965). This technique estimates the oleoresin content of a tree using a sample as small as a few ml taken from the xylem of a tree. Gum yield from two microchips taken from each of 75 slash pines in May, July and September were closely correlated ($r=0.758$) with yields obtained by standard chipping procedures in the same season on the opposite side of the same trees. However, the coefficient of determination was not high enough to select individual trees by the microchipping procedure. Coefficients were developed for predicting gum yield from full-face chipping of trees in various diameter classes. The microchipping procedure has been adapted for use on 2.5 to 3-year-old progeny in closely spaced plantings (Squillace and Franklin, 1968). Progeny testing requires a great deal of time in an advanced generation breeding program and procedures for early detection of genetic traits are needed. Because gum yield is positively correlated with height growth (Squillace, 1965) and microchipping yields are related to full-face yields (Kraus, 1965), the microchipping technique has been adopted for progeny testing (Squillace and Franklin, 1968). No tests have been conducted to show that high microchip yields on a given tree at age 3 also result in high yields 15 to 20 years later when the same tree is full-face chipped for several years. We are in the process of obtaining this documentation.

The potential exists for reducing the progeny testing time to 2 months by evaluating the extractives and/or terpene content in progeny test seedlings (Kossuth, unpublished). The basis for this concept is twofold. First, Franklin et al. (1970) found a positive corelation ($r =.5$) between gum yield and extractives content in slash pine. Second, Funes et al. (1973), using 2-month-old *Pinus pinaster* seedlings from average and high-gum-yielding parents, found that progeny of the high-gum-yielders had 4 times the terpene content of progeny from average-gum-yielders. The system would need to be tested from seedling to microchipping to full-face chipping to verify its applicability and degree of usefulness.

THE RESIN DUCT SYSTEM

Normal resin canals are found in the genera *Pinus*, *Larix*, *Pseudotsuga* and *Picea* (Panshin and DeZeeuw, 1964). Traumatic resin canals arise as a result of stress or injury. Normal and traumatic resin canal differentiation is a post-cambial phenomenon. They arise schizogenously in vertical (longitudinal) and horizontal (radial) rays. The middle lamella disappears, gum is secreted into this region, and the "canal" is created. The vertical and horizontal systems anastomose (Gerry, 1922). The surrounding thin-walled parenchyma cells divide along their long long axis and differentiate, forming the secretory epithelial cells. Epithelial cells of normal resin canals in Pinus are thin walled (Kibblewhite and Thompson, 1973) but those of traumatic origin are thick walled. In slash pine, resin canals have three layers: the inner epithelial cells, a surrounding layer of intermediate cells, and the outer cells (Schierbeek, 1952). Resin canals are always found associated with the ray system.

On a dry weight basis, gum content of slash pine averages 4.7 in sapwood and 25 percent in heartwood. Resin soaking, or the filling of tracheids with gum, normally occurs in heartwood formation. Sixty percent of the vertical resin canals in slash pine were found in the latewood of mature trees, but only 5 percent of rays potentially available for vertical resin canal differentiation actually contained a resin canal (Hobert, 1932). As long as heartwood formation has not occurred, these rays would be available for traumatic resin canal formation. Up to age 8-10 years, resin canals are commonly found in the earlywood as well as the latewood.

Vertical resin canals in slash pine are 70-120 microns wide and are usually found in the heartwood; radial resin canals are always less than 70 microns wide (Koch, 1972). Other reports indicate that widths of both horizontal and vertical resin canals are around 55 microns (Hodges et al. 1981). Slash pines contain 219 vertical resin canals per square inch in cross section, 458 horizontal resin canals in tangentical section, and 20,000 uniseriate rays in tangential section (Koch, 1972).

Hobert (1932) found the number of vertical resin canals in slash pine increased with ring width from 200 to 300 canals per square inch when growth rings were 0.22 and 0.44 inches wide, respectively. The number of horizontal resin canals was not related to ring width. Mergen and Echols (1955) studying 30-year-old slash pine wood samples found: (1) the number of radial resin canals per unit area was highest near the pith (about 86/3.03cm^2),decreased to about the twentieth ring, then remained fairly constant (about 52/3.03cm^2). (2) the number of radial resin canals decreased with decreaseing ring width from about 86/3.03 cm^2 for growth rings 0.3 inches wide to about 53-56/3.03 cm^2 for growth rings 0.1 inches wide and remained at about that level in narrow rings. Ring width declined with age as did the number of resin canals. (3) the size of radial resin canals decreased with age from about 0.0029 mm^2 in 10-year-old wood to 0.0023 mm^2 in 30-year-old wood. (4) radial resin canal size also decreased with ring width from about 0.00285 mm^2 at 0.3 inches ring width to 0.0023 in 0.12-inch ring width.

