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Seventeen Years of Forest Succession Following the Waterfalls Canyon Fire in Grand Teton National Park, Wyoming

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Abstract. Plant species composition has been sampled periodically since the 1974 Waterfalls Canyon Fire in Grand Teton National Park, Wyoming. Prior to the fire, the forests were dominated by mature *Abies lasiocarpa, Picea engelmannii* and *Pinus contorta.* All three tree species have reestablished. After 17 years, *P. engelmannii* sapling density was 1.2-11.2 times greater than the other tree species. *A. lasiocarpa* and *P. contorta* saplings were second in density to *P. engelmannii* in the moderate and severely burned stands, respectively. The understory shrub and herbaceous species that were most abundant during the first 17 years were common the first year after the fire and were also found in the unburned mature forest. Species present in the unburned forest contributed 91-100% of the understory cover in the moderate burn, and 55-74% in the severe burn. Species richness was greatest in the severely burned stand and has increased during the 17 years of succession. While sprouting is the primary mechanism for understory plant establishment in the moderate burn, most species appear to have grown from seeds in the severe burn.

Keywords: *Abies lasiocarpa*; Fire severity; Permanent plots; *Picea engelmannii*; *Pinus contorta*; Species diversity.

Introduction

In the early 1970s, growing awareness of the potential impacts of fire suppression and the threat of intense fires due to fuel accumulation prompted the National Park Service to allow some fires to burn (Kilgore and Briggs 1972, Habeck and Mutch 1973, Taylor 1973). One of the first to be managed under the new fire policy was the Waterfalls Canyon fire (WCF) in Grand Teton National Park (GTNP), Wyoming. The fire was ignited by lightning on July 17, 1974. Amid much public controversy, the fire burned 1414 ha before it was extinguished by snow in late November (Taylor 1976). In June of the following year, two of us (Barmore and Taylor) established permanent plots in moderately and severely burned forests and in an adjacent unburned mature forest dominated by *Abies lasiocarpa, Picea engelmannii* and *Pinus contorta*. Data were collected from the permanent plots in 1975, 1976, 1977, 1983 and 1991. This paper describes the changes that occurred.

Long-term observation of permanent plots provides more precise data than the comparison of stands of different age, but few studies of this nature have been done in the northern Rocky Mountains (Lyon and Stickney 1976, Stickney 1980) and none have focused on forests where *A. lasiocarpa* and *P. engelmannii* were the dominant prefire species. With the WCF data, we examined the effects of burn intensity on plant species composition and life history characteristics during the first 17 years of succession.

Methods

Study Site

Permanent plots were established in 1) a severely burned stand (all trees killed and the above-ground portions of understory species consumed), 2) a moderately burned stand (more than 40% of the canopy trees alive one year after the fire), and 3) a nearby unburned forest. The two burned stands are at about 2070 m elevation and are located on glacial moraines between the east slope of the Teton Range and the west shore of Jackson Lake. The terrain slopes gently (0-5%) toward the east. The underlying glacial till contains Precambrian gneiss, schist, amphibolite and granite (Love et al. 1992). The unburned stand is similar in elevation and topography and is also located on a glacial moraine (though composed mostly of quartzite and volcanic rock, with less gneiss, schist, amphibolite and granite). Soils from all three stands have been mapped as loamy-skeletal, mixed Typic Cryocrepts (Young 1982).

Prior to the WCF, *A. lasiocarpa*, and *P. engelmannii* were the dominant trees throughout the study area (Table 1). *P. contorta* was less abundant (Table 1). Ages of the largest trees suggest that the area had not burned for more than 200 years prior to 1974. A 1936 vegetation map of the Teton Range (Dole et al. 1936) designates the stands which burned in 1974 as *P. engelmannii-A. lasiocarpa-P. contorta* forest, and the unburned forest as *A. lasiocarpa-P. contorta*. This map suggests that *P. engelmannii* may have been less abundant in the unburned forest stand in 1936, in contrast to 1975 when it was second to *A. lasiocarpa*. The three stands occur in a forested area that has been classified in the *Abies lasiocarpa-Vaccinium globulare* habitat type (unpublished map, Interagency Grizzly Bear Study Team), a habitat type that occurs mainly on northerly and easterly slopes at low to middle elevations (Steele et al. 1981).

Continental weather patterns characterize the region. Mean annual precipitation in nearby Moran, at 2064 m elevation, is 59 cm. Seventy-one percent of the annual precipitation falls between November and May, primarily as snow (Martner 1986). Almost annually, in late summer and fall, the dry fuels and high incidence of lightning strikes favor the ignition and spread of fire in the region.

