

Ecosystem Responses to Fire and Variations in Fire Regimes

ABSTRACT

This chapter summarizes the literature available on the effects of fire on Sierra Nevada ecosystems. A general theme that will emerge from the discussion is the intimate, even circular, relationship between fire and postfire ecosystem processes. Fire affects individual species through direct mortality and postfire changes in nutrient, food, and habitat availability. The diversity of species' responses to fire as well as the variety of fire intervals and fire intensities contribute to the overall biodiversity of the Sierra Nevada. The diversity of plants leads to the accumulation of different quantities and quality of fuel. Animals and fire change the quantity and the horizontal and vertical continuity of these fuels, which in turn generate variations in fire behavior. Fire also interacts with other ecosystem processes to create heterogeneity across the landscape. The heterogeneity in the amount, structure, and continuity of fuels across the landscape in turn generates variations in fire regimes. Such diversity, variation, and changes are important components of Sierra Nevada ecosystems.

INTRODUCTION

This chapter compiles and summarizes the literature available on the effects of fire on Sierra Nevada ecosystems. Key elements in the approach were to (1) understand how ecosystem structure and processes respond to variations in fire regimes, for example, fire intensity, frequency, and extent, and (2) understand the role of such responses in generating variations in fire regimes. A general theme that will emerge is the intimate, even circular relationship between fire and postfire ecosystem processes.

The chapter is organized into two major parts: the first part presents general ecosystem responses to fire and variations in fire regimes; the second part deals specifically with the various types of ecosystems of the Sierra Nevada. Successional responses, biodiversity and community-structure responses, fuel-structure changes, landscape-pattern responses, and biogeochemical and soil changes are among the ecosystem structures and processes discussed.

OVERVIEW

Classification of Fire Regimes

The following is a simplified classification of fire regimes (Kilgore 1987; Skinner and Chang 1996), with some examples from the Sierra Nevada. The types of regimes are described in relative terms and would differ if observed from a different temporal or spatial scale. The categories also overlap and have high variations within each type. Nevertheless, they provide a useful structure for discussion.

1. Short-interval, stand-replacement fires: Fire burns frequently and intensively, allowing only fire-adapted species to dominate. One example is the chaparral, but Keeley and Zedler (1978) noted that chaparral is adapted to both short and long fire-free intervals, reflecting how unpredictable fire is in that environment. They suggest a model in which a short fire cycle favors sprouting shrubs over those reproducing entirely from seed, and a longer fire cycle in which "sprouters" and "seeders" coexist.

2. Short-interval, low-intensity surface fires: Fire burns regularly and frequently and, as such, rarely allows organic fuels to accumulate to a point where higher-intensity fires may develop (van Wagtenonk 1972). Examples of such regime types include ponderosa pine forest, mixed conifer forest, and sequoia groves. In such regime types the following effects occur:
 - fire controls species composition by favoring species that require sunlight (such as pines and sequoia) over shade-tolerant forms (such as white fir and incense cedar), and by favoring fire-resistant and fire-dependent types over non-fire-dependent forms.
 - fire recycles understory vegetation without damaging the overstory canopy.
 - crown fires are rare if not nonexistent (Kilgore and Taylor 1979).
 - small patches of intense surface burning often result in small openings and consequent fine-grained landscape.
3. Variable-interval, variable-intensity surface fires: Fire usually spreads slowly and rarely burns the crowns. An example of this regime type in the Sierra Nevada is the upper montane red fir forests: the occasional longer fire-free periods provide the chance for red fir seedlings to survive their fire-susceptible stage and therefore establish themselves.
4. Long-interval, low-intensity surface fires: Fire usually spreads slowly or not at all and rarely burns the crowns or kills stands of overstory trees (Kilgore and Briggs 1972). Examples of this regime type in the Sierra Nevada are the subalpine forests of whitebark pine (*Pinus albicaulis*) and lodgepole pine (*Pinus contorta* var. *murrayana*). The effects of fire on such vegetation vary with species, stand age, and burning intensity.
5. Long-interval, high-intensity surface fires: Fire burns rarely, but whenever it happens, it becomes a high-intensity possibly stand-replacing fire. Kilgore (1987) cited coastal redwood (*Sequoia sempervirens*) as an example of this regime type, but see Brown and Swetnam (1994) for a different observation. For the Sierra Nevada, piñon pine and juniper in the eastern Sierra might fit this category (C. Millar personal communication).
6. Very long interval, stand-replacement fires: Stand-replacing fires burn at mean intervals longer than three hundred years. Such types are typical of very damp forests, for example, spruce fir forests, cedar-hemlock forests, and true fir forests (Hemstrom and Franklin 1982), and are not typical in the Sierra. Even if found in the Sierra, they would be sparse and local. In general, in the long absence of fire, succession shifts dominance to shade-tolerant "climax" species.
7. Variable regime: Both short-interval, low-intensity surface fires and long-interval, stand-replacement fires occur on the landscape. Examples include boreal forests, Great Lakes forests, Pacific Northwest Douglas fir (*Pseudotsuga menziesii*) forests, and Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) forests. Such variable regimes allow complex local variables to give complex results.

The vegetation in these fire-regime types responds differently to fire and consequently responds differently to variations in fire regimes.

Changes in Sierra Nevada Fire Regimes and Their Probable Causes

It is generally agreed that fires in the forest and woodland areas of the Sierra Nevada have become less frequent (e.g., longer return intervals) and generally more severe since about 1850 (Swetnam 1993; Skinner and Chang 1996). Nevertheless, there is considerable disagreement regarding the causes behind these changes. First, climate changes have always had a prominent impact on fire regimes (Swetnam and Betancourt 1990), and because the climate in the region shifted markedly circa 1850 (Stine 1996), some have argued that climate drove changes in fire regimes. However, a closer look at how the climate has changed suggests that such changes would have shifted fire regimes in the opposite direction (Swetnam 1993; Stine 1996).

A second group of explanations for the changes in fire regimes is anthropogenic based on the fact that European-American settlement in the Sierra Nevada also occurred around 1850. Examples include the alteration of fuel loads by sheep grazing and the decrease in ignition sources by the diminished presence of Native Americans. Although many researchers doubt the magnitude of the impact of these two arguments and therefore discount them as important factors, one should still be aware of their impacts on applicable localities. (More detailed discussion of the probable driving forces of fire regimes can be found in Skinner and Chang 1996.)

The most discussed probable cause of the changes in fire regime is the effect of fire-suppression policies. Even so, many question the effectiveness of fire suppression and whether longer fire-return intervals due to fire suppression have dramatically altered ecosystems. Recent research on fire ecology suggests that the influence of historical fire-suppression activities most likely varies depending on ecosystem fire regime: the effects of fire suppression on ecosystem structure and processes is far less important in the longer-interval types than in the short-interval types because more cycles of fire and associated fire effects would have been excluded in the short-interval regimes (Brown 1985; Habeck 1985; van Wagtenonk 1985; Weatherspoon et al. 1992). However, not all short-interval types are equally affected by the longer fire intervals. For example, Keeley (1995) used examples from Hedrick (1954), Keeley (1992a), and Keeley and Zedler (1978) to show

that a hundred years of fire-free conditions do not seem to pose a threat to the persistence of any chaparral species, and the century-old chaparral stands' recovery from fire does not seem to differ from that of younger stands.

The effectiveness of fire suppression also varies across Sierran landscapes. Fire suppression has been more successful in areas where access is easier and less so in remote areas. Fire suppression has also been more successful in areas closer to developments because protecting private property has always been given higher priority. There has been greater success in suppressing low- to medium-intensity fires than in suppressing fast-spreading fires induced by extreme weather. Finally, fire suppression has had greater impact in the middle-elevation zones: the small-area burns typical of the higher elevations usually went out on their own; the fast-spreading fires typical of chaparral sites were often beyond the control of humans and were less successfully suppressed; but the low- to medium-intensity surface fires typical of the middle-elevation zones were more controllable and therefore more successfully suppressed. The variation in the effectiveness and impact of fire-suppression activities has added more intangibles to the understanding of the already complex and variable Sierra Nevada ecosystems.

The Issue of Natural Vegetation and Natural Fire Regimes

In trying to define management goals for the Sierran landscape, people have tried to study past patterns in the hopes of finding what was "natural" (Kilgore 1985). However, it may not be useful to worry about whether the present fire regimes and vegetation are natural, for several reasons. First of all, Native Americans have been influencing the fire regimes for centuries through active burning (Blackburn and Anderson 1993; Skinner and Chang 1996), and thus it would be almost impossible to tell what the vegetation and fire regimes might have been without human influence. Second, because human beings are a part of the environment now, avoiding the influence of people is not realistic and may not even be a desirable management goal (Parsons 1981; Christensen et al. 1989). Third, climate changes often occur on a temporal scale that is within the life span of trees (Delcourt et al. 1982; Davis 1984), and thus the forests often lag behind what would be the equilibrium under such climatic conditions. So even without the influence of people, ecosystems are constantly changing (Sprugel 1991), and a natural state of vegetation or fire regimes throughout time is nonexistent.

Variation and Scale Matter

To extract a take-home message from the literature on fire effects, "Variation and scale matter." The effects of fire and the consequences of different fire regimes vary among ecosystems and among their constituent species, from time to time and from location to location (Christensen 1985). The

magnitude of the variation depends on the temporal and spatial scale of observation. Such variability in fire regimes and its consequences result in a dynamic mosaic of shifting patches that may or may not achieve a higher level of "equilibrium," making fire ecology a complex and fascinating subject.

GENERAL ECOSYSTEM RESPONSES TO FIRE AND VARIATIONS IN FIRE REGIMES

Plant Species Responses to Fire

Conditions for successful reproduction of many fire-adapted plant species are often most favorable immediately following fire, owing to increased fertility, removal of potential allelochemicals, reduced competition, and so on (Canham and Marks 1985; Christensen 1993). Subsequently, many plant species have evolved adaptive traits that help them survive fires or reproduce after fire. Such traits include (1) fire-stimulated germination (e.g., California lilac [*Ceanothus* spp.], manzanita [*Arctostaphylos* spp.], and sumac [*Rhus* spp.]); (2) rapid growth and development that allow a complete life cycle between fires (e.g., many annual species and knobcone pine [*Pinus attenuata*]); (3) fire-resistant foliage (e.g., ponderosa pine [*Pinus ponderosa*], Douglas fir [*Pseudotsuga menziesii*]); (4) fire-resistant bark (e.g., Douglas fir, ponderosa pine); (5) adventitious or latent axillary buds (e.g., oaks [*Quercus* spp.], California lilac [*Ceanothus* spp.]); (6) lignotubers (e.g., manzanita and chamise [*Adenostoma fasciculatum*]); (7) serotinous cones and fire-stimulated seed release (e.g., knobcone pine, giant sequoia [*Sequoiadendron giganteum*]); and (8) fire-stimulated flowering (e.g., soap plant [*Chlorogalum pomeridianum*]) (Sweeney 1968; Christensen 1985; Agee 1993; nomenclature following Munz and Keck 1973).

Plant responses to fire vary and are often determined by a complex interaction among external factors such as temperature, soil moisture, and heat duration (Rogers et al. 1989) and season of burn (Parker and Kelly 1989; Weatherspoon 1988b). More information on plant nutritional responses to fires can be found in Chapin and Van Cleve 1981.

Because fire has been a potent selective force for individual plant species in fire-prone areas (Sweeney 1968; Parker and Kelly 1989), some researchers have suggested that fire and fire-adapted species may have coevolved. Because many of the fire-adapted species are also more flammable and encourage burn, which would in turn facilitate regeneration of these fire-adapted species (Loucks 1970), it has been suggested that higher flammability of these fire-adapted species may also be selected for (Mutch 1970). However, to argue that fire selects for increased flammability of an individual, it would be necessary to show that greater flammability of an individual significantly enhances the likelihood of that individual's being burned, thus resulting in enhanced survival or reproduc-

tion. However, that is not the case. Because the likelihood of *de novo* ignition (e.g., by lightning) of a particular plant is infinitely small, the likelihood of an individual's being burned is less dependent on its own flammability than on the flammability of its immediate surroundings and the overall continuity of flammable individuals in the landscape. Therefore, increased flammability of an individual is unlikely to be selected for (Christensen 1993). The observed higher flammability of fire-adapted species is more likely a secondary effect of herbivory, or other selective forces, selecting for higher contents of secondary compounds that at the same time increase flammability, deter insects, and serve many other purposes (Mooney and Dunn 1970; Christensen 1985).

Community-Level Responses to Fire

Fire, like many disturbances, often resets the successional sequence. However, not all fires are equal: some are stand-replacing fires that completely reset succession, whereas others are surface fires that clear only the understory but leave the canopy intact. Thus, the fire intensities and fire intervals characteristic of a site determine the seral stage most observed on the landscape.