Within 1 to 3 months after the chipping season begins in the early spring, gum yields increase. This increase has usually been attributed to rising temperatures reducing gum viscosity and hence increased rate of gum flow (Harper and Wyman, 1936). However, several anatomical studies have shown that the number of vertical resin canals increases as much as 10-fold, especially in new wood produced above where chipping begins (Gerry, 1922; Busgen and Munch, 1929). The vertical and radial resin canal systems are interconnected (Gerry, 1922). As the bark chipping progresses into the area of new resin canals, these are also contributing to the increased gum flow (Gerry, 1922). Many naval stores workers have successfully used the advanced streak to increase early yields (Herty, 1911). This streak is similar to the common one, but it is put on several weeks before the regular season begins. The early wounding allows time for traumatic resin canal differentiation which takes 4 weeks or less (Gerry, 1922). Although slash pine specifically has not been studied, the length of vertical resin canals in other species has been found to be up to 80 cm and to increase in length with the age of the tree (Werker and Fahn; 1969). This increase may help to account for higher gum yields from older trees. Slash pine has been shown to have more resin canals than longleaf, shortleaf, or loblolly pines (Hodges et al., 1981) and in general, slash pines yield more gum than the other species.

USE OF CHEMICALS TO INCREASE GUM YIELD

Around 1930, a search was begun to find chemicals with which to treat trees to increase gum yields. From 1930 to 1950 a variety of chemicals unrelated to growth regulation were applied to bark-chipped trees in attempts to increase gum yield; among chemicals tested were organic and inorganic acids, bases, salts, solvents, oxidizing and reducing agents, alcohols, poisons, ethers, and oils (Snow, 1944; Schierbeek, 1952). In the 1940's, sulfuric acid, which worked quite well, was introduced for commercial use because it not only increases yields but also prolongs gum flow so workers do not have to chip as often. Gum probably stops flowing because of crystallization of the resin acids and/or tylosoid formation, not because the resin canals are depleted of gum. The mode of action of those chemicals that improved yields was probably to (1) prevent crystallization, (2) prevent tylosoid formation and

(3) enhance the wounding effect.

After 1950, a wide variety of herbicides were tested to improve gum yields. Schopmeyer (1948) conducted the first tests with 2,4-dichlorophenoxyacetic acid (2,4-D) using esters and salts of the parent compound. Although 2,4-D alone was demonstrated to be as effective as sulfuric acid on slash pines, it was not adopted by the industry because effective concentrations of 2 percent 2,4-D on slash pine were toxic to longleaf pine. Most stands are mixed and the effort needed to separate species in the field was too great (Clements, 1964, 1970).

The third generation of chemicals tested to improve gum yield was plant growth regulators. Research begun in 1978 centered on ethylene and ethylene-generating compounds for several reasons. The rubber industry uses a commercial formulation containing 2-chloroethylphosphonic acid (CEPA) to stimulate latex production in rubber trees. At pH levels above 3.5, CEPA degrades to release ethylene (Abeles, 1973). Latex production in rubber trees by laticifers is similar to oleoresin production in slash pine, and both products have the same early precursors in their biosynthetic pathway. Plants respond to wounding such as occurs in the chipping procedure by producing ethylene gas at the wound site (Saltveit and Dilly, 1978). Ethylene is a natural plant hormone that is readily soluble in water and could easily be translocated in slash pine. The addition of ethylene to that already generated by the trees from wounding might increase gum yields through increased synthesis of gum and by increases in the number of resin canals differentiated.