Sampling and Analysis

Three 15 x 25 m plots, marked at each corner with metal stakes, were located about 45-50 m apart within the severely burned, moderately burned, and unburned stands (Barmore et al. 1976). Species composition was sampled between June and August in 1975, 1976, 1977, 1983 and 1991. Height and diameter at breast height (dbh) were determined for all trees (living and dead) greater than 0.5 m tall. Trees between 0.5 and 1.4 meters tall were assigned a dbh of 1.3 cm. Tree density and basal area were not measured before 1983 in the severe burn because the charred dead trees were difficult to identify and no live trees were more than 0.5 m tall.

Tree basal area ($m^2.ha^{-1}$) and density ($number.ha^{-1}$) were determined for each stand by averaging data from the three plots. Tree data were summarized for two height classes: 0.5-7 m (saplings) and >7 m. The sapling size class includes trees which established after the fire, as well as small trees which survived fire (none in the severely burned stand).

Table 1. Relative and total live-plus-dead basal area of tree species in 1975, one year after the WCF, in the unburned and moderately burned permanent plots. Comparable data could not be obtained from the severely burned stand.

	Unburned		Moderate Burn	
Species	%	$M^2 \cdot ha^{-1}$	%	$m^2 \cdot ha^{-1}$
Abies Lasiocarpa	62	17.4	49	17.8
Picea engelmannii	26	7.3	41	14.6
Pinus contorta	12	4.4	10	3.6
Total	100	28.1	100	36.0

To sample the understory vegetation, two permanently- marked 25 m transects were established within each plot and ten 50 x 20 cm quadrats were located at 2.5 m intervals along each transect (for a total of 20 quadrats per plot, 60 per stand). The number of trees <0.5 m was counted in each quadrat, and the percent cover for shrub and herbaceous species was estimated using the cover class method of Daubenmire (1959). Total percent cover for all understory species was determined by summing the mean cover for all understory species (excluding trees). Plant nomenclature follows Dorn (1992).

Early successional species can be characterized by their time of establishment, adaptations for dispersal or survival, and how long they persist during the course of succession (Noble and Slatyer 1980, Rowe 1983, Stickney 1986, Pickett et al. 1987, Halpern 1989). We recognized two classes of early successional species: persistent species and transient species. Persistent species are those found in the mature forest and in the first postfire year. They frequently have underground structures that survive fires, but seed stored in the canopy or soil seed bank, or dispersed from areas adjacent to the burn, may also be important (Stickney 1986, Clark 1991). Transient species are short-lived in recently burned areas and are absent (or nearly so) in mature forest. Some transient species may appear immediately following fire if their seeds remain viable in the soil for long periods (Bazzaz 1979, Stickney 1986), while others are not dispersed to the burned area until 2-3 years later. Our "persistent species" are analogous to the "residual species" of Halpern (1989) and the "forest species" of Turner et al. (1997), whereas our "transient species" resemble the "invaders" and "opportunistic species" recognized by Halpern and Turner et al., respectively.

The three WCF stands were all in close proximity, and they occurred on glacial moraines at the same elevation with similar topography. Therefore, we compared the moderately and severely burned stands to infer the effect of fire severity. We also compared the burned stands with the unburned forest to provide insights on the probable prefire character of the burned stands, especially the understory. If a species known to sprout from underground structures was present shortly after the fire, and the species also occurred in the nearby unburned forest, we assumed the species was present in the burned stand before the fire.

Though permanent plots provide the best data for determining change over time, our study has a major limitation. Due to limited resources and difficulty in finding comparable sites, the treatments were not replicated. Thus, it is not possible to determine if observed differences between the stands are due to fire alone or to differences in environmental characteristics between the stands. Also, our results are not generalizable over a larger area. Nevertheless, the WCF data provide information