Following the previously discussed observation of higher flammability of fire-adapted species, Mutch (1970) proposed that natural selection might have favored the evolution of flammable characteristics in fire-dependent plant communities. Given the probability that burn is a character expressed at the level of a stand, and not an individual, this hypothesis may seem more likely to hold. Furthermore, there is evidence that fuels in fire-prone areas are more flammable than those in less fire-prone areas (Rundel 1981). However, whether this fire-driven natural selection, if it exists, operates at a community level is very questionable (Agee 1993). Natural selection operates at the level of an individual plant, not the whole plant community: if there are traits less adapted to an environment, it is the individuals with those traits, not the whole community, that are out-competed. Conversely, if there are traits that enhance the chance of survival, these genetic traits are maintained within a species and probably are not exchanged among different species. This means that similar adaptations of different species have most likely evolved independently within each species and not as a whole community. Moreover, paleological studies have shown that individual species have migrated at unique rates over time (Davis 1981; Brubaker 1986) and likely changed associated species (i.e., "belonged" to different communities) throughout time. Therefore, even if there were such a thing as an evolving community, each community (the assembly of migrating "accidental tourists") may not have stayed around long enough to evolve and respond to selective pressures together. Therefore, the community-level aspect of the Mutch hypothesis may not hold either. Nevertheless, the hypothesis may still have some intriguing aspects worth testing if restated for kin selection in pure species stands.

Another aspect of the community-level response to fire is the notion of "direct succession" (Romme and Knight 1981) and "accelerated succession" (Abrams and Scott 1989). Direct succession asserts that where fire is less frequent, the disturbance-free period is more likely to be long enough to allow the establishment of later seral species. Therefore, when fire burns through such areas, these sites would have a higher abundance of seed source for the later seral species than would the more frequently burned sites. Consequently, the later seral species would be established much faster in these sites, and thus the term direct succession. Accelerated succession asserts that disturbance, including fire, kills off the overstory seral species and releases the understory climax species, thus accelerating the successional process. Although both notions seem to describe the same observed results, their hypothesized mechanisms are very different. The mechanisms suggested for direct succession seem more probable for fire and may invite more investigation, whereas the scenarios described by accelerated succession (killing overstory trees and releasing understory trees) are seldom observed in burns and seem more likely a result of other disturbances such as windthrow, insects, and disease.

Biodiversity: Floral Community Structure Responses to Fire Regimes

Because fire has been shown to select for fire-adaptive traits in individual species, different fire regimes may also determine the types of plant characteristics dominant in the community. For example, fire regimes have historically varied widely in their interval between occurrences, dimensions, and fire characteristics, and even varied, though on a lesser scale, in the seasons of occurrence. These variable regimes form a diverse set of environmental characteristics and offer a mechanism for promoting and maintaining biodiversity (Keeley 1991a; Martin and Sapsis 1992). Quoting Martin and Sapsis (1992), "Pyrodiversity promotes biodiversity."

If pyrodiversity promotes biodiversity, would fire suppression reduce pyrodiversity and consequently reduce biodiversity? Ledig (1992) and Husari and Hawk (1994) are among those who answer affirmatively, but, as previously discussed, the extent of fire suppression's influence on pyrodiversity and biodiversity will be determined by the effectiveness of fire-suppression activities.

The effect of fire on ecosystem stability, however, is less agreed upon by ecologists, and this disagreement results mostly from different interpretations of stability and scales of observation. One interpretation of stability has been "the ability to resist change" (Vogl 1970). Vegetative cycles maintained and driven by fires were considered stable from this perspective. Another interpretation of stability has been "less prone to disturbance and significant change" (Christensen 1991), and thus many fire-prone ecosystems were thought to become increasingly unstable over the course of succession. Another emerging line of thought asserts that equilibrium

may not always be possible, and for some ecosystems, disequilibrium is the norm (Sprugel 1991). So for these ecosystems, the important question will not be how fire affects ecosystem stability, but how fire affects ecosystem dynamics (see also "Landscape-Pattern Responses to Fire Regimes" later in this chapter).

Biodiversity: Faunal Responses to Fire

The effects of fire on wildlife vary widely depending on fire intensity, duration, frequency, location, shape and size, season of year, fuel types and amount, soils and other site characteristics, as well as the animal species involved (Bendell 1974; Chandler et al. 1983).

Immediate Responses to Fire

Changes in animal populations immediately after fire derive from emigration and mortality during fire and, in some cases, immigration during and immediately after fire. Immigration and emigration behaviors during fire are largely dependent on the type of animal; animal mortality during fire is largely dependent on the type of fire, the type of animal, and the animal's corresponding behavioral responses to fire.

Invertebrate populations decrease immediately after fire, because the animals or their eggs are killed by the flames or heat and their food supply and shelter are diminished. This is true for both soil and surface insects. In some instances, flying insects are attracted by heat, smoke, or dead or damaged trees; thus the population of such species may increase during and after a fire (Lyon et al. 1978).

Amphibians are relatively vulnerable to fire kill because they are less mobile than other animals and often seek shelter in leaf litter or old logs that are consumed by fire. Typically, however, California's amphibians prefer moist habitats, which generally remain unburned except in the most intense wildfires, and thus show better survivorship (Nichols and Menke 1984).

Reptiles generally exhibit low mortality from fire, because they retreat into burrows or rocks to escape the flames. However, some reptile species habitually hide in litter or under logs and thus are vulnerable to fire-induced mortality (Nichols and Menke 1984).

Birds' responses to fire vary, but they generally show no fear of fire. Some fly ahead of a burn or escape into unburned refuges, some ignore fires, and many insectivorous birds, birds of prey, and other birds are attracted to smoke where insects are abundant (Lyon et al. 1978; Nichols and Menke 1984).

Most small mammals react to fire by hiding or seeking shelter. Small nonburrowing mammals live and hide in flammable shelters above ground and thus suffer heavy direct losses in wildfires (Quinn 1979); small burrowing mammals are much less affected directly by wildfires because of the insulation of the soil (Sampson 1944; Lyon et al. 1978; Quinn 1979). Small rodents are also more likely to exhibit panic behavior and have been observed to run in circles or even back into fires, mak-

ing them more susceptible to mortality (Nichols and Menke 1984).

Larger, more mobile animals usually move calmly and can escape fires more easily. This is especially true for predatory animals that have exceptional mobility. Large, rapidly moving wildfires may still trap and kill escaping animals, although recorded incidence is rare (Lyon et al. 1978; Nichols and Menke 1984).

To summarize, large, intense, rapid-moving wildfires are known to trap and kill animals through heat and suffocation, whereas smaller, less intense fires, such as those typical of the presettlement era fire regimes of the Sierra (Skinner and Chang 1996) and present-day prescribed burns, are easier for wildlife to escape and survive (Sampson 1944; Quinn 1979). Animals that either have greater mobility or find shelter in refuges, such as burrows, unburned islands of vegetation and rocky patches, and riparian zones, have better chances of surviving a fire, whereas animals that exhibit panic or find shelter in tinderbox-type shelters, such as woody litter, logs, and brush piles, are most vulnerable to fire mortality. Although there is certainly some vertebrate mortality during fire, the most common opinion is that direct deaths from fires are rare, and such mortality does not have significant long-term impacts on species' populations (Vogl 1977; Lyon et al. 1978).

Postfire Influences

The postfire influence on wildlife is largely related to fire's role in (1) stimulating germination or sprouting of shrubs, herbaceous plants, or trees that are useful to mammals or birds as food or shelter; (2) making openings in the forest understory or canopy that favor wildlife such as deer; or (3) creating snags or hollow trees that provide shelter (Kilgore 1973; Andrews 1994).

Short-term changes following fire are often detrimental to wildlife, especially after intense wildfires, because fires clear large areas of vegetation and litter, removing food and shelter. However, these detrimental effects last only a few years. Vegetative biomass increases shortly after fire, leading to a greater abundance of food, cover, and structural heterogeneity. In fact, some communities, such as the chaparral, attain the highest levels of productivity, diversity, and carrying capacity for consumer organisms during the early stages of succession (Mooney and Parsons 1973; Lillywhite 1977). As with the case of pyrodiversity's maintaining floral biodiversity, optimal wildlife habitat is created when fire maintains a mosaic of different vegetative age classes. Such mosaics lead to higher spatial diversity of food and habitat and create a maximum amount of ecotone or edge areas, both of which help maintain higher faunal biodiversity (Leopold 1932; Wright and Bailey 1982).

Influence of Animals on Fire Behavior

Animals may influence the probability and intensity of fires through alteration of fuel quantity and structure (Chandler et al. 1983). Insects and beavers can increase the amount of

dead fuel on the ground and therefore increase fire hazards (Flieger 1970; Geiszler et al. 1980; Chandler et al. 1983), whereas browsers and grazers such as deer and livestock may reduce the fuel amount (Campbell 1954). Animals that create nests on trees may also increase the flammability of trees (Rowe 1970; Chandler et al. 1983).

Fuel-Structure Changes in Response to Variations in Fire Regimes

Because photosynthesis produces organic matter on a regular basis, vegetative biomass accumulates with time in ecosystems where net primary production is positive. Different types of biomass fall along a gradient of flammability, and the amount available as fuel depends on the prevailing weather conditions and the intensity of the burn. For example, living biomass (especially that in tree boles) does not dry out easily and does not burn in most lower-intensity forest fires. However, in cases of extended drought, high-intensity fires, or fires that burn for long periods of time, part of this biomass may dry out and contribute to the fuel load. This usually nonfuel biomass also becomes fuel when it dies and is added to the fuel complex on the ground. Empirical evidence suggests that fuels are often high immediately following a stand-replacing or intense fire, then decline, and finally build back up again (Romme 1980; Agee and Huff 1987). However, the stochastic natures of ignition, fire weather, and the causes of tree mortality complicate this tendency (Baker 1989). As a result, fuel buildup is not related to stand chronology in a simple way (Paysen and Cohen 1990).

Fire plays an important role in regulating fuel accumulations; fire can decrease dead fuels by consuming them or increase them by killing live vegetation. Fire also affects the horizontal and vertical continuity of fuels. The importance of fire regulating fuel accumulation is especially significant in short-fire-interval types, where natural decay rates are usually very slow. In such types, frequent fires consume and maintain fuels at lower levels. Periodic surface fires also maintain gaps in vertical fuel continuity and prevent fires from moving up to the crown. In cases where fire suppression has effectively lengthened the fire-return intervals in these surface fire types, fuel buildup is more abundant and more vertically continuous, thus increasing the chance of stand-replacement fires (Brown 1985; van Wagtenonk 1985; Kilgore 1987).

In long-fire-interval types, decay, rather than fire, recycles much of the dry matter. In these ecosystems, heavy fuel accumulations are more commonly found historically (Hemstrom and Franklin 1982), and fire suppression does not affect fuel conditions as much as in the short-interval types. Quite the contrary; there has been a concern that fires under a no-suppression regime in these ecosystem types may increase fuels and lead to higher levels of flammability for longer periods of time than under a suppression regime (Brown 1985; Habeck 1985). Still, studies of the Yellowstone fires of 1988

suggest that although the fuel conditions within any individual stand may not be significantly altered by suppression efforts, the extent and continuity of flammable old-growth stands may have been greater in 1988 than they would have been with no previous fire suppression (Romme and Despain 1989).

In the Sierra Nevada, where both short and slightly longer interval types exist, the relationship between fuel structure and fire regimes may be even more complex. In places where fuel has become more continuous in the shorter-interval, low- and middle-elevation zones, the chances that fires originating in these types could spread uphill into the longer-interval, upper-elevation zones are increased. However, the implications of this possibility are still unknown.

Landscape-Pattern Responses to Fire Regimes

Landscapes can be viewed as a collection of patches undergoing successional change (Pickett and White 1985). The character and pattern of landscapes are determined by (1) the underlying physical template, including larger-scale factors such as climate, elevation, and aspect, and smaller-scale factors such as local topographic features and soil characteristics; (2) the frequency, intensity, and spatial extent of disturbances; and (3) the rate and nature of biotic processes (Cooper 1961; Levin 1978; Urban et al. 1987). The importance of disturbances in shaping landscape patterns is determined by the temporal frequency and spatial scale of the disturbance relative to the biotic processes on the landscape.

Patches formed by biotic processes (e.g., succession) are usually at the scale of a tree-fall gap. As individual trees shed branches or die at different times across the landscape, gaps form and undergo successional processes (Runkle 1981; Brokaw 1985). Hence, if the landscape is less prone to disturbance and therefore dominated by biotic processes, the landscape is usually composed of gap-sized patches that are each at different successional stages.

On the other hand, patches formed by stand-replacing fires could have a size ranging from a few trees to thousands of hectares, depending on the characteristic fire size of the landscape. Within each burn, heterogeneity may result from the local variations in the intensity of the burn (Turner and Romme 1994), but each patch created by similar-intensity burns would be relatively homogeneous in regard to stand characteristics such as stand age and community structure. Therefore, if the landscape is dominated by large, stand-replacing burns, the landscape would consist of coarser grains than would sites dominated by smaller stand-replacing burns, other disturbances (e.g., localized insects and diseases), or biotic processes.

In landscapes characterized by surface fires, however, burning does not create distinct patches as stand-replacing fires do. Instead, the patterns of these landscapes are shaped by an interaction among biotic processes, other localized distur-

bances, and the surface burns: the biotic processes and localized disturbances create heterogeneity in fuel levels and fuel conditions within the landscape, which in turn create a higher level of variation in the local burn conditions. Therefore, the patches shaped by surface burns are usually smaller than those created by stand-replacing fires, but larger than those created by biotic processes. There is also higher heterogeneity in both size and stand structure among these patches created by surface fire.

The surface burns also have a secondary effect on the undercanopy composition and vertical structure of these patches (see "Fuel-Structure Changes in Response to Variations in Fire Regimes," earlier in this chapter). The interesting consequence is that a longer fire-free period in these landscapes would increase the probability of a stand-replacing fire, which would in turn create a coarser-grained landscape.

