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Disturbance Patterns in Southern Rocky Mountain Forests

Thomas T. Veblen

INTRODUCTION

The pattern of landscape diversity in the Southern Rocky Mountains has been described as resulting from “two superimposed vegetation patterns: the distribution of species along gradients of limiting factors, and patterns of disturbance and recovery within the communities at each point along the environmental gradients” (Romme and Knight 1982). The previous chapter (D. H. Knight and W. A. Reiners, *this volume*) has emphasized the first pattern whereas this chapter emphasizes the role of natural disturbance in creating landscape patterns. Although human impacts on fundamentally natural disturbances such as fires and insect outbreaks are included, other chapters treat disturbances of exclusively human origin such as logging and road construction.

A conceptual framework for analyzing the characteristics and consequences of disturbance is the concept of *disturbance regime*, or the spatial and temporal characteristics of disturbances in a particular landscape (Paine and Levin 1981, White and Pickett 1985). The key descriptors of a disturbance regime are: (1) spatial distribution, (2) frequency, (3) size of the area disturbed, (4) mean return interval, (5) predictability, (6) rotation period, (7) magnitude or severity, and (8) the synergistic interactions of different kinds of disturbances. Within an area of otherwise homogeneous habitat, variations in these parameters are major determinants of landscape heterogeneity and, consequently, must be considered in evaluating the fragmentation caused by forest cutting and road construction. Although numerous case studies have been done on vegetation and ecosystem response to disturbance

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for the Southern Rocky Mountains, relatively little work has been done on disturbance regimes per se. To inform discussions of the relationship of landscape patchiness to natural disturbances and issues of fragmentation, this chapter will emphasize four “key” questions about disturbance regimes:

1. How do disturbance regimes vary along environmental gradients?
2. How have humans altered natural disturbance regimes?
3. How do disturbance interactions affect vegetation responses as well as the occurrence and spread of subsequent disturbances?
4. How does climatic variability affect disturbance regimes and vegetation response to disturbances?

It will quickly become evident that answers to these questions are very incomplete for the Southern Rocky Mountains. This realization is important both in guiding future research and as a caveat to incorporating the tentative knowledge of disturbance patterns into discussions of fragmentation issues. Although the geographical scope of this review is from central Wyoming to southern Colorado, studies conducted in northern Colorado will be emphasized. For this region, it will be convenient to distinguish the lower elevation montane forests of mainly ponderosa pine and Douglas fir from subalpine forests of mainly Engelmann spruce, subalpine fir, and lodgepole pine (Marr 1961).

FIRE

Historical Documentation of Fire and Its Effects

The earliest reports on the conditions of forest reserves (precursors to national forests) in the 1890s describe landscapes that had recently burned, and much of that burning was attributed to fires ignited by Native Americans mainly for the purpose of driving game (Jack 1899, Sudworth 1899). The observations of early settlers and the high fire frequencies during the prehistoric period (see following section) strongly imply that Native Americans had a quantitatively significant influence on the number of ignitions. Nevertheless, the percentages of fires ignited by humans versus lightning are unknown. During the mid-1800s period of exploration and early settlement (ca. 1850 to 1910), fires were frequently set by EuroAmericans to facilitate prospecting, to justify salvage logging, or to clear brush to find escaped cattle (Jack 1899, Sudworth 1899, Tice 1872, Fossett 1880). At least 20% of the South Platte Reserve had been burned so severely by the 1890s that regeneration had failed, apparently due to destruction of seed sources by

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repeated burns at the same sites in time spans of less than ten years (Jack 1899). Alternatively, regeneration may have failed due to drought that was reportedly responsible for the death of mature ponderosa pine in the same area in the 1880s (Jack 1899). In Boulder County in 1871, there were 51 indictments for illegal forest fires (Tice 1872), implying that contemporary observers perceived a trend towards an unwanted increase in fire occurrence during the latter half of the nineteenth century. Similarly, photographs taken near the turn of the century indicate that vast areas of the Southern Rocky Mountains had been recently burned (Jack 1899, Sudworth 1899, Veblen and Lorenz 1991).

Tree-Ring Based Studies of Fire History

Fire history in forested areas can be described quantitatively on the basis of two types of tree-ring evidence: dates of fire scars (the fire interval approach) or the age of stands that regenerated following stand-replacing fires (the stand origin approach). Because most fire histories of dense subalpine forests have been derived from mapping postfire stands whereas fire histories of open montane forests of ponderosa pine and Douglas fir are from fire-interval data, fire history statistics for the subalpine and montane zones usually are not directly comparable. Furthermore, the reliability of both fire history techniques is limited by numerous problems associated with the collection of the field evidence of fire as well as analytical procedures (Johnson and Gutsell 1994, Finney 1995, Kipfmüller and Baker 1998a). Quantitative comparisons of summary fire statistics for different study areas rarely are valid because of differences in the sizes of the areas sampled, sampling skill and effort, and methods of computing fire statistics. Given these caveats, the interpretation of fire history studies in this chapter will emphasize qualitative differences in fire regimes (e.g., high frequency surface fires versus low frequency crown fires), temporal trends within the same study area, and regional synchrony of fire events.