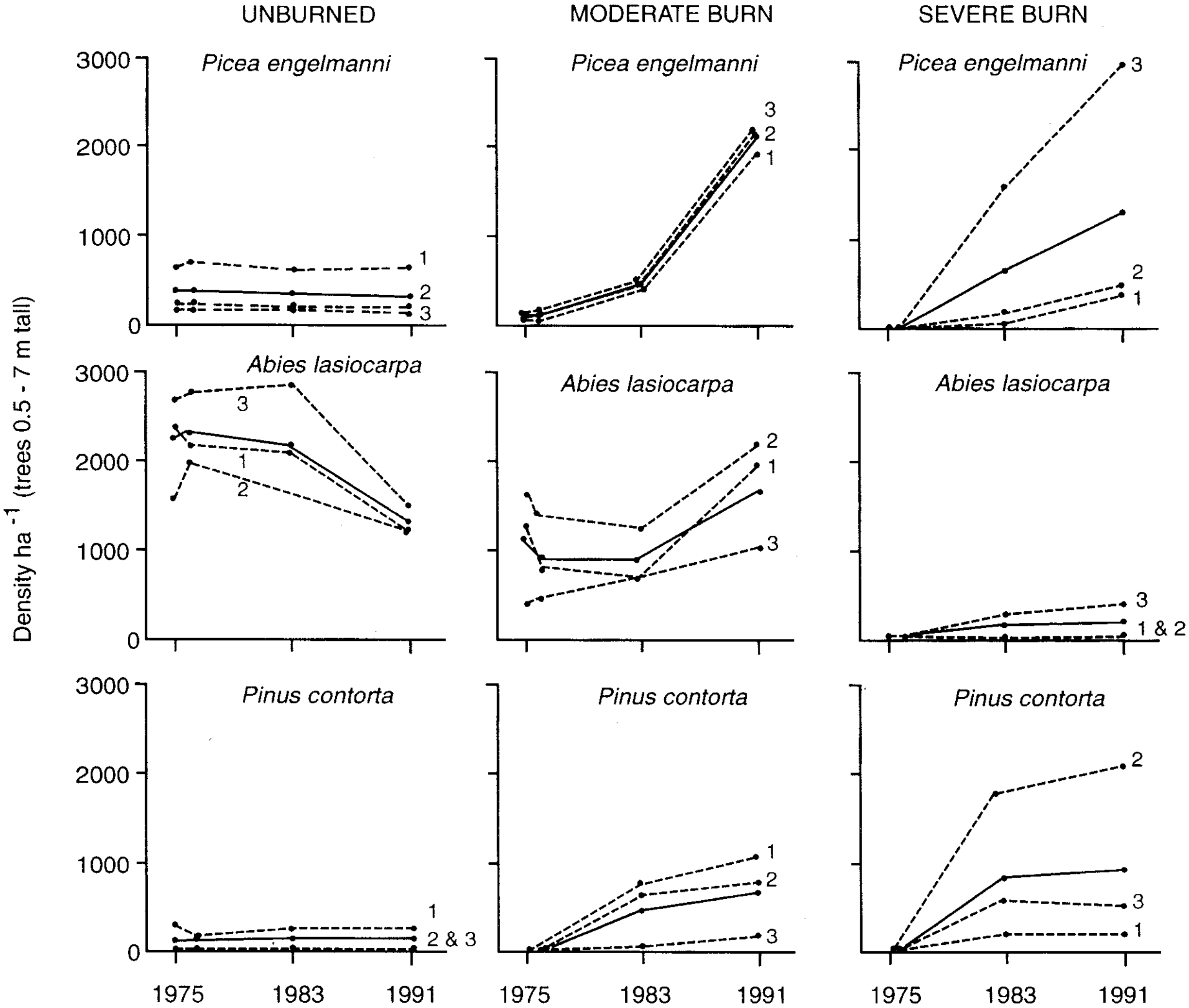

Figure 1. Density of live saplings (0.5-7 m tall) for *Picea engelmannii, Abies lasiocarpa* and *Pinus contorta* in the unburned, moderately burned, and severly burned stands. Data from each of the three plots in each stand are represented by the dashed line and plot number; and the mean of the three plots is indicated by a solid line.

not obtainable in any other manner and such long-term data sets are rare. The data are archived in the Resource Management Office of Grand Teton National Park, Moose, Wyoming.

Results

Postfire tree species composition

Seventeen years after the fire, the sapling density of *P. engelmannii* exceeded that of *P. contorta* and *A. lasiocarpa* in both burned stands (Figure 1). The total density of saplings of all tree species was greater in the moderate burn than in the severe burn. *P. engelmannii* sapling density was consistently high in the three plots of the moderate burn, compared with the more variable density for the plots in the severely burned stand. Notably, *P. engelmannii* seedlings were more abundant than any other tree species in both stands during the first postfire year (Barmore et al. 1976).

