

Fire Effects on Vegetation and Succession¹

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Abstract.—Fire adaptive traits which enhance survival or reproduction of plants are critical in determining post-fire succession. Classical succession concepts which advocate orderly community replacements and retrogression following disturbances fail to describe succession in fire-prone ecosystems. Species attributes and multiple-pathway models provide better post-fire predictors for management.

Although land managers today are expected to predict the short- and long-term ecological effects of different management alternatives, predictions of fire effects on vegetation are particularly difficult due to the wide variability in fire characteristics and vegetation complexes. There is definitely a need for better and more reliable predictions on how various management options affect plant communities and other ecosystem components. These predictions must be incorporated into fire management decision-making and policies (Kessell 1981).

Fortunately, the situation is improving. The past decade has provided a number of significant advances in our knowledge of and ability to predict fire effects and post-fire succession. A better understanding of adaptive characteristics of individual plant species and basic successional processes, coupled with the continued developments in fire behavior models and geographic information system data bases, is already having an impact on fire management decisions.

The purpose of this paper is to briefly summarize the general effects of fire on vegetation, including heat

effects and adaptive characteristics, and to examine the past and present concepts of ecological succession following disturbance by fire. The effects of fire on specific southwestern vegetation types and resource values will not be treated here but will be covered in considerable detail by later authors.

Effects of Fire on Vegetation

Fires in natural ecosystems consume vegetative material, produce residual mineral products, and raise temperatures for short periods. In many fires, plant response depends more on the direct and indirect effects of higher temperatures than on available fuel or release of products. Some heat effects may be immediate and easily observed, i.e., the killing of plant tissue; other effects may be delayed and more difficult to detect, such as damage leading to increased insect and disease susceptibility. This variability can cause problems for managers faced with the task of predicting changes in plant succession and ecosystem dynamics.

Any woody or herbaceous plant can be killed by a fire of sufficient duration and intensity. It is with fires of lower intensity or shorter duration, where only a part of the plant community is killed, that the inherent ability of individual plants to withstand or resist fire becomes significant.

A plant's ability to withstand fire and subsequent heat effects depends upon its heat tolerance and its fire resistance. Heat tolerance is the ability of plant organs and tissues to withstand elevated temperatures, whereas fire resistance is the ability of a plant to survive the passage of a fire.

Heat Tolerance

A plant is directly injured or killed when the temperature of internal living cells is raised to a lethal level. Precise information on the temperatures necessary to kill living plant tissues is lacking (Brown and Davis 1973). Baker (1950) has stated that the heat tolerance of plant protoplasm appears to be the same for all species. This suggests that, although protoplasm coagulation defines lethality for the individual cell, the differences in internal heat effects is due largely to differences in insulation from heat sources.

A temperature of 60°C (140°F) for one minute is often given as the lethal temperature required to kill plant tissue. However, Wright (1970) points out that the temperature at which death of plant tissue occurs is largely dependent upon the tissue moisture content, where tissues with higher moistures are killed at lower temperatures and shorter time intervals. It is possible that a steaming effect may be responsible for increased

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heat susceptibility in plants with higher moisture contents.

Not only is heat tolerance dependent on tissue moisture content, but it also varies for different plant parts. For example, seeds are known to be very tolerant of heat (Daubenmire 1968). Chaparral species with hard, thick seed coats are able to tolerate temperatures of 125° to 150°C (260° to 300°F) (Sampson 1944). Wright and Bailey (1982) indicate that seeds covered slightly with soil can be insulated from the effects of a moderate to intense fire. Furthermore, they speculate that grass fires would probably have little or no effect on the mortality of dormant seeds, even if the seeds were lying on the soil surface. Roots, stems, and foliage also exhibit variations in heat tolerance, as can the presence of salts, sugars, pectins, and other plant tissue substances.

Fire Resistance

A plant's ability to survive or recover from the passage of a fire, defined as fire resistance, is dependent upon its food reserve levels and the presence or absence of fire adaptive traits, i.e., protection of growing areas, resprouting, germination of dormant seeds, etc. Plants are more susceptible to damage from fire during flowering and seed formation or during periods of active growth when carbohydrate reserves are low. Since seasonal trends in food reserves vary considerably between plant species, burning at any particular season can be more detrimental for some species than for others.

Fire Adaptive Traits

In fire ecology literature, four fire adaptive traits of plants have been given special attention. These traits are described as those which enhance survival during a fire, such as (1) bark thickness and protected buds

which result in vegetative sprouting, and those which enhance reproduction, such as (2) fire-stimulated flowering, (3) seed storage on the plant and fire-stimulated dehiscence, and (4) seed storage in the soil and fire-stimulated germination (Gill 1981).