Differences in Fire Regimes by Habitat

A strong contrast exists in dominant fire type between the subalpine and montane zones (Romme and Knight 1981, Peet 1988). The continuous fuels of dense Engelmann spruce, subalpine fir, and lodgepole pine forests generally permit widespread stand-replacing or crown fires. In contrast, most fires in the open ponderosa pine woodlands of the lower montane zone are surface fires carried mainly by grass fuels. However, these two modal fire types represent opposite ends of a con-

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tinuum of fire intensity that can occur in both elevational zones. For example, in ponderosa pine forests, stand-replacing fires are documented for both the fire exclusion period and the prehistoric landscape (Veblen and Lorenz 1986; Shinneman and Baker 1997).

Although statistical comparison of fire parameters from different fire history studies is not feasible, there are consistent qualitative differences in the fire regimes of the subalpine and montane zones. The average time between recurrent fires to the same stand or small area (e.g., <1km²) in subalpine forests has been roughly estimated to be 100 to 500 years versus 5 to 40 years in open woodlands in the lower montane zone (Rowdabaugh 1978, Clagg 1975, Gruell 1985, Romme 1982, Romme and Knight 1981, Peet 1988). In the subalpine zone in southern Wyoming, fire rotation (i.e., time required to burn the entire study area once) has been estimated at 182 years (for 1569–1996 A.D.) for a 3,241-ha area (Kipfmueller 1997), and in northwestern Colorado at 521 years (for 1633–1992 A.D.) for a 594-ha area of subalpine forest (Veblen et al. 1994). The longer fire rotation for the northwestern Colorado site may reflect a moister habitat or topographic restriction of fire spread into the small, high elevation valley where the study was conducted. In contrast, fire rotation in a 113-ha area of open ponderosa pine woodland in the lower montane zone of the Colorado Front Range is estimated at 29 years over the period 1679–1996 (conservatively assuming that years in which $\geq 25\%$ of the trees were scarred were years in which most of the sample area burned; Veblen et al., *unpublished data*). In 73 km² of subalpine forest in Yellowstone National Park, evidence was found of only 15 fire years since 1600 (Romme 1982). In contrast, in only 1.13 km² of open ponderosa pine woodland in the Colorado Front Range evidence was found of 35 fire years since 1679 (Veblen et al. 1996). Although the subalpine zone is clearly characterized by infrequent large fires, repeated burns at short intervals (i.e., <10 years) also occasionally have occurred (Sudworth 1899).

Changes in Fire Regimes over Time

In the context of current forest fragmentation, it is important to consider how EuroAmericans have altered fire regimes over the present century, and in turn may have altered size or intensity of disturbance which affects the spatial heterogeneity of the landscape (Baker 1994). The modern “fire exclusion” period beginning in the early 1900s refers to both suppression of lightning-ignited fires and cessation of widespread, intentional burning by humans. It is widely believed that in

comparison with the nineteenth century, the present century has been a period of reduced fire occurrence throughout the Southern Rocky Mountains (Peet 1988, Knight 1994). However, the validity of this generalization and its ecological consequences vary according to elevation and specific sites. Due to the long fire intervals typical of subalpine forests, the past approximately 80 years of fire suppression have not necessarily had much influence on rates of fire recurrence in some areas of subalpine forests (Romme and Despain 1989, Clagg 1975).

In the montane zone of the Southern Rocky Mountains there is a consistent pattern of reduced fire frequency during the fire exclusion period (Table 3.1). The magnitude of this decline appears small when measured as changes in mean fire return intervals because the computations for the fire exclusion period must be truncated at the date of the most recent fire which in many cases is early in the 1900s. However, simple comparison of the numbers of fire years in periods of approximately equal length before and after the initiation of fire exclusion indicates a 2- to over 14-fold decline in fire occurrence during the fire exclusion period (Table 3.1). The much greater impact of fire exclusion on fire occurrence in the montane zone, compared to the subalpine zone, reflects the inherently higher fire frequency permitted by fuel conditions at low elevation.

In the context of a book on forest fragmentation it is important to emphasize that fire suppression has promoted some forest patch *coalescence* in the montane zone during most of this century. Comparison of historical and modern landscape photographs as well as analyses of tree population age structures document the spread of ponderosa pine and Douglas fir trees into some former grasslands (Gruell 1985; Veblen and Lorenz 1991; Mast et al. 1998). This major change in the montane forests is widely attributed to elimination of the frequent surface fires that formerly prevented seedling survival at most sites. However, climatic variability and changes in herbivore populations also may have influenced the expansion of ponderosa pine woodlands. For example, in southwestern ponderosa pine forests, tree establishment at some sites corresponds with periods of increased moisture availability (Cooper 1960, White 1985), and in western Montana periodic drought is believed to limit Douglas fir expansion into grasslands (Koterba and Habeck 1971). For the Colorado Front Range, climatic influences on ponderosa pine establishment also have been hypothesized, but any association between seedling establishment and short periods (1–5 years) of climatic variation remains elusive (Mast et al. 1998). Confounding influences from livestock grazing make it difficult to detect

Table 3.1. Fire regime descriptors from fire history studies in southern Wyoming and Colorado. Time periods are: NA = the Native American period (pre-1840); ES = the EuroAmerican settlement period; and MFE = the modern fire exclusion period. Years used to define these periods in each study are given in parentheses below the respective mean fire return intervals. For computation of mean fire return intervals (MFI) only complete fire intervals (i.e., fire-scar to fire-scar) within each indicated period were used, except for the two subalpine forest sites where MFIs were computed as the period length divided by the number of intervals. “No. of intervals” is the number of fire intervals in the entire record. “No. of trees sampled” is the number of fire-scarred trees sampled. For computation of the ratios of the number of fire events, the NA period was shortened to approximate the lengths of the ES and MFE periods (i.e., 44 to 74 years).