A. lasiocarpa saplings were at least 15x more abundant in the moderate burn than in the severe burn, due to more successful establishment by seed and greater survival of young trees (Figure 1). Seedling establishment of *A. lasiocarpa* was high in the moderate burn during the first postfire year, but low in the severe burn (Barmore et al. 1976). Also, 81% of the small trees (<7 m) that survived the moderate fire were *A. lasiocarpa* (Figure 1). A small number of *Pseudotsuga menziesii* and *Populus tremuloides* saplings also were found in the moderately burned plots (after nine and seventeen years, respectively).

The density of *Pinus contorta* saplings was variable among the plots in both of the burned stands (Figure 1). In the severe burn, *P. contorta* density was second to *P. engelmannii*, whereas in the moderate burn *P. contorta* was less abundant than either *P. engelmannii* or *A. lasiocarpa*. No saplings of *P. contorta* survived the fire within the moderately burned plots.

The density of all live trees >7 m and the total basal area of live trees (>0.5 m tall) declined for the three predominant species in the moderate burn between 1975 and 1977 (Figures 2 and 3). Consistent with this decline is an increase in dead basal area during the first few years after the fire (Doyle 1994). Between 8 and 17 years after fire, total live basal area increased steadily in the moderate burn (Figure 3).

Understory species composition

Unburned forest

Vaccinium globulare dominated the understory of the unburned forest with a cover that ranged between 30-36% during the study (Table 2). Other important shrubs in the unburned stand were *Lonicera utahensis* (5-9% cover), *Chimaphila umbellata* (4-7% cover), and *Spiraea betulifolia* var. *lucida* (3-5% cover). *Carex geyeri* and *Calamagrostis rubescens* (6-7% and 5-9% cover, respectively) also were common. Species with lower cover (<2%), but which were present every year that data were collected, included *Arnica cordifolia, Goodyera oblongifolia, Hieracium albiflorum, Mahonia repens, Orthilia secunda, Osmorhiza* spp., and *Thalictrum* spp.

Moderate burn

Carex geyeri, Calamagrostis rubescens, Epilobium angustifolium, Hieracium albiflorum, and *Vaccinium globulare* were the most abundant species in the moder-