Because chance factors play more important roles in determining stand composition in early seral stages than in later seral stages (Margalef 1968; Christensen and Peet 1984), if fire recurs at an interval shorter than the time needed for the ecosystem to reach a later seral stage, the seed source may be more variable and thus may result in a wider range of outcomes. It follows that the relative rate of fire return versus the successional process determines ecosystem stability, which in this case means "keeping the same successional trajectory" (Turner et al. 1993).

The size of fire relative to the size of the landscape may also have an effect on landscape stability. The concept of a "shifting mosaic" stability, or dynamic equilibrium, has been asserted by many for ecosystems undergoing frequent disturbances (Heinselman 1978; Bormann and Likens 1979; Kilgore 1987; Clark 1991). Such a concept asserts that whereas individual patches on the landscape may undergo various changes throughout time and the patches may differ greatly from each other at one time, the characteristics of the landscape as a whole change little over time. However, such an argument comes under scrutiny when the sizes of the disturbance and thus the patches become relatively large in comparison to the whole landscape. In this case, the landscape cannot buffer the impacts of the disturbance and shifts out of equilibrium (Christensen et al. 1989; Sprugel 1991). Could this be the case for the present or future Sierra Nevada? We do not have enough evidence to state either way and need more research on this issue.

An interesting aspect of fire is that there is an interaction between its temporal frequency and spatial scale. Because longer fire-free periods allow an increase in both fuel volume and continuity, the relative size of fires generally increases as the average interval between fires lengthens (Heinselman 1981; Baisan and Swetnam 1990). Findings from tree-ring analysis in giant sequoia groves of the Sierra Nevada support this general rule: fires were smaller in size during the higher-fire-frequency period of the Medieval Warm epoch (1000 to 1300 A.D.), whereas fires were more widespread dur-

ing longer interval periods from 500–1000 A.D. and after 1300 A.D. (Swetnam 1993). It has therefore been argued that decreased fire frequency in the Sierra Nevada since 1850 has increased fire size and consequently increased the size of landscape patches (Bonnicksen and Stone 1982; Skinner 1995a; USFS 1995).

Other than the asserted increase in size of landscape patches, landscape-pattern responses to changes in fire regimes are not clear in the Sierra Nevada. Nevertheless, studies from other regions have suggested the complexity of the issue. Baker (1993), for example, studied the responses of landscapes to fire suppression in Minnesota (of variable regime, according to the classification of Kilgore 1987) across several spatial scales. His findings once again supported the importance of variation and scale dependence in fire effects:

- Whereas some characteristics of landscapes respond immediately to fire (e.g., Shannon diversity of patch types), other landscape characteristics (e.g., mean patch size) are slow to respond.
- Variations in the disturbance regime may produce a spatially heterogeneous response, with some parts of the landscape responding immediately after the disturbance, and other parts responding after some time lag.
- This difference in response time becomes more obvious as the scale of observation becomes finer.
- The condition of the landscape at the time of the change in disturbance regime (in this case, fire suppression) can affect the location and timing of a response.
- Even when the disturbance regime is uniform across the landscape (e.g., all fires suppressed), there will still be spatially heterogeneous effects.

To summarize, although Baker was convinced that fire suppression affected the Minnesotan landscape, the spatially heterogeneous character of the responses led him to conclude that it may be difficult to definitively attribute certain vegetation changes to fire suppression (or in general terms, changes in fire regimes).

By shifting down on the temporal scale and looking at the effect of daily burn area on landscape heterogeneity, we further realize the complexity of the issue. Turner and colleagues (1994) found that when burned area exceeded 1,250 ha (3,100 acres) per day in the 1988 Yellowstone fires, the proportions of burned area in different burn severity classes were more fixed, whereas when the area burned per day was smaller, the proportion of burned area in different burn severity classes varied widely.

As an aside, other characteristics of fire besides fire regimes can alter landscape patterns. For example, local variations in microclimate, landform, and fuel beds also influence fire behavior on small spatial scales and contribute significantly to the resulting mosaic of burn intensities, causing a wide varia-

tion in patterns of plant mortality, ash deposition, and soil heating. In addition to variation during fire, postfire climatic patterns may also influence the trajectories of many ecosystem processes. These variations in ecosystem process will eventually determine the ecosystem responses at specific localities, resulting in a complex mosaic of variable patterns (Christensen et al. 1989).

Biogeochemical and Soil Changes after Fire

Although there are studies that suggest prescribed fires had limited effects on soils, nutrient cycling, and hydrologic systems for some ecosystems (e.g., Richter and Ralston 1982), it is commonly believed that fire can have significant effects on soil properties because organic matter located on or close to the soil surface is rapidly combusted. This is particularly true for the studies performed in the Sierra Nevada. Fire has been suggested to alter mineral soil-nutrient concentrations by means of five important mechanisms: (1) Direct volatilization of nutrients reduces the total amount of nutrients in the soil; (2) Mineralization induced by heating increases nutrient availability; (3) Ash deposition and subsequent leaching further add nutrients to the mineral soil; (4) Soil erosion following fires decreases total nutrient amount; and (5) Transportation of nutrients due to the differences in the relative availability of nutrients in the ash versus the mineral soil further influences the relative abundance of nutrients in the mineral soil (Behan 1970; DeBano 1991; Rice 1993). Because intense fires deposit greater quantities of ash than do lighter fires, variations in burning intensities may contribute to the variations in soil-nutrient concentrations following fire.

Because the threshold temperatures for volatilization of nitrogen (N), potassium (K), and sulfur (S) are lower than the glowing combustion temperature (650°C), and all of these nutrients, plus phosphorus (P), have volatilization temperatures lower than the flaming temperatures of woody fuels (1,100°C), these nutrients are readily volatilized and lost from organic matter during combustion (DeBano 1991). However, the amount of nutrient volatilized is related to the intensity of fires, and thus in cooler soil-heating regimes, less nutrient is volatilized (Wells et al. 1979; DeBano 1991). The responses of the different nutrients to heating also indicate that little change is likely to occur more than 4 to 5 cm (about 2 in) below the soil surface, unless a very intense, long-duration fire occurs. Therefore, although volatilization is the most direct response of nutrients to fire, its effects are limited.

Despite the loss of nutrients from volatilization plus the loss due to soil erosion following fires (Behan 1970; Christensen 1995), most nutrients, including phosphorus, potassium, calcium (Ca), and magnesium (Mg), are made more available for use by vegetation by the rapid mineralization induced by fire (Hare 1961; St. John and Rundel 1976; Boerner 1982; Kilgore 1987; DeBano 1991). Such fire-induced mineralization releases nutrients much faster than the decomposition processes, which may require years, or, in some cases,

decades. The increased growth and increased nutrient content in surviving trees following fire may be a direct result of this increased availability of nutrients (Weaver 1947; Hartesveldt 1964; Rundel and Parsons 1980), but it may also be a result of reduced competition due to fire-caused mortality.

Nutrient availability (particularly nitrogen) in the soil can also be increased by the translocation of nutrients downward into the soil during a fire (Wells 1971). For example, although total nitrogen (TN) decreases immediately after burning, available ammonium nitrogen ($\text{NH}_4\text{-N}$) is usually higher in the underlying soil following a fire, because of this transfer mechanism (DeBano 1991). Phosphorus, however, does not appear to be translocated downward in the soil profile as readily as nitrogen compounds. Thus, phosphorus increases mainly in the ash, on or near the soil surface (DeBano 1991).

All these increases in nutrient availability are usually short term. Plant production may increase in the first or second growing season after fire, but soil-nutrient concentration declines to preburn levels with time (Christensen 1995).

Fire may also affect the nitrogen cycle indirectly through vegetation change. For example, Clark (1990) studied fire and its relationship with soil nutrients in a Minnesota forest and suggested that the tendency for species that are more nitrogen-efficient to colonize more mesic sites that burned rarely in the past may have increased the nitrogen content in the litter accordingly. In the Sierra, some chaparral species that follow fire (e.g., California lilac [*Ceanothus* spp.]) are known to fix nitrogen (Riggan et al. 1988). Therefore, given that the plants are not phosphorus limited, they may dominate the site and increase the rate of nitrogen cycling (Delwiche et al. 1965; Kilgore 1973; Christensen 1995).

Fire may also affect nutrient cycling through its effect on microbes. Nitrifying bacteria and endo- and ectomycorrhizae appear to be particularly sensitive to soil heating (Dunn et al. 1985; DeBano 1991). This aspect may be especially important in systems where light burns are typical and ash deposition is lighter (Christensen 1995).

Overall, low-intensity surface fires increase soil pH, stimulate mineralization, facilitate cycling of nutrients, and generally do not increase soil erosion, whereas high-intensity fires may volatilize large amounts of nitrogen and other volatile nutrients, disrupt soil structure, and induce water repellency and erosion (Wells et al. 1979). The trend of increasing intensity in fires, therefore, may have adverse consequences on soil nutrients (Kilgore 1987).

ECOSYSTEM RESPONSES TO FIRE AND VARIATIONS IN FIRE REGIMES

In the Sierra Nevada region, not all ecosystems have been equally studied. For example, most publications concentrate

on the west slope, especially the chaparral and mixed conifer forests, whereas very little of the literature examines the higher elevations and the east slopes. The following is an attempt to synthesize the published materials to date and to provide a more comprehensive picture of what we know today.

Shrublands

Primary Vegetation and Its Historical Relationship with Fire

The major shrubland type found throughout the Sierra is the chaparral, which is characterized by sclerophyllic evergreen woody shrubs. The major types of chaparral found in the Sierra Nevada (Hanes 1977) are the foothill chaparral and the montane chaparral.

The foothill chaparral (chamise chaparral, *Ceanothus* chaparral, scrub oak chaparral, mixed chaparral, and so on) typically occur in the elevation range of 450–1,700 m (1,480–5,580 ft) in the southern Sierra Nevada (Vankat and Major 1978), with different types occurring under different environmental conditions. For the northern Sierra, foothill chaparrals are more widely scattered and are generally restricted to the drier slopes (Hanes 1977). Chamise chaparral is the dominant chaparral type throughout California. It is dominated by chamise (*Adenostoma fasciculatum*) and is associated with hot, xeric sites (south- and west-facing slopes and ridges). *Ceanothus* chaparral is a successional form of chaparral in the southern Sierra but is a climax form in the northern Sierra in the more mesic sites. Its dominant species is buck brush (*Ceanothus cuneatus*). Scrub oak chaparral is also a mesic type, occurring in north-facing slopes below 900 m (3,000 ft) and all slope aspects above 900 m (Hanes 1971) in the southern Sierra, and lies above chamise chaparral in the northern Sierra. Scrub oak (*Quercus dumosa*) is the dominant species, but in the northern parts, interior live oak (*Q. wislizenii* var. *frutescens*) is also abundant. Mixed chaparral consists mainly of chamise, plus tree species such as buckeye (*Aesculus californica*), interior live oak, and canyon oak (*Q. chrysolepis*). It occupies the shady slopes above 900 m in the southern Sierra (Hanes 1977).

Montane chaparral occurs in higher elevations than the foothill chaparral, generally within the same elevation zone as mixed conifers. The dominant species are deer brush (*Ceanothus integerrimus*), manzanita (*Arctostaphylos* spp.), and bush chinquapin (*Castanopsis sempervirens*).

Another type of shrubland found mainly in the northern Sierra is that dominated by Brewer's oak. It generally falls in the upper foothill to lower mixed conifer ecotone and consists mainly of Brewer's oak (*Quercus garryana* var. *breweri*) and deer brush (*Ceanothus integerrimus*).

Although fire-return intervals in chaparral vary among different sites (Skinner and Chang 1996), all the above-mentioned shrublands are believed to be adapted to and intimately related to fire and are suggested to persist where there are recurring fires (Show and Kotok 1924; Skinner 1995b).

Vegetation Responses to Fire

Chaparral is highly flammable and, at the same time, possesses various adaptations to fire. It can sprout massively and quickly from thickened root bases after even severe burning or produce a heavy crop of fire-resistant and fire-stimulated seeds that germinate following fire (Baker et al. 1982; Biswell 1974; Christensen 1985). Vegetative responses on chaparral sites vary and are determined by a complex interaction of temperature, soil moisture, heat duration, depth of burn, and season of burn (Baker et al. 1982; Weatherspoon 1988b; Rogers et al. 1989). Some chaparral shrubs have been shown, through a population model based on size-specific demographic characteristics, to be able to survive more than twenty-three fires (Stohlgren and Rundel 1986). Chamise chaparral regrows more slowly after fire compared to other chaparral types, because of the poor site conditions; montane chaparral responds to fire in a very variable manner (Hanes 1977).

Keeley (1991b, 1992a, 1992b) emphasized the difference between the two types of life-history adaptation to fires: "fire-recruiters" and "fire-persisters." Fire-recruiters, or seeders, establish their seedlings during the first rainy season after fire. Examples of this type are chamise, manzanita, and buck brush. Fire-persisters, or sprouters, are resilient to frequent fires (mostly by vegetative resprouting) but require fire-free periods for recruiting new seedlings. Examples include scrub oak, Christmas berries (*Heteromeles arbutifolia*), holly-leaved cherry (*Prunus ilicifolia*), mountain mahogany (*Cercocarpus betuloides*), and buckthorn (*Rhamnus* spp.). Of the seeders, some *Ceanothus* species are obligate seeders because of their inability to resprout after fire. Zedler and colleagues (1983) found that a seeded chaparral site exposed to a second reburn after one year resulted in the exclusion of buck brush (*Ceanothus* spp.) from the site, providing evidence of the dependence of these species on fire-free intervals.