<i>Location (Source)</i>	<i>Number of trees sampled</i>	<i>Number of intervals</i>	<i>Mean fire return interval</i>			<i>Ratio of fire years</i>	
			<i>NA</i>	<i>ES</i>	<i>MFE</i>	<i>ES/NA</i>	<i>ES/MFE</i>
<i>Montane forests</i>							
Wintersteen Park, northern Front Range (Laven et al. 1980)	n.d.	20	66.0 (1708–1839)	17.8 (1840–1905)	27.3 (1906–1949)	n.d.	13/4
Southern Rocky Mountain Park (Skinner and Laven 1983)	>20	15	21.5 (1703–1839)	12.8 (1840–1928)	6.5 (1929–1942)	6/3	6/3
Fourmile Canyon, northern Front Range (Goldblum and Veblen 1992)	72	14	31.8 (1721–1858)	8.1 (1859–1920)	28.0 (1921–1949)	8/3	8/2
Eldorado Springs, northern Front Range (Veblen et al. 1996)	55	32	8.2 (1703–1858)	4.4 (1859–1920)	no fires (1921–1990)	14/4	14/0
<i>Subalpine forests</i>							
Medicine Bow Range (Kipfmueller 1997)*	73	51	9.4 33.1 (1569–1867)	1.9 10.8 (1868–1911)	3.5 28.0 (1912–1996)	16/5 3/2	16/9 3/2
Taylor Park, Southwestern Colorado (Zimmerman and Laven 1984)	28	38	12.5 (1759–1833)	2.4 (1834–1908)	3.4 (1909–1976)	32/21	32/7

*The top line refers to all fires and the lower line refers to only stand-replacing fires.

any influences of climatic variation on seedling establishment (Mast et al. 1998). Overgrazing by livestock in the late 1800s to early 1900s also has been suggested as an explanation of ponderosa pine increases (Marr 1961). Heavy grazing can reduce competition from grasses and expose bare mineral soil for tree seedling establishment, but tree invasion of grasslands has been continuous during the recent several decades of declining livestock impact (Veblen and Lorenz 1986; Mast et al. 1998). Although the timing and rate of ponderosa pine expansion during the present century probably have been influenced by short-term climatic variation and changes in grazing pressures, without the shift from a high-frequency fire regime to nearly total fire exclusion, this tree expansion is unlikely to have taken its present course. In contrast, in the subalpine zone, conifer invasion into grasslands is linked more strongly to climatic variation or to decreased pressure from livestock (Dunwiddie 1977, Jakubos and Romme 1993). In ponderosa pine woodlands in New Mexico, a decline in fire frequency in the early nineteenth century coincides with increased grazing by sheep that would have reduced fine fuels (Savage and Swetnam 1990). Similar relationships of livestock introduction and decreased fire spread due to fuel reduction probably exist for the Colorado-Wyoming region.

Increased density of ponderosa pine stands during the period of fire exclusion has changed the susceptibility of these forests to stand-replacing fires, pathogen infestation, and perhaps insect outbreak. Qualitatively, it is obvious that very sparse ponderosa pine woodlands did not support crown fires due to lack of woody fuel continuity. Quantitatively, however, the increase in area newly capable of supporting crown fires is difficult to estimate because even prior to any significant effects of fire exclusion some stand-replacing fires occurred in ponderosa pine forests (Veblen and Lorenz 1986, Shinneman and Baker 1997). At more mesic sites, initially open stands of ponderosa pine now have understories of suppressed Douglas fir that are susceptible to insect-caused mortality that further increases the hazard of stand-replacing fires. Dwarf mistle-toe populations are well known to accumulate in both ponderosa pine and lodgepole pine stands where fires have been excluded, and the weakening effects of these hemi-parasites may increase stand-susceptibility to other pests and fire (Zimmerman and Laven 1984; Kipfmüller and Baker 1998b).

A second pattern of altered fire regimes documented for some parts of the Southern Rocky Mountains is an increase in fire frequency in the latter half of the nineteenth century due to burning by EuroAmerican settlers (Table 3.1; Rowdabaugh 1978, Laven et al.