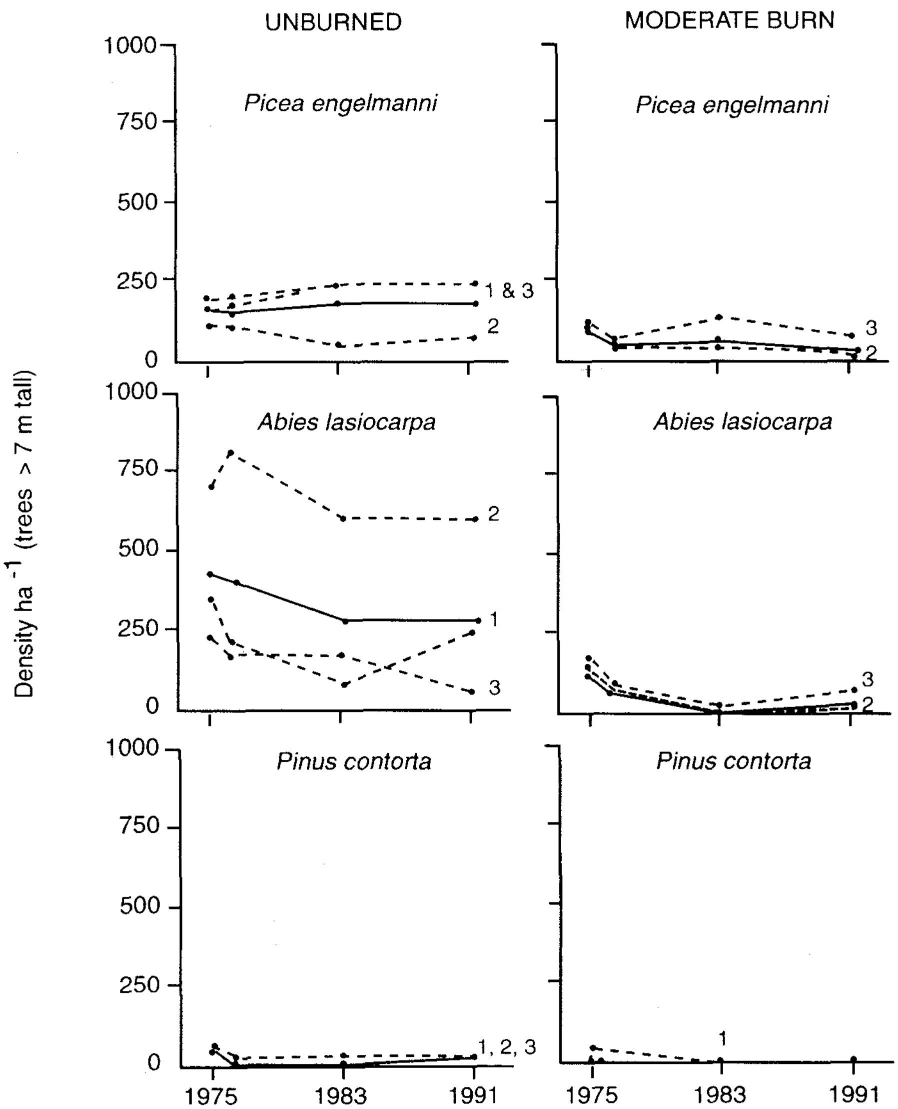

Figure 2. Density of live trees > 7m tall for *Picea engelmannii, Abies lasiocarpa* and *Pinus contorta* in the unburned and moderately burned stands. No trees in the severly burned stand were taller than 7 m between 1975 and 1991. Data from each of the three plots in each stand are represented by the dashed line and the plot number; the mean of the three plots are indicated by a solid line.

ate burn, each reaching at least 7% cover during the first 17 years (Table 2, Figure 4). These species, plus *Chimaphila umbellata*, *Lonicera utahensis* and *Spiraea betulifolia* var. *lucida* (cover ca. 1-3%; Table 2), were present one year after the fire and remained through the first 17 years. No species arriving after the first year (e.g., *Ceanothus velutinus*, *Cirsium arvense* var. *horridum*, *Elymus glaucus*, and *Taraxacum* spp.) had more than 5% cover during the 17-year period (Table 2, Figure 5).

Severe burn

The most important postfire species in the severe burn included *Carex geyeri*, *Calamagrostis rubescens*, *Epilobium angustifolium*, *Astragalus alpinus* and *Arnica cordifolia* (Table 2). All were present throughout the 17-year period, reaching at least 9% cover (Figures 4 and 5). *Spiraea betulifolia* var. *lucida*, *Vaccinium globulare*, *Mahonia repens*, *Aconitum columbianum*, *Galium boreale* and *Viola orbiculata* were also present all years (maximum cover 1-3%). Of the aforementioned species, all except *A. alpinus*, *A. columbianum* and *V. orbiculata* were found in the unburned forest. *Elymus glaucus*, *Cirsium arvense* var. *horridum* and *Taraxacum* spp., which were absent or rare in the unburned forest, reached >5% cover but were not observed until at least two years after the fire (Figure 5). *Iliamna rivularis* and *Dracocephalum parviflorum* were present initially in the severely burned stand (reaching at least 3% cover), but they were absent by nine years after fire and did not occur in the unburned forest. Notably, *I. rivularis* was extremely abundant adjacent to the severely burned plots in the second year after fire (Dale Taylor, pers. comm.).

Species richness and total cover

Species richness (number of species) was greatest in the severely burned plots in all years (at least two times greater than in the moderate burn or the unburned forest after 17 years; Table 2). During the study, a total of 56