Keeley (1992 a, 1992b) found that chamise chaparral stands older than sixty years often are declining in vitality. Old stands were characterized by a high proportion of deadwood, little annual growth, and no new seedling development. Various phytotoxic substances and changes in dormancy related to aging (Hadley 1961, as cited by Parker and Kelly 1989) were suggested to account for the loss of vitality and lack of regeneration, and maintenance of vigorous chamise chaparral was suggested to be dependent on fire (Hanes 1971). Although this "decadence" idea has never really been demonstrated, it is partially supported by Rundel and Parsons (1979), who observed that with chamise chaparral, "between 16 and 37 years, shrub senescence increases with no increase in above-ground biomass and a sharp reduction of available photosynthetic surface area." In contrast, species that survive fire solely by vegetative regeneration from the rootcrown (mainly oaks and Christmas berries) were found to be capable, in the absence of fire, of continuously regenerating their canopy with basal sprouts, had very little mortality even in the century-old stands, and did not show signs of decadence. Obligate seeding shrubs that did not initiate new stems from the

rootcrown, on the other hand, had 100% of the stems date back to the years immediately following the last fire and suffered greatest mortality (Keeley 1992a, 1992b).

Differences in vegetation structure and composition may influence fire behavior in ways that maintain different chaparral types within the same ecosystem. Fires (e.g., the Tower fire in 1980, which occurred west of Redding near Whiskeytown Lake) have been observed to burn rapidly across south-facing slopes dominated by either chamise or annual grasses and to skip or burn slowly through the oak/manzanita-dominated shrub fields on the north slopes (Skinner, personal observations). Such microscale variation in fire regimes allowed for the coexistence of these species of very different life-history strategies (Christensen 1985).

Succession after Fire

For the foothill chaparral, postfire community composition closely resembles that of the prefire community (Hanes 1971), suggesting that chaparral is the norm, if not the climax, of the system. Such communities recover quickly from fire and regain dominance soon after (Biswell 1974). However, at the shrub-herb interface in the more open chaparral types, seeders and sprouters seem to follow slightly different successional paths. After fire, herbaceous plants usually appear in abundance, and the shrub seedlings usually have to invade these pioneer herb communities to regain dominance. The seeder seedlings have higher survival rates under competition from the herbaceous species and stand a better chance of invading the areas covered by herb. Sprouter (e.g., chamise) seedlings, on the other hand, do not compete well with the herbs and require intense fire to clear the site of competitors to survive. Such intense fires usually do not occur on the sites originally occupied by herbs but can occur on the sites occupied by seeder chaparral that has successfully excluded the herbs. Once sprouters are established, they are capable of invading neighboring herb-covered sites by vegetative reproduction. Therefore, it is suggested that at the shrub-herb interface, the seeders "pave the way for the sprouting species" (Biswell 1974).

For the montane chaparral, the shrubs face competition not with the herbaceous species, but with the tree species. Therefore, at the forest-shrub interface, it takes intense fires to remove the forests and allow the establishment of chaparral. After initial establishment, frequent fires help maintain the chaparral by killing the trees before they shade out the shrubs, whereas less-rigorous fire regimes allow the trees to regain dominance.

Biodiversity: Floral Community Structure Responses to Fire and Fire Regimes

During postfire chamise chaparral succession, total woody cover, canopy height, litter, and dominance of chamise increased, while species diversity and herbaceous cover decreased in postfire succession (Parsons 1976). Thus, the observed increase in cover and biomass of chamise in Sequoia

National Park appeared to result from reduced fire frequency (Vankat 1970; Vankat and Major 1978).

Ceanothus chaparral that reproduces only from seed has been known to suffer under rare, low-intensity fire regimes. Black sage (*Salvia mellifera*), California buckwheat (*Eriogonum fasciculatum*), and manzanitas (*Arctostaphylos* spp.) can occupy the resulting openings in the canopy, and their abundant deadwood and compact biomass readily allow the spread of low-intensity fires, thereby further limiting buck brush (*Ceanothus* spp.) establishment (Riggan et al. 1988).

For the mixed chaparral, little information about postfire succession is available, but it is believed that reduced fire frequency has increased stand density and decreased species diversity. In some areas near stands of ponderosa pine forest, observed increases in density and cover of forest species are also thought to result from reduced fire frequency (Vankat and Major 1978).

For the montane chaparral, an increase in both shrub and tree cover and density (thus perhaps invasion of tree species) has been observed for some stands in Sequoia National Park. This increase may have resulted from either reduced fire frequency or recovery from sheep grazing (Vankat and Major 1978). However, Wilken (1967) suggested that for the northern Sierra Nevada, such increases in tree cover and density were temporary and occurred only until the fire-susceptible montane chaparral was burned again.

Fire has been associated with the maintenance of species diversity in nearly all shrubland types (Christensen 1985). In general, species richness and equability tend to be highest immediately following fire. Shortly after, both species richness and equability decline (Christensen et al. 1981). However, when the seed pool is included, species richness changes very little during the fire cycle in many shrublands. In a study of chaparral stands that have been unburned for 56 to 120 years, Keeley (1992a) found that although successional changes in community composition were evident, there was no indication of a decline in species diversity. In addition, he also identified two reproductive modes in chaparral shrubs in response to fire (see preceding discussion) that required very different durations of fire-free intervals for seedling establishment and suggested that both regimes were necessary for the maintenance of both adaptive traits. Also, chaparral communities, unlike other vegetation types, have been found to consist of some fire-adapted herbaceous species that occur only in the burned patches (Sweeney 1968). Therefore, no single, constant fire regime will meet habitat needs of all species. It is thus suggested that to maintain maximum biodiversity, a mosaic of variable fire regimes is required (Keeley 1991a; Husari and Hawk 1994).

Biodiversity: Faunal Responses to Fire

Few quantitative studies of chaparral fire effects on wildlife have been of sufficient duration to assess fully the long-term consequences. General patterns of faunal response to fire have been observed, and these were discussed earlier. Specific

species responses to fire in the chaparral are noted as follows:

Very few data concerning direct effects of chaparral fire on invertebrates are available, except that, generally, mortality of soil invertebrates is low and that certain insects, such as the smoke fly (*Microsamia occidentalis*), are known to be attracted to the smoke of fire in other localities (Nichols and Menke 1984).

Some vertebrate animal species decrease whereas others increase following a burn, but no species is totally eliminated, nor is there any apparent diminution of total life on a burn after plant growth resumes (Lawrence 1966).

Mortality of reptiles in chaparral fires is generally low. Several snake tracks and a live king snake have been found on a fresh chaparral wildfire burn (Tratz and Vogl 1977). Legless lizards and other reptile species that habitually hide in litter or under logs are more directly affected by fire (Nichols and Menke 1984).

Birds seem to be less directly affected by fire in the chaparral, as there are no reported instances of bird deaths attributed directly to controlled burning in this vegetation type (Nichols and Menke 1984). However, birds that normally exhibit a strong preference for chaparral habitat were observed to decrease in numbers in the years immediately following the burn. Conversely, some birds that normally prefer grassland or oak woodland increased in number (Lawrence 1966). Such changes in relative species abundance are less likely a result of fire-induced mortality but more likely a result of migration due to habitat preference. Overall, fire resulted in an increase in density of nesting birds.

Most small mammals are not found in the chaparral immediately after a wildfire. Wood rats and brush rabbits are vulnerable to fire because they often exhibit panicked behavior described previously, whereas dusky-footed wood rats (*Neotoma fuscipes*) and some other small mammals are also vulnerable to fire-caused mortality because they retreat to their woody shelters when frightened (Nichols and Menke 1984). Kangaroo rats are the only abundant rodent species in chaparral immediately after a wildfire. In the second and third years after a fire, the number of species and population densities of rodents increase, and such trends continue for at least five years, and probably much longer (Quinn 1979).

Larger mammals such as mule deer (*Odocoileus hemionus*) are more mobile and generally have little trouble fleeing chaparral fires, but large, rapidly moving wildfires have been known to trap and kill deer. Predatory, fur-bearing animals such as foxes (*Vulpes* spp. and *Urocyon* spp.) and coyotes (*Canis latrans*) are especially mobile animals that can flee from most fires, and there are no reports of direct kills by fire for these species (Sampson 1944). Howard and colleagues (1959) have even observed a bobcat (*Lynx rufus*) trotting away from a controlled burn in a leisurely fashion.

As with birds, mammals that normally exhibit a strong preference for chaparral habitats substantially decreased in numbers in the years following the burn. None of the small

mammals increased in numbers after the burn, but some of the larger predators, such as the coyote and badger, immigrated into the stand during the months following the fire (Lawrence 1966).

As is the case in pyrodiversity maintaining plant biodiversity, it has been suggested that the number of species and the population density of small mammals would be maximized by breaking up chaparral into small areas of different ages, maximizing ecotones, emphasizing physical heterogeneity, and leaving a few areas of unburned brush (Quinn 1979).

Landscape-Pattern Responses to Fire Regimes

Fire in itself is known to cause fragmentation and clumpiness of chaparral vegetation cover at the population level. For example, fire-induced mortality tended to move a chaparral stand toward a more clumped distribution, after which seedling establishment in the patchy empty spots and subsequent self-thinning eventually restored the pattern toward regular spacing (Stohlgren et al. 1984; Keeley 1992a).

Regular fire regimes also increase the clumpiness in shrubland landscape by forming smaller patches than would be formed during longer fire-free periods. Analyzing historical accounts of some chaparral burns in the San Gabriel Mountains, Minnich (1987) suggested that because of frequent burning, chaparral in southern California watersheds before 1900 comprised patches smaller than those seen today. Because these fire-created patches would constrain later burns, the patchiness has tended to persist over time. Irregular fire behavior and development of secondary burns from smoldering or from embers moving long distances beyond the fire zone were also suggested to have added to the complexity of vegetation fragmentation (Minnich 1987, 1989). In Baja California, where regular fire regimes still persist, fires are also recorded as being generally medium-sized fires that form an interlocking mosaic and burn at varied intensities (Minnich 1983).

Conversely, longer fire intervals are expected to push the chaparral landscape toward a more uniform distribution. Minnich (1987), for example, noted that shrubland fuels in the San Gabriel Mountains are more continuous than they were decades ago. Similar findings have been recorded for the shrublands of Sequoia National Park, where instead of a mosaic of different successional stands, old-age stands were found to be dominant across the landscape, and reduced fire frequency was suggested to be the cause (Vankat 1970; Parsons 1976; Vankat and Major 1978).

As a consequence of these continuous fuels, the few fires escaping control under the most extreme weather conditions (usually strong Santa Ana winds) have turned into enormous, high-intensity conflagrations and have resulted in even more spatially continuous landscapes (Minnich 1983, 1987, 1989). A study on fire history of chaparral in the Los Padres National Forests also indicated that fires are getting larger and less scattered (Radtke et al. 1981).

Biogeochemical and Soil Changes after Fire

In general, nutrient availability in the chaparral has been found to be higher immediately following fire (Christensen and Muller 1975; Westman et al. 1981). In a study on nutrient changes after a prescribed chaparral burn, only two (N and K) of the six nutrients studied (N, P, K, Na, Mg, and Ca) showed measurable losses (DeBano and Conrad 1978).

In response to this increased availability of nutrients, chaparral species not only grew more quickly (chamise chaparral, Christensen and Muller 1975), but also increased their consumption levels of nitrogen, phosphorus, and potassium beyond their immediate metabolic requirements (chamise and *Ceanothus* chaparral, Rundel and Parsons 1980). This ability to take up extra amounts of nutrients and store them for future use is an important fire adaptation in plants on low-nutrient soil (Rundel and Parsons 1980).

In addition to being available after fire, soil nutrient concentrations in the chaparral have also been found to be considerably more variable after than before fire (Christensen and Muller 1975). This variation arises because of the previously discussed local variations in fire intensity and uneven distribution of ash.

During the course of chaparral succession after fire, nutrient availability continued to change. Nitrogen availability increased with increasing stand age up to fifty to sixty years. Beyond sixty years, nitrogen availability declined. Phosphorus availability decreased logarithmically with increasing age. Declining nitrogen availability in older stands was attributed to declining total soil nitrogen and a decline in the fraction available, whereas decline in the phosphorus availability was attributed to a decline in the fraction available (Marion and Black 1988).

Nutrient concentrations in the plants also changed over this course. Chamise and buck brush (*Ceanothus* spp.) stands studied in Sequoia National Park showed a rapid decline in foliage concentrations of nitrogen during the first six years after fire, followed by a more gradual decline over succeeding years. Phosphorus concentrations showed a similar early decline but increased in older-age stands. A sharp increase in above-ground nutrients per unit of chamise canopy was found for the first sixteen years of growth, before a plateau was reached. Frequent chaparral fires, such as those observed for the presettlement era, were suggested to promote fire cycling of nutrients at intervals consistent with periods when nutrient availability became limiting (Rundel and Parsons 1980).

The aspects of fire-biogeochemical-plant interactions in chaparral were also discussed by Riggan and colleagues (1988). They suggested that copious nitrogen volatilization during burning is promoted by high concentration of nitrogen in the foliage and fine woody biomass of buck brush and heavy leaf litter of scrub oak (*Quercus dumosa*). They accordingly concluded that communities most prone to severe fires also accumulated and cycled nitrogen and phosphorus rapidly.