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1980, Skinner and Laven 1983, Goldblum and Veblen 1992, Kipfmüller 1997). Although this pattern is also found in additional fire history studies for the Sangre de Cristo Mountains, Colorado (Alington 1998) and the southern Front Range (Donnegan 1999), other studies in progress in Colorado do not report the same pattern (W. Romme, *personal communication*; P. Brown, *personal communication*). For the montane zone of the northern Colorado Front Range, fire dates from 526 trees from 41 sites indicate a nearly two-fold increase in the mean annual percentage of recorder trees recording fire scars for the period 1851 to 1920 in comparison with the previous 70 years (Veblen et al. 1996). Locations of fire-scarred trees in the northern Front Range indicate that there was also an increase in the frequency of large (i.e., >25 ha) burns during the late nineteenth century (Laven et al. 1980, Goldblum and Veblen 1992). Thus, the increased fire frequency associated with settlement was not exclusively an increase in small fires. The importance of large fires during the EuroAmerican settlement period is also consistent with the abundance in today's landscape of extensive, postfire stands of ponderosa pine, Douglas-fir and/or lodgepole pine that originated mostly between 1850 and 1910 (Clements 1910; Zimmerman and Laven 1984; Veblen and Lorenz 1986; Peet 1988; Hadley and Veblen 1993; Parker and Parker 1994; Kipfmüller 1997; Mast et al. 1998). As discussed below, the homogeneity of stand age and structure over such large areas may be influencing fire hazard and susceptibility to pathogen and insect attack at a landscape scale in the Southern Rocky Mountains.

INSECT OUTBREAKS

The most important insect pests of the Southern Rocky Mountains, all native species, are: mountain pine beetle, Douglas fir bark beetle, spruce beetle and western spruce budworm. All of the bark beetles tend to attack larger trees (typically >10–20 cm in diameter) and their attacks are normally lethal. They bore through the bark, create egg galleries, mate, and deposit eggs in the phloem layer. They carry with them fungi, which, in conjunction with the beetle's excavations, results in blockage of water- and nutrient-conducting tissue, killing the tree. In contrast, western spruce budworm is a defoliating moth with larvae that feed on needles and cones. Its attacks may or may not be lethal to the tree depending on numerous factors as discussed in a following section.

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Mountain Pine Beetle

In the Southern Rocky Mountains the mountain pine beetle primarily attacks live ponderosa and lodgepole pines; during epidemics, nearly 100% of overstory trees can be killed over many square kilometers (Schmid and Mata 1996). In the montane zone, outbreaks may convert mixed-aged stands to young stands of ponderosa pine or accelerate succession towards Douglas fir (Amman 1977). In the subalpine zone, elimination of the overstory lodgepole pine by a beetle outbreak can accelerate succession towards the more shade-tolerant Engelmann spruce and subalpine fir.

Mountain pine beetle outbreaks may recur in the same general region within about 20 years and may recur in the same stand in about 50 to 100 years depending on how much of the original stand was killed by beetles (Schmid and Amman 1992). Durations of outbreaks are quite variable (e.g., 2 to 14 years) and may decline rapidly if weather becomes unfavorable to the beetle populations (Schmid and Mata 1996). Numerous mountain pine beetle outbreaks have occurred during the twentieth century throughout the Southern Rocky Mountains (Roe and Amman 1970). It is widely believed that increased stand densities associated with fire exclusion in this century have increased the susceptibility of stands to outbreaks of mountain pine beetle (Roe and Amman 1970, Schmid and Mata 1996). However, no long-term (e.g., based on tree-ring records) studies have been done on the frequency or duration of outbreaks to examine this hypothesis. Also this hypothesis ignores the fact that the larger trees (i.e., those most susceptible to beetle attack) were removed from stands that subsequently have experienced outbreaks. Occurrence of extensive outbreaks in the late 1800s and early 1900s (Roe and Amman 1970) indicates that not all outbreaks can be attributed to the stand structural changes resulting from modern fire exclusion. Outbreaks are believed to increase the likelihood of fire occurrence over a period of about two years while the dead leaves persist on the trees (Schmid and Amman 1992), but longer-term influences on flammability may be quite complex. The fall of the dead leaves may also temporarily decrease fuel continuity in the canopy, but subsequent ingrowth of understory trees in combination with fall of dead trees eventually may increase fire hazard (Knight 1987). Fire-injured trees are generally more susceptible to attack by mountain pine beetle (Amman and Ryan 1991).

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Douglas Fir Bark Beetle

The Douglas fir bark beetle can cause widespread mortality of Douglas fir in the Southern Rocky Mountains, and its epidemics appear to have arisen during and expanded following outbreaks of western spruce budworm (Schmid and Mata 1996). Outbreaks have been observed to last from 5 to over 10 years, and intervals between outbreaks in the same areas may be on the order of 15 to 35 years (Hadley and Veblen 1993, Schmid and Mata 1996). Many of the same potential interactions with fire previously mentioned for mountain pine beetles apply to Douglas fir beetles (Cates and Alexander 1982).