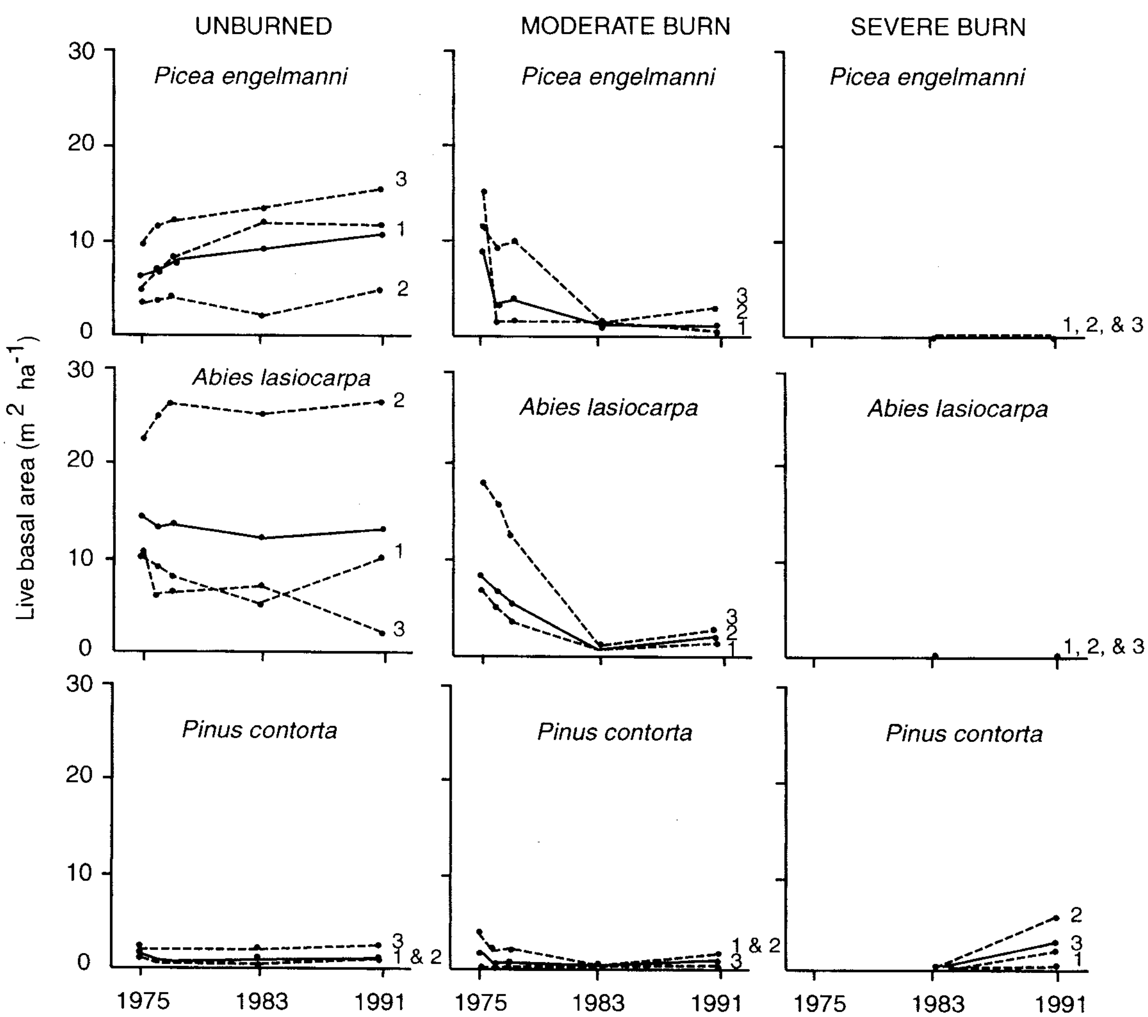

Figure 3. Total basal area for live saplings and trees (>0.5 m tall) for *Picea engelmannii, Abies lasiocarpa* and *Pinus contorta* in the unburned, moderately burned, and the severely burned stands. No trees in the severly burned stand were taller than 7 m between 1975 and 1991. Data from each of the three plots in each stand are represented by the dashed line and the plot number; the mean of the three plots is indicated by a solid line.

Table 2. Mean percent cover and richness of understory species in the unburned, moderately burned and evenly burned stands. t=cover less than 0.5%. Sixty (20 x 50 cm) quadrats were sampled in each stand. Richness = number of vascular plant taxa in each stand, excluding trees.

	Unburned					Moderate Burn					Severe Burn				
SPECIES	75	76	77	83	91	75	76	77	83	91	75	76	77	83	91
GRASSES															
Argrostis sp.														t	
Bromus anamalous															t
Bromus carinatus										1		t	t	1	
Bromus cf. vulgaris					t										
Calamagrostis canadenisi															t
Calamagrostis rubenscens	7	7	9	5	5	1	2	3	13	9	1	4	3	27	9
Elymus glaucus				1					3	1				11	3
Melica spp. (spectabilis/bulbosa)											t	1	1		t
Oryzopsis sp.		t													
Stipa nelsonii var. dorei	t										t	t	1		
Trisetum spicatum														t	
SEDGES															
Carex geyeri	6	6	6	7	7	10	14	18	33	19	4	11	10	21	9
Carex hoodii															1
Carex pachystachya															t
Carex sp.												1	2	2	
FORBS															
Achillea millefolium var. lanulosa														t	t
Aconitum cloumbianum											1	1	t	2	2
Agoseris spp. (aurantiaca/laevigatum)															t
Anaphalis margaritacea									t	t				2	t
Angelica arguta															t
Antennaria microphylla														1	t
Antennaria parvifolia															t
Arabis sp.															t
Arnica cordifolia	2	2	1	2	1	t	t		t	t	5	9	6	1	2
Arnica latifolia														3	
Arnica parryi															t
Aster occidentalis															t
Aster (aceae)sp.							t				t	1	t	2	
Astragalus slpinus											1	3	4	10	4
Campanula rotundifolia															1
Chenopodium sp.											t	t	t		t
Cirsium arvense var. horridum								1	5	t				5	1
Dracocephalum parviflorum											2	7	t		
Epilobium angustifolium						1	4	7	7	3	2	7	11	9	2
Epiloboum sp.								t	t		t	1	1	2	
Fragaria virginiana														t	1
Galium boreale											t	2	1	3	1
Gentianella amarella vaar. amarella															t
Gnaphaloum viscosum															t
Goodyera oblongifolia	t	1	1	1	1	t	t	t		t					
Habenaria sp.		t					t								
Heiracium abliflorum	1	1	t	t	t	t	1	1	8	1			t	1	1
Iliamna rivulareis											1	3	3		
Lacurca sp.											t				
Ligusticum filicinum													t	t	t
Orthilia secunda	1	1	1	1	1	t	t		t						
Osmorhiza spp. (chilensis/depauperata)	2	1	1	1	1				t	t				t	t
Pedicularis racemosa var. alba	1	1	1	t											t
Perideridia montana											t				
Polygonum douglasii var. douglasii														t	
Rudbeckia occidentalis													t	1	1
Senecio integarrimus								1							
Senecio serra var. serra															t