Foothill Woodlands

Primary Vegetation and Its Historical Relationship with Fire

Foothill woodlands can be viewed as a group of variable communities geographically placed between grasslands or shrublands and the montane forests (Griffin 1977). In the Sierra, the oak foothill woodlands (especially the interior live oak woodlands) are closely related to the chaparral (Griffin 1977). A detailed description of the ecological relationships between foothill woodland and chaparral communities can be found in Rundel (1981).

Three major types of foothill woodlands are found in the Sierra Nevada: blue oak, live oak, and black oak.

The blue oak foothill woodland is scattered throughout the western portion of the Sierra Nevada at 150–910 m (500–3,000 ft) (McDonald 1990a). Blue oak (*Quercus douglasii*) is dominant, with manzanita (*Arctostaphylos viscida*) and buckthorn (*Rhamnus crocea*) commonly seen. Soil beneath blue oak stands is found to be significantly lower in total nitrogen, total phosphorus, and organic matter content than adjacent sites with mixed evergreen woodland (Vankat and Major 1978).

The live oak foothill woodland usually occurs above the blue oak woodlands, especially on the north-facing slopes. Interior live oak (*Quercus wislizenii*) is the dominant species, and gray pine (*Pinus sabiniana*) is common. A highly variable mixture of shrubs (e.g., mountain mahogany [*Cercocarpus betuloides*]) and trees (e.g., buckeye [*Aesculus californica*], canyon oak [*Quercus chrysolepis*]) is found primarily on mesic north slopes and at higher elevations (Parsons 1981).

Some live oaks occur in riparian areas, and fires frequently go out or reduce their intensity dramatically when they reach these wetter areas. Most associated plant species have above-ground parts that are susceptible to damage by fire. However, most species quickly resprout after fire (Andrews 1994).

The California black oak woodlands occur on the west slopes of the Sierra from near Lassen Peak to Kings Canyon. Their elevation zones range from 460–1,980 m (1,500–6,500 ft) in the northern Sierra to 1,220–2,380 m (4,000–7,800 ft) in the southern Sierra (McDonald 1990b). California black oak (*Quercus kelloggii*) is the dominant species and is commonly associated with ponderosa pine (*Pinus ponderosa*). Burning by Native Americans has been considered a primary factor in maintenance of black oak stands (Anderson 1993). Without such disturbance, it has been suggested that black oak will eventually be crowded out of most suitable sites and will retreat to scattered remnants in mixed conifer forests (McDonald 1990b).

Vegetation Responses to Fire

Oaks are highly variable in their response and resistance to fire because of differences in their bark thickness, tree structure, and sprouting response. Individual survival is also influenced by understory composition and the degree of fire intensity (Husari and Hawk 1994). Plumb (1980) and Plumb

and Gomez (1983) offer more detailed accounts of the different responses of various oak species to fire.

Blue oak is thought to benefit from fires. Although acorn survival and germination are thought to be negatively affected by fire, the positive association between blue oak ages and fire dates suggests a temporal concentration of postfire sprouting. The low rate of recruitment since the 1940s may be partly due to fire suppression (McClaran and Bartolome 1989).

In contrast, fires are damaging to live oak vegetation, because most associated species are susceptible to fire damage. In particular, canyon oak (*Q. chrysolepis*), interior live oak (*Q. wislizenii*), sycamore (*Platanus* spp.), and cottonwood (*Populus* spp.) have fairly thin bark and are easily top killed by fire. Fire is also known to cause basal wounds and development of hollow trees, which structurally weaken trees, leaving them susceptible to windthrow. However, most species resprout quickly after fire (Andrews 1994).

Succession after Fire

There is very little information about succession after fire in oak stands. In lowland live oak stands, light surface fires may trigger succession through sprouting from resident vegetation in the lower-canopy layers. For succession to proceed from outside seed sources, less-frequent, high-intensity fires are required (Andrews 1994).

Biodiversity and Community-Structure Responses to Fire

For the blue oak stands, livestock grazing has been proposed as the cause of their increase in density. Livestock grazing removes herbaceous competition for blue oak seedlings and decreases fuel levels, so that fires are less intense and thus less detrimental (Vankat and Major 1978).

In lowland live oak woodlands, stand density is controlled by fire frequency, because live oaks are found at their highest density in areas without recent fire (Davis et al. 1988). It is thus believed that interior live oaks and some other woody species have increased cover and density as a result of reduced fire frequency. Before European settlement, some of the stands may have been as open as today's blue oak woodland (Vankat and Major 1978).

Fire also influences faunal diversity in the lowland live oak stands. For example, the basal wounds and hollow trees that can result from fire are thought to provide important habitats for some animals. On the other hand, because riparian live oak stands are less intensely burned, they may also serve as a critical refuge during wildfire (Andrews 1994).

Fuel-Structure Changes in Response to Different Fire Regimes

The Sequoia National Park fire atlas, which maps all fires that burned more than 4 ha (10 acres) since 1920, shows that much of the foothill zone of Sequoia National Park has not burned in at least sixty years. Buildup in both live and dead fuel is

thought to indicate a serious overabundance of "dense, over-mature, highly flammable brush" (Parsons 1981). Loss of distinct age-class boundaries as a result of this longer fire-free period also deprives the system of effective firebreaks and adds to the continuity of the fuel (Parsons 1981).

Biogeochemical and Soil Changes after Fire

Fire running upslope from lowland oak stands is thought to affect runoff and sedimentation. In particular, high-intensity fires are thought to cause water-repellent soil upslope that reduces permeability and increases runoff and erosion (Andrews 1994).

Ponderosa Pine Forests

Primary Vegetation and Its Historical Relationship with Fire

Ponderosa pine forests dominate the xeric sites on the lower-elevation west slopes of the Sierra Nevada, from about 300 to 610 m (1,000 to 2,000 ft) in the north, and from 1,615 to 2,225 m (5,300 to 7,300 ft) in the south (Burns 1983). Their range of occurrence also differs on different aspects, starting below 1,220 m (4,000 ft) on north-facing slopes, and 1,830–2,440 m (6,000–8,000 ft) on south-facing slopes. Ponderosa pines (*Pinus ponderosa*) are dominant, and sugar pine (*P. lambertiana*) and incense cedar (*Libocedrus decurrens*) are commonly found associates. At the upper margin, ponderosa pines are often replaced by Jeffrey pines (*P. jeffreyi*) (Rundel et al. 1977).

Historically, surface fires were most common in this type, with occasional flare-ups occurring in brush patches. Crown fires were unlikely in most stands (Husari 1980). Long, loosely packed pine needles and herbaceous species maintained frequent and mild surface burns. These fires created openings for pine seedling establishment, thus maintaining its persistence. These fires also thinned saplings and maintained the relatively open understories documented by early settlers (Muir 1894; Sudworth 1900; Leiberg 1902; Cooper 1961). The recent increase in understory density has been attributed to the current longer fire intervals, which in turn have been suggested to result largely from fire suppression.

Vegetation Responses to Fire

Ponderosa pine is fire-adapted in all stages of its life history and is especially well adapted to light, regular surface fires (Rundel et al. 1977). The seeds prefer openings with mineral soil usually prepared by fire for seedbed. For the seedlings and young trees, early development of insulative bark, shielded meristems, high moisture content in living needles, and rapid extension of taproots reduce their mortality from fire (Husari 1980). For the mature trees, thick bark, deep roots, and low-flammability crown structures help them survive most fires (Starker 1934).

Generally, well-spaced ponderosa pine seedlings and saplings are able to survive low-severity fires, as are pole-sized

and mature trees. Moderate- to high-severity fires, however, kill pole-sized and smaller trees, and crown fires kill mature trees. The main cause of their mortality following fire is crown scorch rather than damage to the cambium or roots. Crown scorching has also been noted to make pines more vulnerable to bark-beetle infestation, thus adding to the indirect mortality caused by fire (Andrews 1994). Fortunately for the pine stands, self-pruning of lower branches and open crown structure reduce the chance of crown fires, and such incidences rarely have been observed in this vegetation type historically (Husari 1980).

Succession after Fire

Following a stand-replacement fire, the successional sequence in these types proceeds from herbaceous species to shrub and hardwood, and finally ponderosa pine stages. Occasional sugar pines and incense cedars are found with the ponderosa pines when seed sources are available. The lower-intensity surface fire typical of this type generally does not completely reset succession but, rather, thins the understory and allows pine establishment in slightly more intensely burned small patches where fuel loads are locally higher.

Biodiversity: Floral Community Structure Responses to Fire and Fire Regimes

Under the presettlement fire regime of frequent, low-intensity fires, the ponderosa pine forest canopies were kept open with spaced trees of an uneven-aged structure (Weaver 1943, 1967; Husari 1980; Andrews 1994). Herbaceous species were much more common, and except for brush fields, shrubs in the forest were rarer and younger. Multilayered stands existed but were less extensive than today (Andrews 1994).

At present, the understories of ponderosa pine forests are dense in many places with unthinned pine seedlings and increased hardwood and shrub cover. The resulting high-intensity crown fires shift species dominance to hardwoods, because these stand-replacing fires kill all conifers and the above-ground portion of hardwoods, but hardwoods sprout vigorously after fire and capture the site. It has been suggested that such early seral vegetation will dominate the site for some time after fire (Andrews 1994).

Following large, severe fires, shrubs may also occupy sites for very long periods before the pine can again attain a superior position (Husari 1980; Andrews 1994). But instead of giving way to pine, these brush fields may also maintain a continual cycle of fire, therefore maintaining itself (Andrews 1994). The exclusion of fire has also been noted to allow the establishment of brush, usually manzanita (Husari 1980).

Biodiversity: Faunal Responses to Fire

Bock and Bock (1983) studied bird and deer mouse populations in response to a prescribed burn in a ponderosa pine forest. They found that total breeding birds were more abundant on burned than on unburned sites during the first postfire summer. In the second summer, however, one of the four

burned sites had fewer birds than its control, whereas the remaining three paired sites did not differ. Although species composition of burned versus control areas remained almost the same through both years, seven species were more abundant on the burns during the first postfire nesting season, whereas none was more common on control plots. In the second summer, however, only one species was more abundant on the burns, whereas two were more common on the controls. Deer mice were also more abundant on the burned sites during the first summer, whereas there was no difference between burned and unburned sites during the second summer. It seems that for the birds and rodents, the population change after fire is short term.

Fuel-Structure Changes in Response to Different Fire Regimes

Fuel loads from the ponderosa pines are relatively light (Blonski 1980, as cited by Husari 1980) and are known to have carried frequent, light surface fires under the presettlement regimes. But with fire exclusion, large amounts of pine needles and small branches have accumulated over time and created a bed of fine fuels with large surface-to-volume ratios that often lead to fast-moving, intense fires. The dense understories also increase the chance of crown fires.

There has also been an increase in the accumulation of downed logs and snags in these forests as a result of the increased mortality from recent, severe fires, from insects, and from stressed, overcrowded pine stands. Such mortality increases the debris and the vertical and horizontal structural development of fuels in ponderosa pine stands. As a consequence, large (4,000 ha [10,000 acres] or more), high-severity fires, once rare, have become commonplace in recent years, as have many small (less than 4 ha [10 acres]), high-intensity fires (Andrews 1994).

Landscape-Pattern Responses to Fire Regimes

Ponderosa pine stands are a classic example of how gap-sized local variation shapes the heterogeneity of the landscape. Within a stand, single mature trees or groups of trees are killed by insects, disease, lightning, or windthrow. These dead trees form gap-sized patches of concentrated fuel in the landscape. When a characteristic low-intensity surface fire burns through the area, these "tinderboxes" result in patches of higher-intensity burns, open up the ground, and allow young pines to germinate. In the remaining areas where mature trees still stand, heavy accumulations of flammable needles, cones, and bark scales build up, and when the next fire comes through, it burns more intensely under these canopies than in the openings, thereby killing seedlings and saplings under their canopies. The young pines in the gap-sized openings, however, survive the event, because the small accumulation of needles in the openings will not support a surface fire. Hence, until the pines are large enough to build up fuels under themselves, fires are not intense enough to kill them, and by the time the pines do create such heavy fuels, many of them are also large

enough to withstand the surface fires (Kilgore 1973; Husari and Hawk 1994). The periodic fires typical of the area in the presettlement era are thought to support this process and thereby maintain a mosaic of different-aged patches.

At present, because of the increased continuity of fuels, high-intensity fires typically kill all vegetation over large to very large areas, increasing the homogeneity and patch sizes in these forests (Andrews 1994).

Mixed Conifer Forests

Primary Vegetation and Its Historical Relationship with Fire

Mixed conifer forests are largely restricted to the west slope of the Sierra Nevada at middle elevation, from about 760 to 1,400 m (2,500 to 4,600 ft) in the north, and from 915 to 3,050 m (3,000 to 10,000 ft) in the south (Eyre 1980). Dominant species include ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), incense cedar (*Libocedrus decurrens*), white fir (*Abies concolor*), California black oak (*Quercus kelloggii*), and Douglas fir (*Pseudotsuga menziesii*). Jeffrey pine (*Pinus jeffreyi*), red fir (*A. magnifica*), lodgepole pine (*P. contorta*), and patches of giant sequoia (*Sequoiadendron giganteum*) are also found (Eyre 1980; Tappeiner 1980). The proportion of each species in different stands is highly variable (Eyre 1980) and is thought to be determined by elevation, precipitation, and fire frequency: more frequent fire favors a higher percentage of fire-adapted ponderosa and Jeffrey pines; less frequent fire favors the less fire-tolerant white fir and incense cedar. Fire scar analysis indicates that the majority of this forest type was historically subject to low- to moderate-severity fires (Show and Kotok 1925; Wagener 1961). There was a great deal of variation in fire intensity and effect within similar sites, even within a single fire (Stephenson et al. 1991).