Spruce Beetle

The spruce beetle in the Southern Rocky Mountains mainly infests Engelmann spruce (Alexander 1987, Schmid and Mata 1996). Endemic spruce beetle populations infest fallen trees and scattered live trees but during outbreaks can kill most canopy spruce over extensive areas. Spruce less than 10 cm in diameter usually are not attacked, nor are the subalpine fir, and their accelerated growth following the death of canopy trees can be used to date outbreaks (Veblen et al. 1991*b*). Stands containing large (i.e., >55 cm diameter) spruce and especially those in valley bottom sites are the most susceptible to outbreaks. Blowdowns or the accumulation of logging debris are usually the immediate triggers of outbreaks (Schmid and Frye 1977), which is an important distinction from outbreaks of mountain pine or Douglas fir beetle.

In 1939 a strong windstorm blew down extensive areas of subalpine forest in western Colorado, promoting the growth of endemic spruce beetle populations into the largest recorded epidemic of the twentieth century that killed 4.3 billion board feet of timber in White River, Grand Mesa, and Routt National Forests (Massey and Wygant 1954). Tree-ring methods and historical photographs document the occurrence of a spruce beetle outbreak in the mid-1800s in an area of northwestern Colorado at least as large as the 1940s outbreak (Baker and Veblen 1990; Veblen et al. 1991*b*, 1994). This widespread spruce beetle outbreak in the mid-1800s, as well as outbreaks recorded in fossil records (Feiler and Anderson 1993), occurred prior to any significant impact of EuroAmericans on the subalpine forests of northwestern Colorado in the form of either logging or fire suppression. Thus, widespread spruce beetle outbreaks are clearly a natural component of disturbance regimes in the subalpine zone.

Spruce beetle outbreaks result in a massive shift in dominance in basal area from spruce to fir due both to mortality of large spruce and

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the ingrowth of formerly suppressed seedlings and saplings of subalpine fir that are typically the most abundant tree species in the understory (Veblen et al. 1991*c*). Some new seedling establishment of spruce and fir is favored but not of the seral lodgepole pine, probably due to lack of heat for opening its serotinous cones and inhibition of seedling establishment by an already established understory. Spruce beetle outbreaks probably increase the hazard of fire ignition during a relatively short period of two to five years when fine fuels from dead needles and twigs are more abundant. The slow decay and fall rate of the dead-standing trees (Hinds et al. 1965) implies that there is an increased potential for more intense fire over many decades, but effects on stand flammability are complicated by the reduced continuity of fuels in the canopy.

The frequency of severe outbreaks in the same stand is limited by lack of trees large enough to be susceptible to beetle attack (Schmid and Frye 1977). At a stand scale, lack of large-diameter spruce for 70 to 100 years after a severe outbreak or a stand-replacing fire prevents that stand from being attacked even when surrounding older forest is attacked (Veblen et al. 1994, Schmid and Mata 1996). However, at a landscape scale, the White River area was affected by two major outbreaks in a span of only about 100 years (Veblen et al. 1991*b*). At a smaller scale in a 594-ha area of subalpine forest in northwestern Colorado, tree-ring methods documented three extensive spruce beetle outbreaks since the early 1700s (Veblen et al. 1994). Mean return interval and rotation period were 117 and 259 years, respectively, which made disturbance by spruce beetle more important, at least spatio-temporally, than disturbance by fire in this valley.

Western Spruce Budworm

The western spruce budworm primarily defoliates Douglas fir and white fir in the Southern Rocky Mountains (Schmid and Mata 1996). Extensive defoliation by budworm over several years can produce high levels of tree mortality. Suppressed trees and trees stressed because of poor site conditions suffer higher rates of mortality (Cates and Alexander 1982). Young, vigorous postfire stands may show minimal defoliation by budworm whereas multitiered stands with high stem densities and a range of tree sizes are more severely affected (Hadley and Veblen 1993). Spruce budworm outbreaks in mixed stands of Douglas fir and ponderosa pine tend to shift dominance towards pine (Hadley and Veblen 1993). During outbreaks, western spruce budworm larvae also consume cones and seeds which further impedes the ability of stands

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Table 3.2. Major historic insect outbreaks in the northern Colorado Front Range. *Source:* Barrows (1936) and Schmid and Mata (1996).

<i>Mountain pine beetle</i>	<i>Western spruce budworm</i>	<i>Douglas fir beetle</i>
1920s	Early 1940s	Mid-1930s
1930s	Late 1950s	Early 1950s
Late 1950s	Late 1970s–1980s	Mid-1980s
Mid-1970s		

to recover from attacks (Schmid and Mata 1996). During this century, several outbreaks of western spruce budworm and Douglas fir bark beetle have greatly altered the structure and composition of the montane forests of the northern Colorado Front Range (Table 3.2; Hadley and Veblen 1993). Durations of outbreaks are highly variable but average about eleven years (Swetnam and Lynch 1993). Tree-ring studies indicate that since the early eighteenth century epidemics in the Southern Rocky Mountains have occurred at a frequency of about 20 to 33 years in the same stands (Swetnam and Lynch 1989, Shimek 1996).