Table 2. Continued.

Solidago multiradiata vcar. scopulorum								t	t	t					1
Tarazacum spp. (laevigaum/officianale)						t			1	1		t	t	7	10
Thalictrum spp. (fendleri/occidentale)	2	1	1	2	2						t	t	2	2	t
Viola orbiculata											t	t	1	1	t
Wyethis sp.												t			
SHRUBS															
Amelanchier alnifolia	1	1	t	t											
Ceanothus velutinus							1	2	1	1					
Chimaphila umbellata var. occidentalis	7	6	6	6	4	2	3	1	1	t			1		
Lonicera utahensis	8	9	8	8	5	1	1	1	1	t	1			t	
Mahonia repens	1	t	1	1	t	t					t	1	1	2	1
Ribes lacustre								t	t	t					
Sorbus scopulia	t	t		1	t										
Spiaea betuilifolia var. lucida	4	3	4	5	3	1	2	3	1	1	t	2	2	1	1
Vaccubuyn globulare	33	36	36	30	36	6	4	5	7	5	1	t	1	1	1
Vaccinium scoparium							t		t			t	t	t	1
Species richness	17	18	15	17	15	11	16	15	20	20	21	25	26	32	44
Total percent cover	75	77	76	71	67	22	32	42	82	42	20	54	50	116	54

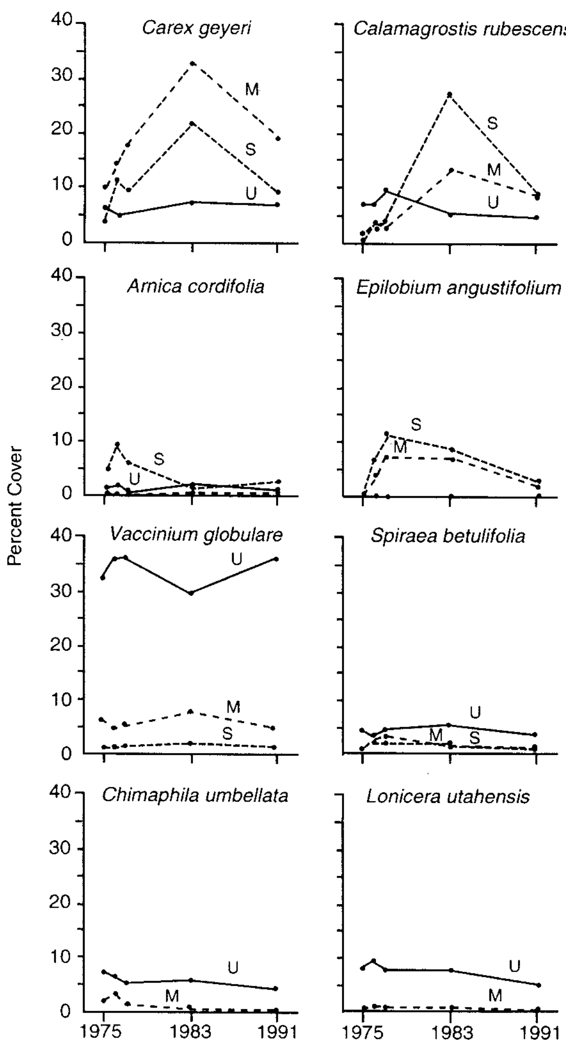

Figure 4. Mean percent cover of persistant species in the unburned (U), moderately burned (M) and severly burned (S) stands.