Vegetation Responses to Fire

Weatherspoon (1988a) discussed the relative fire tolerance of the various species in the mixed conifer forests. Sugar pine, Douglas fir, red fir, white fir, and incense cedar typically survive less crown scorch as a percentage of crown volume than do ponderosa and Jeffrey pines. A study of mortality in four species in the mixed conifer forest showed that ponderosa pine is able to survive longer flame lengths than sugar pine, incense cedar, and white fir (van Wagtenonk 1983).

The various species in the mixed conifer forests also responded differently to the various burning conditions in terms of seedling establishment. Ponderosa pine and Jeffrey pine seedlings benefit from high-intensity surface burns that open up the understory (Vlamis et al. 1956; Bock and Bock 1969), whereas sugar pine and giant sequoia are known to require patches of stand-replacing burns that create canopy gaps (Stephenson et al. 1991). Kilgore and Biswell (1971), for example, found the largest number of sequoia seedlings in places that experienced the most intense fire, and vice versa. Both white fir and red fir germination also seem to be favored by

fire (Agee and Biswell 1969; Laacke and Fiske 1983), although both firs also do well without fire (Kilgore 1973; Taylor 1990a).

Although the fewest numbers of shrubs were found in patches that had gone through intense fires (Kilgore and Biswell 1971), deer brush (*Ceanothus* spp.) and manzanita (*Arctostaphylos*) species are known to be stimulated to germinate by fire and can persist only within canopy gaps (Andrews 1994). Although there is no totally fire-dependent herbaceous species associated with the conifer forests in California (Sweeney 1969), most herbs are known to prefer more open habitats and may be affected by pine litter. Several species of herbs have been found to increase in coverage or frequency following burns in the giant sequoia-mixed conifer forest (Kilgore 1973).

Denser stands that have resulted from the exclusion of fire cause more competition for available water and, therefore, greater moisture stress. Extensive mortality thus results from droughts, either directly from drought stress or from stress-induced bark-beetle outbreaks (Weatherspoon et al. 1992).

Succession after Fire

During the first few years after fire, a herbaceous layer develops but is eventually shaded out by the growing woody layer. Among the many tree species in the mixed conifer zone, the pines and sequoia benefit most from postfire conditions and dominate the site in the years following fire. Although white fir and incense cedar also benefit from improved seedbeds after fire, their seedlings do not grow as fast as pine and sequoia seedlings do and thus are suppressed in the early seral stages. However, these two species are more shade tolerant and are known to be released at the chance of a gap formation, even after many years, and thus benefit from longer fire-free periods. Under presettlement conditions, forest succession was influenced by generally low-intensity fire with inclusions of localized patches of vegetation that were either completely burned or unburned (McBride and Sugihara 1990).

Biodiversity: Floral Community Structure Responses to Fire and Fire Regimes

Fire affects the character of the mixed conifer forests by effectively decreasing woody plant density and influencing species composition (Rundel et al. 1977). The frequency of fire determines the percentage of fir in these forests (Agee et al. 1978; Husari and Hawk 1994): frequent surface fire eliminates the less fire-resistant white fir and incense cedar seedlings and favors the more fire-resistant but shade-intolerant black oak and pine seedlings, whereas longer fire-free periods allow the shade-tolerant fir to dominate the canopy with time (Sellers 1970; Lyon et al. 1978). White firs in Sequoia National Park have been observed to increase in density during dates that correspond to the onset of reduced fire frequency (Vankat and Major 1978). Other observations of present white fir dominance in the understory are abundant (Parsons and DeBenedetti 1979; Bonnicksen and Stone 1982; van Wagtenonk 1985; Weatherspoon et al. 1992). In addition to pine, sequoias

also may be severely affected by fire-suppression policies (Parsons and DeBenedetti 1979). Periodic fire has been thought to maintain a mix of fire-tolerant and fire-intolerant conifers (Husari 1980), whereas fire exclusion is thought to be leading toward fir dominance. A prolonged period with intense, stand-destroying fires is thought to convert the habitat to a montane chaparral type (Husari 1980).

Before European settlement, these ecosystems were probably more open than they are today (Weaver 1974) and sufficiently open to support a well-developed herbaceous-layer community of forbs, perennial bunchgrasses, and dispersed shrubs. These understory components are now lost from the system and impossible to describe in detail from available historical data. Shrubs are also thought to have been present in the understory but were patchy and variable in the percentage of ground covered (Andrews 1994). Vankat and Major (1978), for example, documented a decrease in some shrub species, especially manzanita (*Arctostaphylos viscida*), in Sequoia National Park following European settlement. They suggested that this decrease may be a result of decreased germination of their fire-stimulated seeds.

Fire also affects the forest structure of the mixed conifer zone. Periodic fire thins the trees, and thus fire suppression has been thought to be the reason for the observed increase in the density of small trees (Parsons and DeBenedetti 1979). Periodic fires before European settlement were also thought to maintain uneven-aged stands (Weaver 1974), which were dominated by larger, older trees as compared with today's predominant smaller, younger trees (Andrews 1994). Fire also changes forest structure by altering the species composition. For example, the fire-sensitive tree species, especially white fir, have been observed to have increased dramatically in abundance, particularly in small to medium size classes. The resulting multiple-canopy stands consisting largely of these shade-tolerant species are now common but are thought to have been much less common previously, except in the cool and moist extremes of the type (Parsons and DeBenedetti 1979; Bonnicksen and Stone 1982; van Wagtenonk 1985). Consequently, stands have become more complex vertically but less complex and more homogeneous in terms of aerial arrangement (Weatherspoon et al. 1992).

Biodiversity: Faunal Responses to Fire

The findings of the few studies on faunal responses to fire in the mixed conifer forests show that deer populations have increased after burns (Lawrence and Biswell 1972); bird populations also have increased in numbers or biomass following fire (Lawrence 1966; Bock and Lynch 1970), but elimination of saplings less than 3.5 m (11.5 ft) tall did not make major changes in species composition of a breeding-bird population (Kilgore 1971a).

There is no evidence to suggest that the overall wildlife species richness before European settlement was markedly different from that currently found in the mixed forest. However, it is likely that the species' relative abundance has

changed (Andrews 1994). Also, the shift from open- to closed-canopy forests with a more complex vertical structure has probably benefited wildlife associated with closed forests over those associated with open forests, such as chickadees. Spotted owls may have been affected by this change in forest structure too, because the increased vertical stand structure could close their flyways and affect their hunting success (Andrews 1994).

Fuel-Structure Changes in Response to Different Fire Regimes

The mixed conifer forests before European settlement were thought to be uneven-aged, patchy, broken, and varied in cover type. This discontinuous structure made the forest fairly immune to extensive, stand-replacing crown fires. Although local crown fires may have occurred, they probably extended at most over a few hundred acres (Show and Kotok 1924).

Because of the lack of periodic fires, fuels on the forest floor (including coarse, woody debris) have accumulated over time (Parsons and DeBenedetti 1979). Increased mortality due to drought stress (see earlier discussion) has also added greatly to fuel loads. The increase in snags and large woody fuels is likely to increase fire spotting and make fires harder to suppress. Because pine fuels are easier to burn and reduce, the species-composition shift from ponderosa and sugar pines to a white fir-incense cedar mix makes the system less readily and thus less frequently burned (Agee et al. 1978), therefore further adding to fuel accumulation. Opening of the canopy as a result of tree mortality also results in warmer and drier fuels (Countryman 1955), which ignite more easily and support faster-spreading fires (Weatherspoon et al. 1992).

In addition to changes in fuel amount, fuel structure has also changed following the change in species composition. Increased prevalence of white fir in the understory has created multilayered structure and fuel ladders, linking surface fuels to upper canopy layers. In addition to having increased the vertical continuity of fuels, the lack of periodic fire has also resulted in a more homogeneous landscape and horizontally continuous fuel. This increase in both the horizontal and vertical continuity of fuels, combined with the greater quantity of fuels, has substantially augmented the probability of large-scale, catastrophic fires (Kilgore 1973; Kilgore and Sando 1975; van Wagtenonk 1985).

Landscape-Pattern Responses to Fire Regimes

Present fire regimes within the mixed conifer forests are characterized by infrequent, high-intensity surface fires or infrequent, stand-replacement fires. These fires range from medium to very high severity. With present fire recurrence rates, it is thought that stands will generally convert to an "infrequent, very high intensity fire regime with uniformly severe effects" (Husari and Hawk 1994).

Before European settlement, fire regimes were characterized by periodic low-intensity surface fires. Because these low-intensity fires were very much influenced by local variables,

they varied in intensity and effect even within similar sites (Lindenmuth 1960; Sweeney and Biswell 1961). These fires also had large fluctuations in the timing of fire frequency and set various scenarios for vegetation establishment, composition, and survival. As a consequence, each patch bore a distinct aggregation of trees that developed successionally as an independent entity, creating a complex mosaic of aggregations with patch sizes typically 0.2 to 2 ha (.5 to 5 acres) (Bonnicksen and Stone 1982; McBride and Sugihara 1990; Stephenson et al. 1991). Fire patterns similar to those ascribed to the presettlement period are currently found in the ponderosa pine and mixed conifer forests of the Sierra San Pedro de Martir National Park, Baja Norte, Mexico, where historical fire patterns still persist (Barbour et al. 1994; Minnich et al. 1995).

Toth and others (in Andrews 1994) agreed with Bonnicksen and Minnich's assertion that the presettlement mixed conifer landscapes had a fine-grained patch structure, in which small patches of single-storied, even-aged, and uniformly sized stands shifted in time across the landscape. They noted that these small patches were typical on flat terrain and most aspects. However, they asserted that the presettlement mixed conifer landscapes also had coarser-grained seral stage patterns (larger patches). These larger patches, though scarce, were thought to be found in areas of catastrophic fires or with longer fire-return intervals, particularly on moister north and east aspects. Such big patch patterns were also thought to be more uniform in nature and to have initially formed a more coarse-grained mosaic. However, such homogeneity in the landscape would have persisted only until both age and localized disturbance events, such as insects, diseases, blow-downs, and other disturbances, blended these areas into the overall landscape pattern of finer grains. Because of the general big tree character, they also asserted that age-class distinctions would have blurred at the landscape level, so that the fire-induced vegetation pattern in the presettlement landscape appeared "relatively uniform on a broad scale."

At present, the landscape pattern is changing from the fine-grained, open, presettlement forest, which generally contained large numbers of large-diameter, older trees, toward a patchy, coarse-grained mosaic of openings and more closed-canopy forest, with a much larger proportion of the landscape in younger stands (Andrews 1994).

Heterogeneity is a relative term, and it is useful to note that earlier discussions of landscape heterogeneity are based on the comparison of presettlement and post-settlement Sierran landscapes. Even the relatively heterogeneous presettlement landscape could be seen as relatively homogeneous: Parker (1984), for example, compared Yosemite forests to those in Glacier National Park and concluded that the surface fire regime promoted "uniformity of structure and compositional dynamics" in Yosemite forests, whereas a broader spectrum of disturbance regimes in Glacier forests promoted "heterogeneity of structure and complex patterns of compositional dynamics."

Biogeochemical and Soil Changes after Fire

Fire plays a significant role in recycling various mineral nutrients back to the soil in all Sierran conifer forests. Light burns typical of the presettlement mixed conifer forests are thought to increase soil pH, stimulate nitrification, and increase available phosphorus, potassium, calcium, and magnesium through ash deposition (Hare 1961). The effects of burning on soil nitrogen, though, are more complex: some studies show a loss of nitrogen from the forest floor (Knight 1966), while others report a net gain (Klemmedson et al. 1963).

However, because the exclusion of fire has resulted in a change in fuel structure, when a wildfire occurs in dry weather, it is much more likely to develop crown fire behavior. This type of fire behavior has been thought to "seriously disrupt energy and nutrient cycle stability" (Agee et al. 1978). The increased amount of large materials (downed logs and snags) has also raised the concern of "greater heating damage to soils" because of these localized concentrations of fuels (Weatherspoon et al. 1992).

Upper Montane Fir Forests

Primary Vegetation and Its Historical Relationship with Fire

Two major species of firs are present in this type: red fir (*Abies magnifica*) and white fir (*A. concolor*). In the northern Sierra, the elevation range of these firs runs from about 1,520 to 2,440 m (5,000 to 8,000 ft). From Mount Lassen to as far south as Sonora Pass, where peaks extend above the 2,440 m (8,000 ft) level, red fir extends to (or near) timberline. An exception is the Warner Mountains, where there is no red fir (Skinner personal communication). To the south and on the east side of the Sierra crest, the elevational limits gradually shift upward to about 2,130–3,040 m (7,000–10,000 ft) (Andrews 1994).

In the northern Sierra Nevada, there is a gradual transition from mixed conifer forests, to more or less pure white fir stands (up to 1,830 m, or 6,000 ft), to a mixed red and white fir zone, and finally to red fir forests (above 2,130 m, or 7,000 ft). White fir is frequently the dominant species on mesic sites between 1,500 and 2,000 m (5,000 and 6,500 ft) (Conard and Radosevich 1982).

In the southern Sierra Nevada, the transition goes directly from mixed conifer forests to red fir forests, although the lower portions of these red fir forests often contain white fir, and upper portions often contain lodgepole pine (Vankat and Major 1978).