A series of factorial experiments were undertaken to test the effect of several levels of CEPA alone and in combination with several levels of sulfuric acid on gum yield in slash pine (Kossuth and McReynolds, 1982, 1983). Both liquid and paste sulfuric acid formulations were tested because producers use both. Gum yield was increased by 37 percent over the commercial 53 percent sulfuric acid paste by lowering the sulfuric acid level to 25 percent and adding 5 percent CEPA (McReynolds and Kossuth, 1983). In treatments with CEPA alone, yields increased with increasing CEPA levels but all were at least 22 percent less than that from the commercial 53 percent sulfuric acid paste. Spraying to runoff with 21.6 percent CEPA (applied as the full-strength commercial formulation of Ethrel [3] over the rossed bark surface at the beginning of the year or spraying the 21.6 percent CEPA on the bark just above each streak as it was chipped also increased gum yields close to the best sulfuric acid plus CEPA pastes. Gum yields decreased at the higher CEPA levels.

Results with liquid sulfuric acid formulations (McReynolds and Kossuth, 1984) were similar except that higher CEPA and acid concentrations were required to increase gum yields. The greatest increase over the commercial control was 20 percent in the 50 percent sulfuric acid plus 15 percent CEPA treatment. In these treatments, gum yields did not decline at the 25 and 50 percent sulfuric acid plus 15 percent CEPA levels and higher sulfuric acid and/or CEPA levels may increase gum yield even more.

There was no synergistic interaction of the sulfuric acid and CEPA. The sulfuric acid is essential and CEPA seems to only add to the increase in gum yield. The paste formulations were more effective at lower concentrations because the paste bead stays at the application site and soaks in, whereas the liquid runs down the face of the tree. Long-term studies may show that with the liquid treatments resin soaking occurs on the lower part of the face which receives repeated application because of runoff from above.

The mode of action of CEPA is probably to release ethylene which induces (1) added gum production in existing resin canals and (2) differentiation of new resin canals, perhaps above the number induced by the normal chipping procedures.

A fourth generation of chemicals for increasing gum yields has already received preliminary testing (McReynolds and Kossuth, 1983). These are chemicals which alone, or in combination, stimulate the tree to produce ethylene. High auxin concentrations induce plants to produce ethylene (Kang et al., 1971). The success with 2,4-D treatments is probably attributable to this process. Calcium plus kinetin (Lau and Yang, 1974) and auxin plus kinetin (Lau and Yang, 1973) stimulate plants to produce ethylene and these treatments have increased gum yield from chipped slash pines (McReynolds and Kossuth, 1983).

More research is needed to identify chemicals which may stimulate resin production versus those which cause the formation of traumatic resin canals. Basic research on the biosynthetic pathway for the components of oleoresin is also needed. The oleoresin resulting from CEPA treatment has been much less viscous than that from the commercial control, indicating that there is preferential synthesis of the terpene fraction of the gum.

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[3] Mention of trade names is to identify materials and does not constitute endorsement by the USDA.

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PANEL QUESTIONS

FOURTH SESSION: Forest Productivity: Problems and Achievements

QUESTION (A.M. Carey): What do you consider to be more important for maintaining long term forest productivity on these sites, increasing the root density by more intensive initial site preparation or improving the nutrient status of the affected rooting zone. The reason I'm asking this is that I think within our career spans what we are going to be seeing is more intensive forest culture because of more intensive pressure and competition between forest uses and agricultural uses.

RESPONSE (S.J. Riha): One of the points I was trying to make for mature stands is that I think in a lot of situations root density is not limiting water uptake; on the other hand root density very well may be limiting nutrient uptake. In that situation more intensive cultural practices, such as fertilization, would be useful. In terms of site preparation for tree seedlings, the volume of soil that the roots are exploiting definitely limits water uptake. The idea for mature stands is that they have already exploited the total soil volume that is available to them and basically if they've got a few roots in wet soils they are going to make it somewhere down deep enough. But for tree seedlings, anything that would stimulate root growth and increase the rate at which those roots exploit the soil volume would be useful for decreasing water stress.

QUESTION (A.M. Carey): Has there been any work done in altering root resistance chemically; in other words, the application of another chemical to decrease root resistance.