Bark thickness and protected buds.—The insulating qualities of bark are well recognized. Reifsnyder and others (1967) have stated that the primary factor in determining whether a tree is fire resistant or not appears to be bark thickness. Wright and Bailey (1982) report that trees suffer very little heat damage if the bark thickness is 1.0 to 1.3 cm. Many plant protective mechanisms vary during growth and development so that susceptibility to fire damage may also change with age. In general, bark tends to be quite thin in small trees, considerably thicker at maturity, and declines in thickness with senescence.

Plant survival following fire can frequently be attributed to the location of meristems and the protection buds receive from reaching lethal temperatures. Packham (1970) noted that the amount of rising convective heat from a surface fire is three times that of radiated heat. The exposed location of terminal and lateral apical buds of many shrubs make them highly susceptible to top-killing from rising convective heat, whereas surface and subterranean buds are well-protected against major heat inputs. The basal meristems of a number of grass and forb species provide a distinct fire survival advantage. Basal sprouting may be common in shrubs after fire has destroyed the foliage. Sprouting is thought to be an ancient adaptation which occurs when the foliage is removed by an external agent (Chandler and others 1983). While the leaves are alive, an inhibiting factor prevents bud activity, but when the foliage is killed the inhibition disappears and the dormant buds begin sprouting. Resprouting after fire appears to be related to the age of the plant, stem size, season of

the year, fire frequency, and fire intensity.

Fire-stimulated flowering.—Among fire-resistant plants, the phenomenon of fire-stimulated flowering has been observed (Chandler and others 1983, Gill 1981). Although not widely reported in the western United States, a number of observations have been made in Australia, Israel, New Zealand, and South Africa. This trait appears to be most frequently associated with the monocotyledons, especially the amaryllis, grass, lily, and orchid families.

The mechanisms responsible for the triggering of flowering by fire are still unknown. The results, however, are that prolific flowering is followed by increased seedling establishment. This may be a consequence of greater seed set, lower on-plant seed predation, or lower predation of seeds following dispersal (Gill 1981). Chandler and others (1983) speculate that either a change in diurnal temperatures following fire or an increase in the amount of light reaching the soil may cause heating of the floral reproductive organs and induce flowering. The removal of shrubs could also promote more effective pollination of certain species by insects and wind.

Seed retention and fire-stimulated dehiscence.—For many shrubs and trees, retention of seeds on the plant and stimulation of dispersal is an important mechanism for survival in fire-prone environments. Two examples of tree species that possess this trait are jack pine (*Pinus banksiana*) and lodgepole pine (*Pinus contorta*). A number of other pine species have cones that dehisce (split open) after fire or under the effects of fire, a trait known as serotiny. The cone scales of these pines are held closed by a resinous or waxy material sensitive to high temperatures. As fire passes and heat melts the resins, the cone scales exfoliate and seeds are released. Lodgepole pine is particularly interesting because its cones can vary from serotinous to freely dehiscent (Brown 1975; Lotan

1975, 1976). In stands where fires are frequent, serotinous cones are common, whereas cones are freely dehiscent in forests where fire is less frequent. Lotan (1975) also reported that young lodgepole pine trees tend to have open cones while older trees possessed either open or closed cones.

When seeds from serotinous cones are released by fire, they often fall on a favorable seedbed. The ash and minerals provide nutrients while the lack of overstory foliage increases the amount of sunlight reaching the soil to assist in seedling germination and growth.

Seed storage in the soil and fire-stimulated germination.—The storage of seeds in the soil and stimulation of their germination by fire can be seen as an adaptive trait. Seed germination in recently burned plant communities can usually be attributed to the release of seeds retained by the plants or to the germination of seeds stored in the soil from past years. Some transport of seeds to the burned area from sources in adjacent unburned sites is also possible.

Hardseededness is a term applied to seeds with a physical barrier to germination, commonly typified by the lack of imbibition, swelling, and softening when exposed to water (Gill 1981). However, when the seed coat is scarified, germination does occur. A number of woody and herbaceous species, perennials, and annuals exhibit this trait. Fire is one of the mechanisms capable of scarifying seeds and breaking seed dormancy. Similar results can be achieved by the movement of seeds in ephemeral streambeds and softening of seed after passage through birds and animals (Gill 1981).

Research by Muller and others (1968) on the allelopathic conditions in California chaparral indicates that profuse flowering and appearance of herbaceous species after fires is due to the destruction of a chemical inhibitor produced by the woody plant cover and deposited on buried seeds.