Given the apparently greater susceptibility of stands with suppressed understories of Douglas fir saplings, it is likely that fire exclusion during this century is creating a more homogeneous landscape of increased susceptibility to budworm outbreaks. Studies from Montana to New Mexico suggest that since the early 1900s budworm outbreaks have become increasingly severe and synchronous over larger areas (McCune 1983, Anderson et al. 1987, Swetnam and Lynch 1989, Hadley and Veblen 1993). Increased nineteenth century burning in the upper montane zone also would have created extensive areas of postfire even-aged stands that more or less synchronously become susceptible to budworm outbreaks (Hadley and Veblen 1993). During the initial decades of stand development, these postfire stands are not highly susceptible to outbreaks, but as stands continue to age they take on a multitiered structure with subcanopy populations of suppressed Douglas fir that increase stand susceptibility to outbreaks. This hypothesis is consistent with a period of reduced budworm outbreaks in the Front Range from the 1880s through the 1920s that is followed by several widespread and severe outbreaks (Swetnam and Lynch 1989, Shimek 1996).

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WIND

Exceptionally strong windstorms occasionally cause extensive blowdowns in the forests of the Southern Rocky Mountains, especially in the subalpine zone, and are important determinants of stand development patterns (Alexander 1987, Veblen et al. 1989). In the subalpine zone, frequency of high wind events may be greater; the rugged terrain creates greater turbulence, and the probability of heavy snow loads is greater (Alexander 1987). In the subalpine zone most tree species also are shallow rooted and development of dense, postfire stands increases stand susceptibility to blowdown (Alexander 1987). Single windstorms can produce enormous blowdowns. For example, in 1987, a tornado blew down 6,000 ha of forest in the Teton Wilderness (Fujita 1989, Knight 1994), and, in 1997, easterly winds of 200–250 km/hr blew down over 8,000 ha of forest on the western slope of the Park Range, Colorado, in Routt National Forest (USDA Forest Service 1998). In addition to these rare but spectacularly large blowdowns, small blowdowns of 0.2 to several hectares are common in the subalpine forests (Alexander 1964, Veblen et al. 1991*a*).

Despite the importance of small and large blowdowns to the dynamics of the subalpine forests, few studies have been done on either the frequencies or consequences of such events. Windthrow is greater where topographic or logging patterns constrict and therefore accelerate wind speed (Alexander 1964). Other features that increase the hazard of windthrow in relation to cutting operations include shallow soils, poorly drained soils, location on leeward cutting boundaries, dense stands, infestation by root and butt rots, and steeper slopes (Alexander 1964). Time elapsed since last fire, and therefore stage of seral development, is an important determinant of the successional consequences of disturbance by blowdown. For example, a 1973 blowdown of a 15-ha stand of a 350-year-old postfire forest in Rocky Mountain National Park accelerated succession from dominance by lodgepole pine towards subalpine fir and Engelmann spruce (Veblen et al. 1989). Similarly, comparison of wind disturbances in old-growth spruce-fir stands versus an adjacent approximately 250-year-old postfire stand revealed the latter to be less susceptible to small blowdowns (<0.3 ha) (Veblen et al. 1991*a*). As postfire stands dominated by lodgepole pine age, they appear to become more susceptible to moderate-sized blowdown (e.g., >10 ha), and blowdowns strongly accelerate succession towards spruce and fir (Veblen et al. 1989). This change, in turn, increases stand susceptibility to spruce beetle outbreak (Schmid

and Frye 1977). Thus, where humans have altered forest structures through changes in fire regimes and logging they have also altered the potential response to natural windstorms. Although disturbance by wind should be sensitive to changes in atmospheric circulation patterns that change either the frequency of windstorms or the directions of major gusts, no long-term data evaluate whether such changes have occurred over the last several centuries in the Southern Rocky Mountains.

INFLUENCES OF CLIMATIC VARIATION ON DISTURBANCE REGIMES

Fire

Although the focus of this book is on fragmentation caused by humans, it is important to recognize that variation in regional climate is also an important influence on landscape heterogeneity through its effects on fire and insect disturbances. On an interannual scale, synchronous occurrence of fire-scar dates from areas too large for fire to have spread from a single ignition point is strong evidence that regional climate is influencing fire regimes. For example, widespread burning in 1879 and 1880 is recorded in early, albeit fragmentary, documentary sources (Sudworth 1899, Jack 1899, Plummer 1912) as well as tree-ring studies of fire history from southern Wyoming to southern Colorado (i.e., Skinner and Laven 1983, Zimmerman and Laven 1984, Goldblum and Veblen 1992, Kipfmueller 1997, Veblen et al. 1996). Other individual years that recorded fire scars at disjunct locations over this large area include 1684, 1809, 1872, and 1893 (Kipfmueller 1997) which suggests that at a regional scale climatic anomalies increase fire hazard over extensive areas.

In the montane zone of the northern Colorado Front Range, comparison of tree-ring records of fire and climatic variation from 1600 to the beginning of fire suppression in 1920 indicates that fire is strongly associated with below average spring precipitation during the fire year and with above average spring moisture availability two to three years prior to the fire year (Veblen et al., *in press*). These records also show that for the two to three years following increased spring precipitation associated with El Niño events, fire occurrence increases. ENSO (El Niño–Southern Oscillation) signals are also found in fire records from ponderosa pine woodlands in Arizona and New Mexico (Swetnam and Betancourt 1990). North of the Front Range, however, sensitivity to ENSO events weakens (Kiladis and Diaz 1989), and it is likely that mid-latitude circulation anomalies will have greater influences on fire

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regimes. From an understanding of the effects of interannual variation on fire regimes, it may be possible to link longer-term trends in fire occurrence to longer-lasting (i.e., multidecadal) changes in atmospheric circulation patterns such as frequencies and intensities of ENSO events. However, the challenge is to discriminate between the influences of human activities and climatic variation on fire regimes.