RESPONSE (S.J. Riha): That's interesting. I haven't seen any work like that. There has been a lot of controversy in the past 10 years or so about root resistance. In the 1960's Gardner wrote an article basically talking about how slowly water moves through dry soils; and most of you who have ever taken a soils course probably got that impression that water moves very slowly through dry soils -- so the assumption was that water uptake was limited by movement through soils. Then it was physiologists really who started trying in various ways to measure root resistance. -- It's not an easy thing to measure; and I would say there are still a lot of problems with the way root resistance is measured. They found that it was quite high and, in fact, a lot of people reported it was much higher than soil resistance. Now there is still some debate about how much contact resistence there is - right between the soil and the root; and that is very difficult to delineate from either end. The problem right now is that no one has really concluded where that big resistance in the root is. It is basically thought to be in the endodermis with the casparian strip; but exactly how water moves from the cortex into the xylem; how much it moves apoplastically and how much it moves simplastically is not known. So in terms of chemical alterations, that would just be a hit or miss thing because it would be difficult to say exactly what kind of chemicals you should use and where you would want to affect this. The controversy right now over resistance is how much temperature affects it, how much something like dormancy might affect it, how much variability there is say between suberized and unsuberized roots, and also whether the resistance in the root itself is flux-dependent. There has been a lot of suggestion that the quicker the water flow through the plant, the higher the resistence to flow. That may just be an artifact of the measurement system. So I would say at this point, no, there has not been any work with chemical alteration of root resistance.

QUESTION (S.L. Stout): I would like to start by saying, Kathleen, that I really enjoyed your paper and I have several questions, many of which arise from my own very deep interest in the topics you covered. What are the more important management implications of what you are doing then, in terms of a large landowner - a landowner who say has holdings across the whole south? Could he use your model in conjunction with maps of rust hazard to choose management strategies for stands and manage for solid wood products in low risk areas, for example?

RESPONSE (K.E. Moore): Yes, that is definitely one way you can avoid impact - just adjust your expectations. I think that is a very feasible kind of thing, because the tall resin yields are higher from the galls themselves. There is quite a bit of resin in those galls; so while the pulp yield from the galls themselves goes down, it turns out economically, as shown by McVeld, that is more than offset by increased tall resin yields. If you go ahead and pulp those trees chances are you are not going to see that kind of product loss.

QUESTION (S.L. Stout): In some of your most recent work, it seemed to me as if there was some implication of yield loss associated with higher levels of aggregation incidents.

RESPONSE (K.E. Moore): I think it went the other way. The position of the line decreases .. that's why it didn't do what I expected it to do. What I would anticipate is that the intercept for the uninfected stands should be the same, but the slope should be steeper. What I found was that the slopes were the same for the two levels of aggregation. It may just be that I haven't done enough runs yet to be able to get a good line out of that.

QUESTION (S.L. Stout): You mentioned that the disease cycle is dependent upon an essential phase in an alternate host; I wondered if you could talk some about whether or not a large-scale landowner could find information about where alternate hosts are versus where pine plantations are, to either control or minimize impact of disease on pine plantations.

RESPONSE (K.E. Moore): My opinion is yes, very much so. That goes contrary to almost anyone else's opinion regarding this disease. Part of that is the history you may or may not be familiar with -- the control attempts earlier in this century with respect to white pine blister rust. It was an eradication program to get rid of the alternate host. Everybody kind of scoffs at that now, because -- who had the picture of all the men in the trees trying to get rid of the egg masses -- it was the same kind of thing. They just sent out these huge crews of men, I understand, to get rid of the alternate host for white pine blister rust. I think that is part of why people laugh when I talk about oak control. Nonetheless, the fact of the matter is the history of fusiform rust is such that one of the major reasons that we are experiencing an epidemic of this disease now is that our forest management practices have brought the alternate host in closer contact with the pine host. The fact of the matter is you have got to have the alternate host -- it has got to be there in order for new infections to occur. What we need to know more about is the dispersal process and find out in a very sophisticated way what conditions affect dispersion and which plantations may respond to management of the altermate host.

QUESTION (J.R. Flack): Laura, first of all I would like to thank you very much for the paper that you gave, I thought it was excellent -- it was very well presented and gave the kind of detail that I really like to see. When I knew that I was going to have to make some comments to Laura at this meeting I did a quick search of the literature to find out who has been working in this area recently and it dawned on me every quickly that Laura isn't just one of the few, but she is certainly in the forefront of this work that is going on in the northeast. So I feel very priviledged to have been able to meet with her and look at her work. I would like Laura to explain how it is that she can do such refined work now, whereas in the past it was much more difficult. Where she can use not only tree ring width but also the cellwood density to come up with fairly precise data, so that she can arrive at an apparently accurate set of data from only 30 cores out of 15 trees. Please explain to us the density in the tree ring width differences.