The authors concluded that heat is not required for germination, but germination is stimulated by the removal of the inhibiting ligneous extracts. The degree of seed coat inhibition removed is dependent upon the intensity and duration of heat exposure. When woody plants return, the inhibition becomes reestablished; however, the seeds remain viable until another fire takes place.

Gill (1981) refers to these four vegetation adaptations as the "classical" fire traits. He points out that there are other developmental patterns of plant species which could be considered fire adaptations. Mentioned as possibilities are seed burial, plant longevity, chemical composition, time to first flowering, and patterns of leaf shedding. Many adaptive mechanisms are able to facilitate the reproduction or survival of plant species in fire-prone environments.

Fire Characteristics

Chandler and others (1983) state that adaptive traits have been considered in relation to the occurrence of a single fire, but, in actuality, an individual plant may be exposed to several fires, each with different fire characteristics and fire effects. To determine the significance of adaptive traits consideration must also be given to the life cycle of the species and fire regimes to which the species is subjected.

Fire frequency determines the vegetative composition of an area by selecting species which will continue to occupy a site. A species can be removed if fire occurs too often, too early, or too late in its life cycle. For instance, a non-sprouting species may be lost if fire occurs before seed has been produced, or if fire occurs after the species has died and the seed pool is unavailable (Chandler and others 1983). Two strategies typically characterize the response of different species to fire frequencies — those that sprout can withstand re-

peated fires while those that produce seed are favored by infrequent fires (Keeley 1981).

Understanding the effect of fire intervals is important because it can significantly affect the survival probability of an individual, population, or species. In general, a pattern of less frequent fires burning with higher surface temperatures due to increased fuel accumulations, and vice versa, has been recognized. Fire regimes, then, modify the evolution of plants and any changes in these fire regimes will precipitate a change in the floristic composition and structure of a vegetative type.

The season of fire occurrence is a very important factor affecting plant survival and flowering. Frequently, substantial fire effects differences can be observed between spring and fall burns. Spring fires tend to damage annual grasses that emerge following winter rains and have not had the opportunity to produce seed. On the other hand, many perennial species are still dormant during a spring fire and could resprout later in the season (Wright 1969, 1974).

The size of the area burned by a stand-consuming fire can influence recolonization if plants are unable to regenerate by sprouting. Seed carriers, such as wind or animals, may not provide adequate distribution of seeds if the burned area is extensive.

Vegetative responses to intensity and duration of heating vary considerably depending on the natural role of fire in an ecosystem. With fire-sensitive species, a low-intensity fire may be very damaging, while a moderate- to high-intensity fire in a vegetative type dependent upon fire may stimulate reproduction and cause little change in floristic composition. Fire intensity is one of the more difficult fire characteristics to assess. Some observers rely on the visual post-fire changes evident on vegetation or soil, others install temperature sensors or attempt to correlate intensity with flame lengths using different indices.

A fire that creates high surface temperatures for a long duration can result in heat penetrating into the surface soil. The survival of subterranean organs, i.e., roots, rhizomes, and seeds, is dependent on the depth of heat penetration. If penetration is extensive, organs are killed and reestablishment of the species will be difficult. A low intensity fire does not destroy these organs which allows the vegetation to become reestablished on the site quickly.

Effects of Fire on Succession

The preceding discussion was specifically directed to heat effects, fire adaptive traits, and fire characteristics. This information can now lead to an examination of ecological succession in a fire-prone environment. Before considering the present-day concepts of fire-disturbed succession, it is important to look back at the early or classical version of succession and to see why it fails in disturbed ecosystems.

Classical Succession

The classical definition of succession is simply the replacement of the biological community of an area by another community. Classical Clementsian succession can be described as (1) an orderly process of community change which is reasonably directional and predictable, (2) resulting from the modification of the physical environment by the present community which creates conditions suitable for the establishment of another community, and (3) ultimately reaching a biologically stable ecosystem stage (climax community) (Clements 1916, 1936).

Clements has also identified the successional development of vegetation as a sequence of five processes: immigration, establishment, site modification, competition, and ecosystem stabilization.

Two types of succession are often recognized — primary and secondary. Primary succession is the development of communities on newly exposed bare areas which have not previously supported vegetation. Primary succession, also known as autogenic or self-induced succession, starts with a pioneer stage (usually mosses and lichens) and progresses to larger and taller species, each creating a microclimate or soil condition which induces the emergence of a new community and the loss of the old.