Although red fir appears to be a climax species in many stands at high elevations, it is rarely found in extensive, pure stands. Common associates include white fir, lodgepole pine (*Pinus contorta* var. *murrayana*), incense cedar (*Libocedrus decurrens*), sugar pine (*P. lambertiana*), Jeffrey pine (*P. jeffreyi*), western white pine (*P. monticola*), western juniper (*Juniperus occidentalis*), mountain hemlock (*Tsuga mertensiana*), and quaking aspen (*Populus tremuloides*) (Eyre 1980).

Although lightning-ignition frequencies are much higher in the upper montane zone (Vankat 1983), fires spread less readily because (1) biomass accumulates more slowly; (2) the fuel is more compact; (3) weather conditions that will support a fire occur less often; and (4) the high-elevation areas of the Sierra contain many natural fuel breaks, including sharp or sparsely vegetated ridges, barren rocky areas, streams and draws with relatively fire-resistant riparian vegetation, and large areas of sparsely spaced vegetation, that do not support fire well (Kilgore and Briggs 1972; Husari 1980; Weatherspoon et al. 1992). It has been observed, for example, that although red fir type constitutes only 8% of Yosemite National Park, 16% of the fires recorded in the park between 1930 and 1983 were in this zone. The majority of those were of single trees, and larger fires occurred when red fir was mixed with montane chaparral (van Wagtenonk 1986). Crown fire is unusual in this type except under rare high winds, partly because of the sparse understory vegetation (Kilgore and Briggs 1972; Rundel et al. 1977). The potential for stand-destroying fire exists on steep, south-facing slopes with heavy fuels and dense regeneration (Husari 1980). As a consequence, fires in the red fir zone were historically less frequent and usually far less intense than fires in the lower elevations, but the fire regimes varied from landscape to landscape (Kilgore and Briggs 1972; Husari 1980; Skinner and Chang 1996).

Fire-suppression actions are thought to have had less effect on the red fir type, both because suppression activities began later (1920s to 1930s) in red fir forests and because fewer fires would have burned there without suppression anyway.

Vegetation Responses to Fire

The relationship between red fir and fire is paradoxical. On the one hand, red firs seem to do well without fire and may even suffer under prolonged periods of frequent fires: they can germinate and grow in light litter and thus do not require fire-generated openings to establish themselves (Laacke and Fiske 1983; Taylor 1990a); they are shade tolerant and do well under canopies (Fowells 1965; Helms and Standiford 1985); and they are highly susceptible to fire when young (Kilgore 1971b). On the other hand, red firs seem to be at the same time fairly resistant to fire and may even benefit from fire: they develop thicker bark as they mature and become moderately resistant to the low- and medium-intensity fire typical of the vegetation type (Kilgore 1971b; Husari 1980); they establish best in postfire bare mineral soils (Laacke and Fiske 1983; Parker 1986); and episodes of their regeneration seem to be associated with fire events (Weatherspoon et al. 1992; Andrews 1994). It has been argued that the decrease in fire frequencies in this century may have led to a decrease in red fir establishment (Pitcher 1987).

Thus, we can conclude that red fir requires some fire for regeneration but does not do well during prolonged periods of frequent fires. Frequent fire eliminates fir seedlings and favors pine (Husari 1980). Firs benefit most from a variable-interval, low-intensity fire regime with occasional longer fire-

free periods that allow young fir trees to survive through the fire-susceptible age. The short growing season and heavy snowpack may be important in limiting the frequency of fire, thus benefiting fir in this vegetation zone (Husari 1980).

Succession after Fire

Fir forest is the climax community over much of the coniferous type in the upper montane zone. Small fires produce openings where lodgepole seedlings may become established. Stand-destroying fires replace red fir stands with montane chaparral type, but subsequent seral changes will shift the dominance back to red fir (Husari 1980; Conard and Radosovich 1982). On older sites, openings in the canopy caused by tree mortality allowed patchy understory development (Conard and Radosovich 1982).

Biodiversity and Community-Structure Responses to Fire and Fire Regimes

Because of its ability to regenerate in both shade and sunlight, it has been suggested that red fir will be able to reach dominance in this vegetation zone even under different fire regimes. Given the present seed source in the area, fire suppression may not alter species composition in this vegetation zone by shifting the dominance of species. However, fire-dependent associates of red fir (e.g., lodgepole pine, Jeffrey pine, western white pine, and quaking aspen) may decrease with continued fire suppression (Andrews 1994).

As in other conifer types, fires are thought to have historically thinned young fir patches, leaving scattered trees that then developed into scattered, mature individuals. Therefore, although fire suppression may not have had as significant an effect in the red fir forests as in the lower-elevation forests, decreased fire frequency still may have resulted in denser red fir forests (Vankat and Major 1978).

Stand age structure is also influenced by fire events. A study of the relation between stand age structure of red fir and disturbances in the southern Cascade Range revealed that the red fir forest patches may be even-aged or multiaged, depending on the disturbance history of the site. Even-aged patches were a result of synchronous postdisturbance establishment. Gaps in the study area were created mostly by frequent wild-fire and by windstorms. Severe fire cleared larger openings, initiated mass establishment of red fir and white fir, and resulted in larger even-aged patches, whereas smaller gaps created by windthrow released already established individuals, resulting in smaller, even-aged patches. Low-intensity fire stimulated little recruitment and probably caused thinning but did not affect the age structure of patches. Multiaged patches, on the other hand, were a result of continuous recruitment of seedlings moderately tolerant of shade during disturbance-free periods. Thus, both episodic and continuous recruitments, as determined by the type and severity of natural disturbances, were thought to be the driving forces shaping the complex age and structures of these red fir forests (Taylor 1991, 1993).

Because the patchy distribution of red fir forests in the Sierra Nevada originates not only from fire and windthrow, but also from a wide variety of other agents (including insect attacks, diseases, avalanches, or landslides), and because fires are not as regular as in the lower-elevation zones, changes in stand structure due to fire suppression are much less marked than in lower-elevation mixed conifer forests. Nevertheless, continuous establishment of red fir due to fire suppression will likely lead to changes in the vertical structure of forests, especially along the red fir–white fir ecotone (Andrews 1994).

Regarding fire influence on faunal biodiversity in red fir forests, no changes in deer or bird numbers were noted after a prescribed surface fire (Kilgore 1971b).

Fuel-Structure Changes in Response to Different Fire Regimes

Fir types tend to accumulate fuels of larger size classes (Husari 1980). The finer fuels that accumulate are made up of short needles that form a dense litter layer, which is further compressed by a heavy snowpack (Weatherspoon et al. 1992). Such fuel structure is capable of supporting only slow burns and thus does not promote rapid fire spread. The historical low-to medium-intensity fires in the red fir forest tend to spread to and from large, downed logs, burning the areas around the logs lightly, often spotting from log to log. Distribution of the large, decaying logs, therefore, tends to be spotty and concentrated in areas that missed being burned for a variety of reasons. One potentially important change in the ecosystem is the slight increase in the amount of large, downed woody material, which may now be more uniformly distributed throughout the forest (Andrews 1994). However, because this trend has not been commonly reported, whether it is representative of the whole Sierra Nevada is unknown.

Landscape-Pattern Responses to Fire Regimes

The level of heterogeneity in the Sierra Nevada fir forests changes from north to south: the mix of species becomes more variable and diverse, and spatial heterogeneity increases from north to south. A range of severity and frequencies of fire, in addition to a variety of other disturbances, has shaped the landscape into a complex pattern of various patch sizes and tree ages (Agee 1989; Weatherspoon et al. 1992; Andrews 1994). These fires burned irregular-shaped areas with varying spread rates (Kilgore 1971b) and were thought to behave so because of the variations in fuel-type pattern and fuel-moisture content (Kourtz and O'Regan 1971; van Wagtenonk 1972) and local topographic variations and weather conditions (Kilgore 1973).

Stand-replacing fires occasionally occur in these zones, and they initiate large cohorts of red and white firs (example from Cascade Range, Taylor 1993), but lower-severity fires that create smaller canopy openings and consequent smaller patches of thinned saplings are most common (Kilgore 1971b; van Wagtenonk 1986; Taylor 1993).

Biogeochemical and Soil Changes after Fire

Few studies of the biogeochemical and soil responses to fire have been done in the fir zone, but it has been suggested that fire may be an important factor in nutrient cycling by releasing nutrients from the accumulated litter on the forest floor, which would otherwise decompose very slowly (Andrews 1994). Water quality of creeks in this vegetation zone was not altered by prescribed surface burn (Kilgore 1971b).

Lodgepole Pine Forests

Primary Vegetation and Its Historical Relationship with Fire

The elevation range for lodgepole pines is about 2,000–3,000 m (6,560–9,840 ft) for the central Sierra Nevada, and slightly higher, 2,150–3,400 m (7,050–11,160 ft) for Sequoia National Park in the southern Sierra.

Lodgepole pine (*Pinus contorta* var. *murrayana*) is the dominant tree, whereas western white pine (*P. monticola*), ponderosa pine (*P. ponderosa*), and Jeffrey pine (*P. jeffreyi*) are common associates. Gooseberry (*Ribes montigenum*) is the most common shrub.

Small or moderate-intensity fires are thought to favor perpetuation of the lodgepole habitat in the north (Husari 1980), although Vankat and Major (1978) have suggested that the elimination of sheep grazing could have triggered a major pulse of lodgepole pine reproduction in the south.

Vegetation Responses to Fire

The mature lodgepole trees have very thin bark, deep roots, and medium to low foliage flammability and are considered intermediate in fire tolerance (Starker 1934; Husari 1980; Kilgore 1971b). Mature lodgepole trees are most commonly killed by scorching cambium or crowning (Starker 1934). Lodgepole seedlings are shade intolerant and thus require openings for growth. These seeds germinate best in openings and sterilized mineral seedbeds produced by high-intensity fire, and they seem to be stimulated by fires (Kilgore 1971b, Husari 1980).

In many regions, lodgepole pine owes its prominence to repeated fires, particularly in the Rocky Mountains (e.g., Brown 1975). In the Sierra, this dependency varies with location. For example, lodgepole pines seem to be fire dependent in the north (Husari 1980), but not quite so further south (Parker 1986).

Sierran lodgepoles do not have serotinous cones as the Rocky Mountain lodgepoles do, but they produce seeds in abundance each year and can set seed at an early age. The combination of heavy, early seed production and the ability to reseed in any openings that occur gives lodgepole pine a competitive advantage over its associates in the presence of fire, whether the intensity is low, medium, or high (Husari 1980).

In the central Sierra Nevada, an observed small-scale clumping of lodgepole seedlings suggests that tree falls may

often create regeneration sites for these trees. Despite the virtual absence of crown fires in these areas, lodgepole pines apparently persist in these stands by continuous successful establishment in these tree-fall gaps (Parker 1986). Thus, for the central Sierra, lodgepole pines do not appear to be fire dependent.

Succession after Fire

Lodgepole has long been considered mainly a seral stage, to be replaced by fir in the absence of fire in most locations. Some localities seem to support a lodgepole climax, however, and Husari (1980) has suggested that for the northern Sierra and the Cascades, frost pockets and poorly drained soils may be the edaphic factors that define a lodgepole climax.

Biodiversity, Community-Structure, and Landscape Responses to Fire and Fire Regimes

Not much information is available on the compositional changes of lodgepole forests after fire, except that many areas in the north are found with developing understory of white and red firs (*Abies concolor*, *A. magnifica*), especially white fir, and that the suspected cause of this encroachment of firs is the exclusion of fires (Husari 1980).

Lodgepole pines in the Rocky Mountains are known to have a relatively even-aged structure and unimodal or bimodal diameter distribution, which have been associated with the crown fires typical of that area. For the northern Sierra, however, uneven-aged stands are more commonly seen, and low-intensity, small fires are suggested to be the process maintaining this structure. For the central Sierra, negative-exponential distribution of age classes, random dispersal of trees, and aggregated seedlings in small clumps are typically observed, and tree-fall gaps are thought to have had a major influence on the forest structure. Differences in community structure and landscape heterogeneity are due to the regional variations in site productivity and in the scale and frequency of disturbance: tree-fall or small-fire gaps in the Sierra Nevada lead to a more heterogeneous landscape, while larger crown fires in the Rocky Mountains create a more homogeneous landscape (Parker 1986).

Fuel-Structure Changes in Response to Different Fire Regimes

Not much is known about the effect of fire on fuel structure in the Sierran lodgepole pine forests, except that the recent development of understory fir in the northern Sierra creates fuel ladders that increase crown fire potential (Husari 1980).

Subalpine Meadows

Very little information exists for fire effects on subalpine meadows, like lodgepole pine ecosystems. But fortunately a case study on a lightning-ignited burn that ran through Ellis Meadow, a subalpine meadow in the Kings Canyon National Park, in 1977 (DeBenedetti and Parsons 1979, 1984) recorded

detailed descriptions on the immediate postfire responses and a follow-up of four years of succession. Although the Ellis Meadow study may not be representative of all meadow burns, it contains valuable details. Most of the following discussion derives from this study.

Primary Vegetation and Its Historical Relationship with Fire

Subalpine meadows consist mainly of grasses and sedges, with some lodgepole pines invading from the borders. Ratliff (1982) presents a description of the herbaceous species in these meadows.

Rather than focusing on "what maintains meadows," the literature available on meadow ecology is most concerned with "what leads to tree invasion of meadows."