RESPONSE (L.E. Conkey): The whole technique of taking wood density was developed in areas other than the arid southwest where correlation between tree ring width and climatic factors is so prevalent and so easily done. The first people working in wood density from a forestry point of view were in France. The technique has spread to places in Switzerland. There are many instances of use of this technique in different applications, but in dendrological applications it is very limited in where this is taking place. Part of that is due to the greatly increased cost, both in time and in finance, of getting density information. The technique involves taking cores from trees, but then subjecting them to x-rays, deriving an x-ray film that one can develop and analyze for relative opacity of the rings from one part of the growing season to the next. That is what produces those density traces that I showed you on that one slide. That is done merely by figuring out how the density of the x-ray film, which is cellulose acetate, how that relates directly back to the wood density itself. There is a lot more equipment needed, a lot of expense and a lot more time involved in getting that information -- and in a lot of places it hasn't seemed to greatly increase the amount of information obtained over what can be obtained much more easily by just looking at ring widths themselves, which you can do by just looking and counting and measuring, cross-dating. For instance, in the Colorado plateau there has been some work done with wood density versus ring width that shows that the ring widths have more information from a climatic point of view than do the densities themselves. But in an area such as this where the ring width correlation to the climate is so low, density definitely appears worth the added investment.

QUESTION (J.R. Flack): Thanks. One other question that I have has to do with your historical analysis -- and we talked about this a little bit at the break. But maybe you could further elucidate why it is that you think changes are insect related when you look at your 19th century record as opposed ot merely a temperature differentiation in your data.

RESPONSE (L.E. Conkey): When I did climatic analyses I used two major sources of information, one involved just the weather bureau records that we have for the last hundred years; that is readily available - temperature, precipitation, drought severity, disease, water stress and other such factors. That will take us back to the very latest 1800's in Maine -- Most climatic stations only go back to 1895 maximum. But there are some researchers at the University of Maine who have been culling records from historical sources -- diaries, records that people kept a long, long time ago whether in association with their own farms and crops or just for a very esoteric academic kind of interest. At almost every university there was somebody taking records of temperature and precipitation as soon as some of these places got going. These researchers at the University of Maine have put together a very impressive record of historical climate based on such records -- qualitative and quantitative. The quantitive records are easy, the qualitative records they subject to content analysis to get some kind of quantitative information from the qualitative records. I was able to use those records in comparison with my own climatic reconstructions that I derived from the density and the width, and came up with some very good correlations in some instances. That is on a more specific level. On a more general level, I mentioned the 1816 year without a summer; there was another cold spring in 1812. Things of that nature that are more generally known and talked about, different kinds of things that happened in the past in terms of climate. But there are two significant sources of deriving climatic correlations with the tree ring data. As far as insect infestation, disease, wind throw, things like that -- at this point it is entirely qualitative. On my point I found very little historical information on that, and as I was talking with one of you just a little while ago, when people say there have been budworm infestations in the northeast over the last 300 years, well they are getting that information form the same kind of data that I have. That is, the tree ring records themselves, so it gets rather circular rather quickly -- and I can't really rely on that kind of information.

QUESTION (M.Morselli): Susan, the other Susan, I am very happy to have to comment on your paper because for once I will not speak of maple sap flow but resin flow. The first question -- you are talking about genetic differences, naturally; you said that the maximum yield in a progeny test is after about two months; but what is the optimum age for resin yield in a natural stand? Did you way 10 years at some point?