Secondary succession is the sequence of vegetation development on areas which have supported vegetation but now vegetation has been destroyed, in part or in total, by an agent such as fire, flood, windstorm, etc. The term allogenic (externally-induced) is often used with secondary succession because changes are precipitated by forces independent of the community itself. Secondary succession can appear at any stage of primary succession and, theoretically, causes a retrogression or resetting of succession back to an earlier stage. The essential distinction between primary and secondary succession is that pioneer communities of a secondary succession receive the benefit of soil already in place.

Probably one of the most confusing aspects of classical ecological succession is the concept of a climax community. A postulate advanced by Clements (1936) and his followers states that community succession leads to a climax and that the concept of succession cannot be separated from that of climax. Clements felt that with sufficient time and competition, an undisturbed plant community would approach the same species composition and structure in a given climatic region. This monoclimate or climatic climax concept placed only secondary importance on other site factors such as soil, topography, or repeated disturbances. Over time, ecologists recognized that stable vegetative commu-

nities can also be attributable to site or other environmental conditions. This has led to a number of additional definitions of climax attributes such as polyclimax, subclimax, physiographic climax, edaphic climax, disclimax, preclimax, and postclimax.

Notwithstanding the debate on climax, ecologists acknowledge that some ecosystem changes accompany the successional growth and maturation of vegetational stages. For example, there appears to be a progressive increase in community complexity and diversity from early to mature stages, an increase in the total biomass and gross productivity, and an increasing development and maturation of soils.

Fire Disturbances

The classical concept of succession subscribes that, following a disturbance, such as fire, the present community disappears and is replaced by an earlier vegetation type which results in a retrogression or backing up of succession. Succession then moves forward through the intermediate or seral stages to the stable, climax community. This classical succession has been described in the literature as the facilitation model (because of its emphasis on changes within successional areas facilitating the establishment of new species), the relay floristics model (due to the replacement or relay sequence of successional stages or seres), or the single pathway model where succession follows a predictable sequence of steps (Connell and Slatyer 1977, Egler 1954).

Not all successions necessarily proceed stepwise through to a climax community. If disturbances, such as fire, are part of the natural environment of a plant community, then the term climax loses meaning since all species that persist are climax species. Climax implies stability; however, plant communities cannot be completely stable. With different

ages and lifespans, there are weak and overmature individuals that disappear and are replaced. Openings, either natural or human-caused, allow the establishment of new individuals or species. Thus, communities are characterized by continual change rather than by stability. It is interesting to note that Patterson (1986) has recommended that the word "climax" be stricken from forest terminology. He argues that Clementsian climax theory is known to be based on assumptions that cannot be met, and that continual changes in time and space make ecosystems dynamic instead of stable.

As the failure of classical succession concepts to describe vegetational changes resulting from disturbances became more apparent, scientists began to propose other models of succession. In 1977, Connell and Slatyer suggested two additional pathways of succession. They identified these as the tolerance and the inhibition models; both were attempts to explain the site occupancy of certain species following disturbances. The tolerance model describes the situation in which later species are successful whether or not earlier species have preceded them. The inhibition model considers the condition where later species cannot grow to maturity in the presence of earlier ones. Although these two models provide some insight on species establishment, they did not deal effectively with species changes being observed following fire disturbances.

As more information on fire disturbances and succession became available, Noble and Slatyer (1981) stated that several generalizations could be made. These were:

1. Species composition immediately following a fire is dependent upon propagules (reproductive structures) which have arrived from adjacent areas, have persisted through the fire, or have re-

sprouted vegetatively from organs surviving the fire. Therefore, it is not surprising that replacement sequences following fire tend to be reproducible and often lead to development of communities similar to those existing before fire (initial floristic composition) or existing on nearby undisturbed areas.

2. Shortly after fire, there is a surge of recruitment and regrowth under conditions of low competition for site resources.
3. There is a slowing in recruitment following the initial surge as individuals become established and are more difficult to displace.
4. Further recruitment of new species may be facilitated by prior occupancy, but it may also be restricted or inhibited by present occupants.
5. In the absence of further fires, species that are long-lived and those that can regenerate and grow under an adult canopy will become dominant.

For understanding successional pathways following fire, evaluation of responses by individual plant species leading to community development may be considerably more useful than the community replacement approach of Clements. Fire-induced succession is related to the adaptations possessed by individual plant species to colonize, grow, and survive. Therefore, specific life-history characteristics of key species in a particular community can be used to describe successional patterns which follow fires of varying intensities and frequencies.