Three major factors have been suggested to define forest-meadow boundary dynamics: climatic change, livestock grazing, and fire (Husari 1980; Taylor 1990b). Although climate has been identified as an important force behind forest-meadow dynamics in the Sierra Nevada over thousands of years (Wood 1975), the effect of climate over shorter temporal scales is less clear. In the Pacific Northwest, warm, dry weather has been associated with a period of tree establishment in subalpine meadows (Franklin and Dyrness 1973; Agee and Smith 1984). In the Cascade Range, tree establishment was associated with wetter periods (Vale 1981; Taylor 1990b). For the Sierra Nevada, tree invasion has been associated with drier periods (Boche 1974; Helms 1987). The paradoxical relationship between climate and tree invasion along the Pacific Coast suggests that climate alone cannot explain the forest-meadow boundary dynamics observed over the past few decades.

The most commonly held hypothesis on such tree invasion is that past grazing activities resulted in increased precipitation runoff, soil erosion, and stream entrenchment and that these in turn lowered the water table, dried the meadows, and improved conditions for tree seedling establishment (Vankat and Major 1978). However, because sheep ate the tree seedlings and kept them off, tree invasion did not start until grazing activities ceased (Magee 1885; Bradley 1911). Large fires were also an important factor determining the meadow-forest boundary (Vankat and Major 1978), and there has been a concern that meadows are being lost to lodgepole invasion because of the exclusion of fire (Husari 1980).

Charcoal layering indicates that meadows in Yosemite National Park and Sequoia National Park burned once every 250 to 300 years (Leonard et al. 1968; Botti 1979). However, because charcoal layers are less indicative of less severely burned periods, these subalpine meadows historically may or may not have burned less frequently than the surrounding forests. An observation that some fires burning in the nearby forests may stop at the edge of meadows (e.g., Sugarloaf Meadow in 1974, as described by DeBenedetti and Parsons 1979) provides a mechanism that could result in a reduced fire frequency. Meadows characterized by high productivity

and biomass are most likely to carry fires through, and prolonged drought greatly facilitates fire spread (DeBenedetti and Parsons 1979).

Vegetation Responses to Fire

Generally, fire does little damage to grasses and sedges (Husari 1980). Hot fires may kill well-established trees and may greatly damage meadows, but light fires do little harm to trees or meadows (Ratliff 1985). In the case of the Ellis Meadow burn, the fire killed many lodgepole seedlings but only a few of the numerous sapling or pole-sized pines found around the perimeter of the meadow (DeBenedetti and Parsons 1979).

Succession after Fire

In Ellis Meadow, grass and graminoid species recovered quickly after fire, increasing from an 8% ground cover one year after fire to a 75% ground cover four years after fire. In areas that burned less severely, above-ground biomass and cover of grass and graminoid appeared comparable to those of unburned sites the following year. Broadleaf species also increased, but at a much slower rate, from a 28% ground cover one year after fire to 49% four years after fire. Absolute cover by annuals declined steadily during the second through fourth years after fire. Postfire succession brought the vegetation back toward the characteristics of the preburn state (DeBenedetti and Parsons 1984).

Many of the lodgepole pine seedlings and saplings located around the boundaries of Ellis Meadow were killed by fire. Lodgepole pine seedlings were not found in burned portions of the meadow during any of the four years following fire (DeBenedetti and Parsons 1984).

Biodiversity and Community-Structure Responses to Fire and Fire Regimes

In Ellis Meadow, the total number of vascular plant species increased from the first year after fire to the second year after fire and remained essentially constant through the fourth year after fire. Although the number of species remained relatively constant, the composition fluctuated considerably from year to year. Species that appeared in the first year through the fourth year following the fire constituted the most important plant group for every postfire year, in terms of their contribution both to the number of species present and to total cover. No species was found only during the first year following fire (DeBenedetti and Parsons 1984).

Landscape-Pattern Responses to Fire Regimes

In Ellis Meadow, the burn was more intense in flat places dominated by wideleaf sedge. In these areas, subsurface fires did not carry well through the above-ground fuels and smoldered around them. In hummocky microtopography, patterns of burns varied: in places where burns were of low intensity, fires were largely confined to the trough between hummocks, and green vegetation was rarely totally consumed, leaving

the landscape patchy with surviving vegetation on top of hummocks, whereas in places where fire intensity was high, the surfaces of both troughs and hummocks were continuously burned, leaving the landscape relatively homogeneous.

The same pattern occurred for lodgepole seedlings: those growing on flat topography were mostly killed by the fires, whereas those growing on top of the hummocks, where the fire was usually not hot enough to burn through the bases of the trees, were rarely killed (DeBenedetti and Parsons 1979).

Biogeochemical and Soil Changes after Fire

In Ellis Meadow, where the topography was flat, the fires smoldered for some time, consumed the organic layer, and left an ash layer 10 to 30.5 cm (4 to 12 in) deep. Where the fire was most intense, the surface of the meadow was lowered between 10 and 25 cm (4 and 10 in) relative to adjacent vegetation. Soil puddling occurred in most of these areas, and initial stages of channelization in the form of shallow rills were sometimes present, probably a result of a heavy rain that occurred one year after fire. DeBenedetti and Parsons hypothesized that this would alter overall meadow drainage patterns and change the distribution of major plant communities, but subsequent observation has not supported this hypothesis (DeBenedetti and Parsons 1984).

East-Slope Vegetation Types

The literature on east-slope Sierran ecosystems is sparse. There are several vegetation types on the east slope, including piñon-juniper, sage-bitterbrush, and east-side lodgepole (which is slightly different from the west-side lodgepoles discussed earlier), and east-side pine and mixed conifers. But of these various types, only the east-side pine forests have received enough study to be comprehensively reviewed here. Also, it is important to keep in mind that these following statements have relatively little scientific support and are mostly from the workshop supporting the California spotted owl environmental impact statement (Andrews 1994), which consists of ad hoc summarization by scientists and managers from the area.

East-Side Pine Forests

Primary Vegetation and Its Historical Relationship with Fire

Generally, the east-side pine forest is roughly defined by the region dominated by various pine species east of the Sierra Nevada crest (McDonald 1983). Because the east-side pines have not been widely studied, they are poorly described both geographically and ecologically. In the northeastern California region, they fall in the elevation range of 1,220–1,980 m (4,000–6,500 ft) (McDonald 1983). Ponderosa and Jeffrey pines (*Pinus ponderosa*, *P. jeffreyi*) are the dominant species, and white fir (*Abies concolor*), incense cedar (*Libocedrus decurrens*), and, on poorer sites, juniper (*Juniper* spp.) are commonly found

associates (Andrews 1994). Fire is an important factor in maintaining this vegetation type (Sweeney 1968), but because the rate of the biotic processes is slow, the system is less resilient and requires a longer recovery period after fire than the west-side vegetation types (Andrews 1994).

Succession after Fire

The plant succession sequence following severe fires in this type generally proceeds from herbs, to shrubs, to pine, to fir (Sweeney 1968). For the Inyo area, the postfire sequence proceeds from herbs to a shrub and pine mix (Millar personal communications). Succession of western juniper is usually a function of disturbance: after severe fire, western juniper is usually reduced greatly in abundance, sometimes almost to elimination, and perennial grasses increase in both abundance and productivity (Andrews 1994).

Biodiversity and Community-Structure Responses to Fire and Fire Regimes

Concerning biodiversity, east-side pine forests have low species diversity when compared to their west-side counterparts (Andrews 1994). Understory grasses and herbaceous vegetation were thought to be generally abundant historically, because of the frequent fire and open canopy conditions in the past. Although many junipers are believed to germinate better after fire (Millar personal communications), western junipers are thought to be susceptible to fire and would decrease with fire (Andrews 1994). A major regeneration pulse of white fir (*A. concolor*), shrubs, western juniper (*Juniperus occidentalis*), whitebark pine (*P. albicaulis*), ponderosa pine (*P. ponderosa*), and Jeffrey pine (*P. jeffreyi*) was observed for the early 1900s (before 1930), but the driving forces behind these changes are largely unknown. Suggested candidates include the cessation of sheep grazing, logging of large trees, fire suppression, and a concurrent wet climatic period.

Fire exclusion and selective logging have been suggested to have caused the observed shift toward shade-tolerant conifers, especially white fir and, in some places, incense cedar. Andrews (1994) has suggested that high-severity fires may benefit species adapted to such fires (e.g., deer brush [*Ceanothus* spp.] and manzanita [*Arctostaphylos* spp.]), introduced herbaceous species (e.g., cheat grass [*Bromus secalinus*]), and persistent herbaceous species (e.g., mule ear [*Wyethia glabra*]).

Historically, tree canopies in this area were characteristically open and exhibited a high degree of horizontal diversity but relatively low vertical diversity. There was a diverse mosaic of seral stages and slow-growing, long-lived tree species. In the recent past, vertical diversity in this area has increased, and horizontal diversity has decreased. It has also been observed that the small patches of older, large trees have been lost from the system extensively (Andrews 1994).

Fuel-Structure Changes in Response to Different Fire Regimes

Because of the dry climate, the rates of both fuel accumulation and decay are slower on the east slope than on the west. Before European settlement, fuel structure was thought to consist mostly of low levels of small, woody fuels, litter, and duff. Coarse, woody debris was thought to have been patchy. Snags were thought to have stood longer than they do now, but for exactly how long is unknown (Andrews 1994).

Fire suppression is thought to have greatly changed the fuel complex to more small, surface fuels, more vertical fuel distribution favoring crown fires, and greater fuel loading overall. Together, these changes increase the probability of large, high-severity fires (Andrews 1994).

Landscape-Pattern Responses to Fire Regimes

Fires in this region were primarily of low severity, with patches of high severity corresponding mostly to areas with heavy fuel accumulations or dense patches of small trees. More mesic sites burned less often, but fires were somewhat more severe when they did occur. Such fire patterns resulted in a mosaic of diverse, small, even (or similar) aged (or sized) patches, which exhibited little vertical diversity. Such "fine-grained" forest mosaic was occasionally fragmented into a more "coarse-grained" mosaic by a number of landscape elements common to the east-side pine type, including sagebrush flats, low sites, rock outcrops and scarps, meadows, springs, cold air pockets, brush fields, lava flows, and occasional large, high-severity burns. Large, intense fires create large patches that remain for a long time in early- and mid-seral stages (Andrews 1994).

Biogeochemical and Soil Changes after Fire

East-side pine forests are characterized by low levels of stocking, productivity, and growth rates, and nutrient cycling and decomposition are slow. Fire seems to help increase the rate of nutrient cycling. There has been a significant loss of soil productivity, and Andrews (1994) has suggested that the large, high-severity fires and earlier impacts from logging and harsh mechanical site preparation are the major causes.

CONCLUSION

Because of variations in fire tolerance, the time needed to reach maturity, and reproductive strategies, different species respond differently to the various fire intervals and fire intensities. Some species (e.g., obligate seeding chaparral shrubs and ponderosa pine) respond well to frequent fires, but others (e.g., sprouting chaparral shrubs, incense cedar, and firs) are favored by slightly longer fire-free periods. The successional process depends on the seed source at the time of burn and the consequent competition among the seedlings.

Different plant species also produce different amounts and types of fuel accumulation and, therefore, have the potential of supporting different fire regimes. Some (e.g., chaparral and mixed conifer types) accumulate fuels more rapidly than others (e.g., montane fir forests) and thus are capable of supporting fires at shorter intervals. Some (e.g., ponderosa pine) create loosely packed fuel that favors fast-spreading surface fires; others (e.g., firs and incense cedar) create ladder fuels that facilitate crown fires.

Depending on the relative temporal frequency and spatial scale of fire, other local disturbances, and the biotic processes on the landscape, landscape structure also responds differently to the various fire regimes. Landscapes characterized by stand-replacing fires (e.g., chaparral) are composed of coarser grains with patch sizes reflecting the typical range of fire sizes in the system. Landscapes characterized by surface fires (e.g., mixed conifer forests) have higher levels of variation in their patch sizes and stand structures. Patches created by stand-replacing fires often define the boundary of the next burn; patches shaped by surface fires often create local heterogeneity in burning intensities during the next burn. Because both horizontal and vertical fuel continuities increase as the fire-free period lengthens, longer fire-free periods result in larger burns. In ecosystems characteristically visited by surface burns, longer fire-free periods also increase the probability of stand-replacement fires. Therefore, a longer fire-free period often results in an increase in patch size, and the landscape becomes coarser grained compared to the landscapes that experience more frequent burns.

The complex geography of the region also has a significant effect on fire spread. The rocky exposures near the mountain ridges serve as natural firebreaks, limiting the spread of fire in and across that region, whereas the continuous sheet of fuel bed from the foothills to the mixed conifer zones often results in a larger area burned, especially when the fuel within each type is continuous.

Today, many of the issues in the Sierra Nevada surround debates in land use and forest management: Active or passive management? To burn or not to burn? If to burn, how often, and how intense? If not to burn, what to do instead?

From the ecology of the Sierra Nevada, we have learned that change is constant and that ecosystems have a wide range of variation in their responses to fire. We should not study past patterns of change in the hopes of recreating them. Rather, we should seek to understand how change will determine the patterns of the future. We have to decide what it is we want and work with the natural processes to achieve those goals. If we seek biodiversity, a diversity of fire regimes may be critical. If we seek to control fires in vegetation close to residential areas, lower fuel loads and lower fuel continuity may help us gain that control. But if it is stability in terms of persistence of some "steady state" that we are after, we are bound to fail; change is the very heart of nature.

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