Despite the availability of instrumental climatic records and more complete fire records (e.g., USDA Forest Service and National Park data) for the present century, it is difficult to clearly relate long-term changes in fire regimes to climatic variation. For all the national forests of northern Colorado, there appears to be a trend towards increasing numbers for all fires, lightning-ignited fires, and forested area burned per year during the 1970s and 1980s (Fig. 3.1). Increases in areas burned during the last few decades of the twentieth century generally for the western United States (Auclair and Bedford 1994, Balling et al. 1992) have multiple and nonmutually exclusive explanations. These explanations include: (1) improved accuracy of estimates of areas burned based on the use of aerial photographs since ca. 1940; (2) fire suppression effects on fuel accumulation; (3) adoption of "let burn" policies during the 1970s and 1980s in some areas; (4) altered fuel conditions due to increased insect-caused tree mortality; and (5) for some areas, increased temperatures.

Although it has been hypothesized that a trend towards warmer temperatures over the past few decades has contributed to increased burning and insect outbreaks generally in western North America (Auclair and Bedford 1994), for the Rocky Mountain region the evidence is equivocal. Analysis of approximately 100 years of climatic trends based on 79 climatic stations from northern Montana to southern Colorado reveals substantial differences in temperature and precipitation trends according to seasonality, latitude, and elevation, rather than a regionally uniform warming trend (T. Kittel, *personal communication*). For example, in the northern Colorado Front Range for high elevations there is evidence of a post-1951 decline in mean annual temperature in contrast to warming at the same time in adjacent low elevations (Williams et al. 1996). Furthermore, widespread fire occurrence at low elevation can be favored by enhanced production of fine fuels associated with above-average moisture availability (Veblen et al. 1996), whereas widespread fires in the subalpine zone are favored mainly by drought (Clagg 1975, Romme and Despain 1989, Renkin and Despain 1992). Thus, asynchrony in climatic trends with elevation as well as differential climatic sensitivity of fire regimes at high versus low

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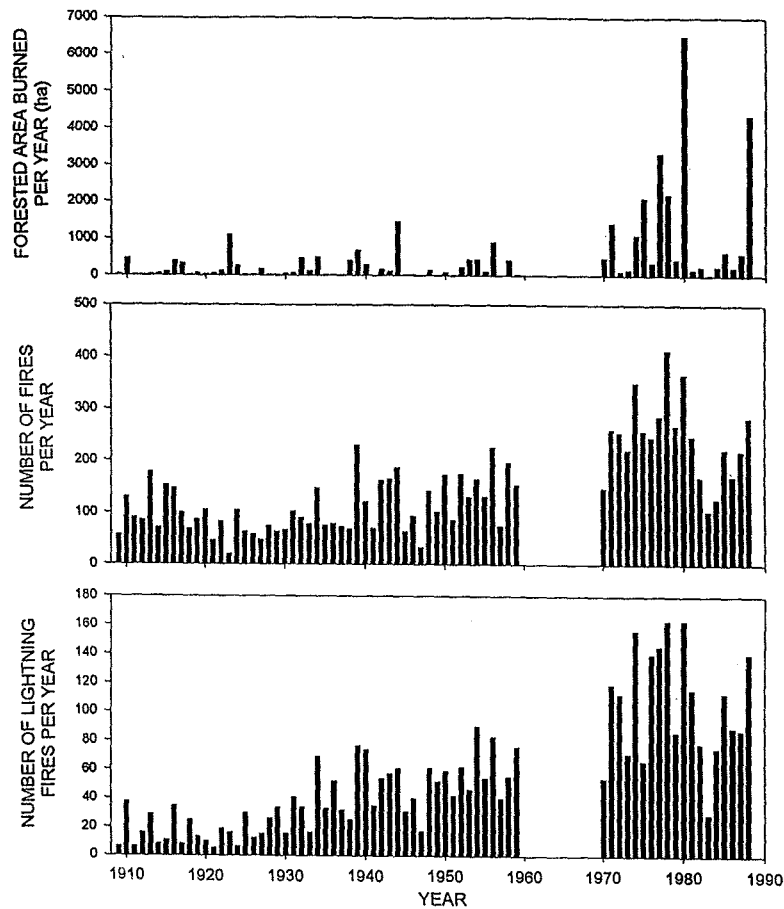


Fig. 3.1. Records of fire occurrence from five national forests in Colorado: Pike, Arapaho, Roosevelt, Routt, and White River National Forests for 1909 to 1988. No data are available for 1960–1969.

elevations greatly complicate the determination of causal influences of regional climatic variation on trends in fire regimes.