Fire is now recognized as one of the most common disturbances of natural ecosystems and it is becoming

widely acknowledged that the properties of individual species are one of the key factors in determining successional patterns in fire-adapted communities. Noble and Slatyer (1977, 1980, 1981) and Noble (1981) have provided the foundation for much of today's work on plant adaptive traits and post-fire succession. These authors sought to identify a small number of attributes which are vital to terrestrial, higher plant community species which occur in areas subject to recurrent fires. They developed a "multiple pathways" model for predicting major shifts in species composition and dominance in fire-prone ecosystems which is based on selected plant "vital attributes."

Three main groups of species attributes which are vital in a vegetation replacement sequence have been recognized. These are (1) **method of persistence** (the method of species arrival after, or persistence during, a fire), (2) **mechanisms for establishment** (attribute associated with the site conditions in which the species become established and grow to maturity), and (3) **critical life stages** (time needed for the species to reach critical periods in its life history, i.e., reproduction, maturity, senescence, extinction).

In recent years increasing numbers of authors have reported the use of the vital attributes approach to describe successional changes following fire (Hobbs and others 1984, Noste and Bushey 1987, Rowe 1983). Some excellent fire ecology information and fire management guidelines using species attributes and fire characteristics for specific forest habitat types in Idaho and Montana have been published (Crane and Fischer 1986, Fischer and Clayton 1983, Kessell and Fischer 1981).

Although it is evident that this method is providing managers with a more realistic prediction of post-fire succession, there are situations where its application is difficult. For example, the wide variability in cone serotiny for lodgepole pine has direct

applicability to its reproductive success after fire. Some difficulties also arise because of the lack of vital attribute information on key plant species. It is recognized that this approach works best for forest and brush overstories, but little attention has been given to understory herbaceous species. As additional data on plant adaptations, life histories, and site-specific fire characteristics become available, the use of the multiple pathway vital attributes model of succession will become a more valuable tool for the land manager in fire prone areas.

Management Implications

The land manager attempting to predict the effects of fire on vegetation and subsequent successional sequences is facing a difficult task. This individual is being asked to integrate information which ranges from plant heat tolerances, fire resistances, and plant adaptations, to specific fire and weather characteristics, into a reasonably comprehensive and meaningful fire management plan. The magnitude of the task is readily apparent. Thus, a major function of this paper was to provide an overview of fire effects and their relationship to succession and to furnish managers with information on changes and new approaches for use in decision-making.

One of the more important points for today's land managers who deal with fire is to recognize that the application of classical succession concepts to predict post-fire vegetation patterns is not appropriate. Therefore, managers should become as familiar as possible with the individual plant species in their area and, particularly, try to determine what attributes these species have to survive or persist following fire. Some of this latter information may be available in the literature but, ultimately, close field observations and records of plant responses during

and after fire by researchers and managers together may be most valuable. Researchers and managers need to determine precisely what information is required to do the job (USDA FS 1981). Although some researchers disdain the concept of "good enough," often managerial objectives can be adequately met by procedures and models that are neither the "best" nor the "most complete." The cost of improving or expanding such procedures may not be financially justifiable to the manager or the agency. A program of cooperation and communication between research and management will yield greater benefits than individual efforts.

An example of such cooperative efforts is the development of a Fire Effects Information System (FEIS), a new computer-based storage and retrieval system. This FEIS is being developed at the Intermountain Fire Sciences Laboratory in Missoula by Forest Service prescribed fire and fire effects research personnel and the Computer Science Department at the University of Montana. The Bureau of Land Management and the National Park Service have provided support for the project. The purpose of the system is to provide land managers easy access to up-to-date information on fire effects in plant communities and associated individual plant and animal species. Managers interested in this system may wish to contact the Intermountain Fire Sciences Laboratory, the Boise Inter-agency Fire Center, BLM State Offices in Idaho, Colorado, Nevada, and Oregon, or personnel at Wind Cave National Park.

In the coming years continued advances will be made in our understanding of and ability to predict post-fire plant succession. Work has already progressed on several fronts, including the knowledge of basic successional processes, the adaptive characteristics of species populations, the effects of fire intensity and periodicity, and the ability to integrate

successional sequences with ecologic and managerial concerns.

The challenge of the 1990's will be to continue to build upon this knowledge base and to expand application to include how fire disturbances and their management affect other terrestrial and aquatic community components. Fire impacts on water quality, nutrient cycles, ecosystem dynamics and energetics, fish and wildlife, fuel complexes, and soil properties are directly and indirectly related to floristic changes and successional patterns. Additional information on these components in a fire disturbed community will, undoubtedly, substantially enhance the value and applicability of fire management plans.

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