RESPONSE (S.V. Kossuth): The industry people have established a rule of thumb that they don't work trees that are smaller than 9 inches. The reasoning is that on the smaller trees the 1/3 circumference area is less and therefore they will be getting less yield from it, and that it takes a certain amount of time just to get to each tree and to make each treatment and collect. So, in the end they don't get enough gum from working smaller trees. So they usually work larger ones. One of the problems that one has in reading the literature is that initially, especially with the breeding program, they would take say high gum yielding trees and plant them with commercial checks, and after 10 years or whatever go in there and chip and say -- ah ha, the high gum yielding trees are high gum yielding -- look at all this gum we have. Well, they were also fast growing, so they were also larger in diameter -- and no corrections were made for the diameter size; so, yes, larger trees yield more gum, but that is because you are chipping a larger surface area to get that gum. So all of the data I presented was corrected for -- I forget what the units were, I think I had barrels per crop, that's 435 pounds in a barrel per 10,000 trees in a crop -- but those numbers came from grams per inch dbh. The face width was whatever the dbh was on the tree. So you can get good yields from smaller trees, it is just that it is not economical to go back that often for small amounts at a time -- you need larger amounts.

QUESTION (M. Morselli): How long does the season last?

RESPONSE (S.V. Kossuth): In Florida they start in March and go right through October. That is based on the assumption that it needs to be warm. I guess I forgot to follow that up the advanced streak I promised. The empirical observations were that the increasing gum yield came sooner if you put on thad advanced streak; and they would put it on in the cooler months, like January-February, and start chipping in March and April and get much larger yields at that time because of the advanced streak, which I believe was simply the woulding effect, production of ethylene, and it takes about a month for resin canals to differentiate -- so after 6 weeks or more, after an advanced streak, they'd start chipping and they would have more resin canals all ready to be contributing gum.

QUESTION (M.Morselli): The other question was on elaborating a little more on the ethylene production, in terms of the exudation pressure. I would like to know a little more about the mechanism. Is the exudation pressure correlated with the higher ethylene production in a normal situation?

RESPONSE (S.V. Kossuth): The exudation pressure is a heritable character, so there will be a correlation of what kind of pressure you get in progeny with the parents form which they came. What I don't know is if there is a relationship between ethylene production and that pressure. The physical factors involved in gum flow that have been considered are the size and number of resin canals, the flow rate, the viscosity and pressure have been shown to be under genetic control, but their affect was not of a high enough magnitude on total yield that they were used as selection criteria in the breeding program.

QUESTION (M. Morselli): Has anybody studied the pressure -- where it comes from really?

RESPONSE (S.V. Kossuth): Yes, it has been studied and it shows a diurnal fluctuation in that the pressure is very high early in the morning and it drops off during the day, on towards the night, then builds up again at night. It follows the same pattern as the water stress situation would during the day. What is probably happening is that the pits in the tracheids which are conducting the water, are in contact with those parenchyma cells, and that as less water is taken up or high transportation rates occur, there is a decrease in the amount of water available to those epithelial cells around a resin canal -- so they become a little bit flaccid and that reduces the pressure. Then it builds back up again in the night.

QUESTION (M.Morselli): That is exactly what I wanted to hear, because you didn't mention it. The other thing is if there was any correlation with temperature in any way?

RESPONSE (S.V. Kossuth): Very much so. What they had done was they would go out with ice packs and put them on a tree, then they would chip; when they would cool the tree it would increase the viscosity and decrease the flow rate; and I doubt that it was having an effect particularly on the pressure. In the same way, they would wrap them up in blankets and so on early in the spring and try to insulate them against cold nights; then they could get better flow early in the day. But there is a very definite seasonal pattern in how much flow of gum there is in that very first day after chipping; it at least quadruples the amount that you get in the first day from, say early March to July, is when it would peak. So some of that is bound to be temperature and some of that, I believe, is also the number of resin canals.

QUESTION (M. Morselli): Speaking of this, does tree exposure make any difference?

RESPONSE (S.V. Kossuth): It should, but doesn't. You would think if chipped on one side or the other -- the data never showed that there was a difference, but you would think there would be, but they haven't been able to show that.

QUESTION (M. Morselli): The other question I think is the last, because I;d like to let the other scientists here ask questions. What is the damage to the tree, not only by the act itself of cutting so much of it around the bark, but also the damage of the acid -- and certainly you are saying from your studies that acid needs to be used on 53% -- I don't know what really in the long range is effect to the tree in terms of opening this to bacterial invasion, insect invasion, fungi invasion, mortality of the trees?