Insect Outbreaks

Weather profoundly affects the life cycles of insect pests as well as the capability of trees to respond to insect attacks, yet the effects of climatic variation on the occurrence of insect outbreaks are poorly understood (Swetnam and Lynch 1993, Logan et al. 1995). For example, mortality of mountain pine beetle is increased by cold winters, and cool temperatures are believed to be the major restriction on mountain pine beetle outbreaks at high elevations (Logan et al. 1995). Gener-

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ally, warmer temperatures promote bark beetle outbreaks both through their favorable influence on the life cycle of the insect and drought-related declines in the tree's ability to withstand attack (Frye et al. 1974, Amman 1977). However, nonclimatic factors related to stand structure also play such important roles that the association of outbreaks with particular types of weather is difficult to verify quantitatively.

Although it has long been believed that drought predisposes Douglas fir stands to outbreaks of western spruce budworm (Cates and Alexander 1982), recent research from Colorado and New Mexico suggests that wet periods may favor outbreaks. For example, in northern New Mexico tree-ring records of outbreaks from 1690 to 1989 indicate a tendency for outbreaks to coincide with years of increased spring precipitation (Swetnam and Lynch 1993). These records contrast with findings for the northwestern United States and eastern Canada where shorter-term records indicate an association of budworm outbreaks with periods of moisture deficit (Kemp et al. 1985). Tree-ring records from the northern Colorado Front Range indicate an association of initiation dates of budworm outbreaks with a sequence of one year of below-average spring moisture availability followed by a couple of years of above-average moisture availability (Veblen et al., *unpublished data*). Although the mechanisms relating budworm population dynamics and tree susceptibility to attack are not clear (Swetnam and Lynch 1993), there is strong evidence that climatic variation influences the occurrence of budworm outbreaks. However, nonclimatic changes in stand structures may play an equal or greater role.

CONCLUSIONS

Returning to the four key questions about disturbance that were stated in the introduction to this chapter, it is evident that there are only preliminary and partial answers to those questions for the Southern Rocky Mountain forests. For example, in a broad sense, subalpine forests are characterized mainly by stand-replacing fires whereas lower montane forests support more surface fires, but robust quantitative analyses of fire behavior along elevational gradients are lacking. Similarly, although potential links among different disturbance types in the Southern Rocky Mountains are widely recognized and numerous examples are given in this review and elsewhere (e.g., Knight 1987), there are few studies that quantitatively document these linkages (e.g., Malanson and Butler 1984, Suffling 1993, Veblen et al. 1994). In terms of human impacts on fire regimes in the montane zone, the

pattern of fire exclusion during this century is well documented for many sites throughout the Southern Rocky Mountains. The increase in burning associated with late nineteenth century EuroAmerican settlement is strong for some areas and absent for others; it may be limited to areas of more intensive land use such as the mining areas of the northern Colorado Front Range. Vegetation managers should regard both trends as common patterns that for any particular area must be corroborated by fire history studies based on adequate numbers of sample trees and sample sites. The high degree of spatial variation in fire history associated with differences in habitat and human activities implies that many more fire history studies are required in the Southern Rocky Mountains.

In contrast to the quantitatively large impact of fire exclusion on fire frequencies in the montane zone, in the subalpine zone fire exclusion over the past 70 to 90 years probably has only moderately increased mean fire return intervals from their pre-twentieth century levels. This needs to be recognized in evaluating forest health issues in the subalpine zone. For example, extensive outbreaks of spruce beetles, such as the mid-1800s and 1940s outbreaks affecting most of northwestern Colorado, cannot be attributed to fire exclusion. In contrast, for the montane zone there is strong evidence of changes in stand structures and susceptibility to insect pests during the fire exclusion period. For example, in the montane zone of the northern Colorado Front Range there is evidence of a shift during the twentieth century towards a more homogeneous landscape of stands that are increasingly susceptible to both insect outbreaks and stand-replacing fires. Even within the montane zone, however, there is substantial variation in disturbance history and patterns of vegetation change, and some of the generalizations made in this review may not be valid for a particular site. In discussion of management options, it is important to recognize the high degree of variation in disturbance histories along environmental gradients and to avoid taking generalizations out of their appropriate context.

Interannual climatic variability can create conditions favorable to exceptionally widespread burning in individual years as well illustrated by the 1988 Yellowstone fires, and multidecadal climatic variation potentially can have similarly dramatic influences on patterns of disturbance by fire and insects. In the context of forest fragmentation, it is important to consider the potentially large role of climatic variation in altering disturbance regimes and vegetation patterns. For the forests of the western United States in general, it has been suggested that

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recent increases in fire and insect outbreaks reflect a combination of synchronization of forest structures by nineteenth century burning, fuel accumulation under modern fire exclusion, and fire-promoting weather associated with more frequent El Niño events since the mid-1970s (Auclair and Bedford 1994). Although the Southern Rocky Mountains appear to conform to that general pattern, much more site-specific research is needed on how humans and climatic variation affect disturbance patterns and landscape structure (Baker 1994, 1995). A better understanding of landscape patterns in relation to disturbance patterns requires that researchers more fully consider the potential influences of both humans and climatic variation on disturbance regimes.

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Forest Fragmentation
in the
Southern Rocky Mountains

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