RESPONSE (S.V. Kossuth): The main problem has not had to do with wood quality because that outer part of the tree in making any form of lumber is usually cut off as the outer slab; so the wood quality doesn't suffer. We do have to be very careful about insect attacks; and I was telling Barbara about lindane becasue the industry regularly will spray the lower part of the tree, the bottom 3 or 4 feet, with lindane to prevent initially bark beetles, but also ambrosia beetle attacks, because that oil resin has a lot of the volatile terpines in it which are very good insect attractants. If all goes well, that is not a problem to a naval stores operation; if we have a very dry year it creates a water stress in the tree. We already have created a tremendous stress by chipping the tree, and those combinations are devastating. The reason that I know that is because we did a pilot type test with a producer and it was on a flat wood site and it was very wet and shortly thereafter the industry came in and ditched the area. So it lowered the water table because they were now draining off the water, and it changed the water relations -- tremendously stressed the trees. Normally a producer would have just stopped everything when they came in and ditched, recognizing that that was going to create a water stress and in combination the operation would be no good. So we have some data that does say precautions need to be taken, we are increasing the stress on the trees, and that when these combinations start adding up they can be lethal. All of the trees that are worked are not owned by the people working them. They are leased -- so if you are the timber company and you are leasing trees and somebody comes in andkills 30% -- it's a very bad situation.

FROM THE AUDIENCE

QUESTION: For Laura, also, Given your knowledge of state-of-the-art dendrochronology, do you believe it is possible to isolate our climatic factors such that one can attribute growth loss or a decreased wood density to acid precipitation?

RESPONSE: What a tricky question. It is very much a concern right now in dendrochronology to try and isolate that climatic factor, and has been done with varying degrees of success in different areas. In a very closely controlled study, I think one can differentiate the effects of climate from other environmental factors. It gets exceedingly difficult in areas of, for instance, the eastern US where the climate, as I've shown I think, the varying influences on growth are very, very difficult to differentiate one to another. There are some techniques of deriving what might be the climatic response of growth, but this too is being revised at the moment -- there is a dissertation underway at the University of Arizona where these response functions are being very intensely studied to see if that indeed is a good way of deriving what the climatic influence might be. But that is a hot topic.

QUESTION: Laura, I was wondering if you could comment on whether there are techniques that you use in dendrochronology that could be used in studies like fertilizer response, or response of a stand to insect attack -- to actually determine if there is an effect -- in a more spbphisticated way than just looking from a volume of growth response over a long period of time.

RESPONSE: I think a lot of the studies that have been done on fertilizer effects have included what kind of differences there are in growth, certainly by looking at diameter growth. Now whether that, what is usually a short-term, study can be extrapolated for a whole stand for instance over a long period of monitoring might be of great use. Certainly, in that regard, once you start working with long time periods dendrochronology becomes very useful. On the short term you have much greater control over what is happening in what year in terms of growth, and so dendrochronology per se is less useful, but certainly there is potential for its use in long term studies of insect infestation or fertilizer studies, I would think.

QUESTION: If you look at the data base of what people work on new, like what is known about how trees respond to insect attack and fertilizing application, where do you see the biggest gaps in information that wuld be useful to you? Is there good data on those types of responses?

RESPONSE: There isn't always, and maybe I'm just unaware of it. I've looked at -- for instance, the University of Maine Extension Service has put out a number of publications on the effects of fertilizer in this or that individual situation. The difficulty from my point of view is that there is very little generalization made -- and maybe it is just not possible -- but I would like to be able to say in looking at the record in the past I can see this or that piece of evidence that seems to fit is with what has been seen on the shorter time period -- and that has been hard to do. It is very hard to generalize, I think.

QUESTION: Susan, what effect do soluable heavy metals have on water uptake?

RESPONSE: Well that is an interesting question. I think it would depend which heavy metal you are talking about. Something like aluminum, which I know you may be interested in, there is so many possible modes of action of aluminum toxicity in the roots -- there are so many that have been proposed in the literature, it would be difficult maybe to say. But one of the things some of the people at Cornell are hot on, they feel like aluminum might -- they have done some work, I believe it is with corn, aluminum tolerant and intolerant species -- they think that aluminum is complexing in the cell wall and that in turn would decrease the elastic modules of the cell wall, and therefore there would be problems with growth and expansion of the cell carying the cell wall. This would break up the integrity of the root. Now, my guess is that given that whole scheme of things in terms of water transport through roots, through the endodermis and into the xylem, that just breaking up the cell wall would probably have more effect on disease infestation. Probably some of the pathologists would be better able to comment on that than myself, than on water flow itself. I think you would have to actually change either the simplastic or apoplastic movement of water and I'm not sure at this point how heavy metals alone would affect that. Maybe some of the other physiologists have some comments on that.

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FIRST SESSION:

Biological Aspects of Forest Pest Control

Moderator:

Ann M. Spearing, Assistant Dean, Graduate College. Assistant Professor of Forestry, University of Vermont, Burlington

"Predicting response of forest defoliators to insecticides"

Molly W. Stock, Associate Professor, Department of Forest Resources, University of Idaho, Moscow

Jacqueline L. Robertson, Project Leader, U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California

"Differential population characteristics of western spruce budworm"

Jacqueline L. Robertson and Molly W. Stock

"Nucleopolyhedrosis virus transmission in the gypsy moth, *Lymantria dispar* (Lep.: Lymantriidae)"

Kathleen S. Shields, Research Entomologist, U.S. Forest Service, Northeastern Forest Experiment Station, Hamden, Connecticut

"The short- and long-term effects of insect attacks on trees"

Barbara C. Weber, Project Leader, U.S. Forest Service, North Central Forest Experiment Station, Carbondale, Illinois

PANEL:

Joan M. Herbers, Assistant Professor, Department of Zoology, University of Vermont, Burlington

Patricia M. Hanson, Graduate Research Fellow, College of Agriculture, University of Vermont, Burlington

Barbara S. Burns, Forest Protection Specialist, Vermont Department of Forests, Parks, and Recreation, Montpelier

Katherine Carter, Assistant Professor of Forest Resources, University of Maine at Orono

SECOND SESSION:

Perceptions of the Forest and Its Uses

Moderator:

Betty Wong, Plant Physiologist, U.S. Forest Service, Northeastern Forest Experiment Station, Burlington, Vermont

"Displacement: One consequence of not meeting people's needs"

Dorothy H. Anderson, Research Social Scientist, U.S. Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota

"The handicapped user in outdoor recreation resource environments: Implications for resource planners"

Lou G. Powell, Assistant Professor, Recreation and Parks Department, University of New Hampshire, Durham

THIRD SESSION:

Wildlife within Forest Ecosystems

Moderator:

Betty Wong, Plant Physiologist, U.S. Forest Service, Northeastern Forest Experiment Station, Burlington, Vermont

"Amphibian and reptile habitat association in selected forest types in the Northeast"

Deborah Rudis, Associate Wildlife Biologist, U.S. Forest Service, Northeastern Forest Experiment Station, Amherst, Massachusetts

"Deer densities and forest regeneration"

Nancy G. Tilghman, Research Wildlife Biologist, U.S. Forest Service, Northeastern Forest Experiment Station, Warren, Pennsylvania

"Patterns of wolf predation and effects on moose feeding habitats"

Joan Edwards, Assistant Professor, Department of Biology, Williams College, Williamstown, Massachusetts

FOURTH SESSION:

Forest Productivity: Problems and Achievements

Moderator:

Margaret M. Harris, Research Soil Scientist, U.S. Forest Service, Northeastern Forest Experiment Station, Burlington, Vermont

"Water transport in soil and roots: Influence of root properties on water uptake"

Susan J. Riha, Assistant Professor of Forest Soils, Cornell University, Ithaca, New York

Mary Ann Levan, Graduate Research Assistant, Department of Agronomy, Cornell University, Ithaca, New York

"Impact of fusiform rust on loblolly pine plantations"

Kathleen E. Moore, Research Forest Pathologist, International Paper Company, Tuxedo Park, New York

"Dendrochronology and forest productivity: red spruce wood density and ring width in Maine"

Laura E. Conkey, Assistant Professor, Department of Geography, Dartmouth College, Hanover, New Hampshire

"Multipurpose slash pine: Genetics and physiology of gum naval stores production"

Susan V. Kossuth, Project Leader, U.S. Forest Service, Southeastern Forest Experiment Station, Olustee, Florida

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