understory species were recorded on the severely burned plots, 26 on the moderately burned plots, and 21 on the unburned forest plots. Species richness increased until nine years after fire in the moderate burn, but increased throughout the study in the severe burn. Ninety-five percent of the species in the unburned stand were found in one or both of the burned stands (Table 2). Conversely, 62% of the taxa in the moderate burn and 29% of the taxa in the severe burn were present in the unburned forest (Table 2).

Total cover of all understory species in the two burned stands increased ca 400-600% during the first 9 years and then declined 40-60% between years 9 and 17. Total cover was 20-60% higher in the severe burn than in the moderate burn during all years, except in the first postfire year, but remained fairly constant during the study in the unburned stand (67-77%; Table 2).

Persistent species

Persistent species were important during early succession in both of the burned stands. In the moderate burn, 90% of total understory cover was comprised of persistent species during the 17-year period (Table 3, Figure 4). In the severe burn, persistent species made up about 70% of total understory cover during the first 9 years after fire, but dropped to 55% of total understory cover 17 years after fire (Table 3).

Five persistent herbaceous species (*Calamagrostis rubescens, Carex geyeri, Arnica cordifolia, Hieracium albiflorum* and *Epilobium angustifolium*) appear to have increased following fire. *C. rubescens* and *C. geyeri* had greater cover in both burned stands than in the unburned forest during much of the 17-year period (Figure 4). *A. cordifolia* was abundant in the severe burn during the first

Table 3. Relative cover (percent of total understory cover) of persistent species in the moderately and severely burned stands. Persistent species are those found in the unburned forest and which presumably occurred in the stands before the fire.

Stand	1975	1976	1977	1983	1991
Moderate burn	100	96	94	91	92
Severe Burn	74	67	73	68	55

few years following fire, but later decreased to levels found in the unburned forest (Figure 4). *H. albiflorum* was most abundant in the moderate burn 9 years after fire, but by 17 years postfire its cover fell to levels similar to those in the unburned forest and severe burn. Notably, *H. albiflorum* was not recorded in the severe burn until three years after the fire and its cover never exceeded 1% (Table 2). *Epilobium angustifolium,* rare in the unburned forest, increased rapidly during the first three postfire years before declining markedly over the next 14 years (Figure 4).

Other late-successional species, especially shrubs, had lower cover in both burned stands than in the unburned forest (Table 2). *Vaccinium globulare*, *Lonicera utahensis*, and *Chimaphila umbellata* sprouted one year after the fire in the moderate burn, but during the study they did not reach the level of cover found in the unburned forest (Figure 4). These shrubs were even less successful in the severe burn. *V. globulare* was present in all years after the fire in the severe burn, but was much less abundant there than in the moderate burn or unburned forest. In contrast, the cover of *Spiraea betulifolia* in the moderate and severe burns was similar to that in the unburned forest during the early postfire years — suggesting high survival of rhizomes — but it subsequently declined.

Transient species

Several species common in the burned stands were not found or occurred only sporadically in the unburned forest (*Elymus glaucus, Cirsium arvense* var. *horridum,* and *Taraxacum* spp.; Figure 5). All have small seeds that can be dispersed long distances by wind, and none was present one year after the fire. Following their arrival 2-3 years after the fire, *E. glaucus* and *C. arvense* var. *horridum* increased and then declined in both burned stands (Figure 5). *Taraxacum* spp. has increased over time in the severe burn and has maintained low cover in the moderate burn during the 17-year period. *Iliamna rivularis, Dracocephalum parviflorum* and *Astragalus alpinus* also appear to be transient species (Figure 5), but unlike the others, they were found the first year after fire in the severely burned stand. Presumably they developed from seed already in the soil at the time of the fire (Bradley et al. 1992).

Discussion

Data from the WCF suggest that the plants, seeds and other propagules present at the time of disturbance are important in postfire succession. Most of the species important during the first 17 years of succession, in both severely and moderately burned stands, emerged in the first postfire year and were apparently components of the prefire vegetation (as indicated by their presence in the nearby unburned forest). In contrast, only a few species absent from the unburned forest were important during the 17-year period. Other studies on Rocky Mountain vegetation also indicate that most plant species found on a site will re- establish during the first postfire year (Lyon

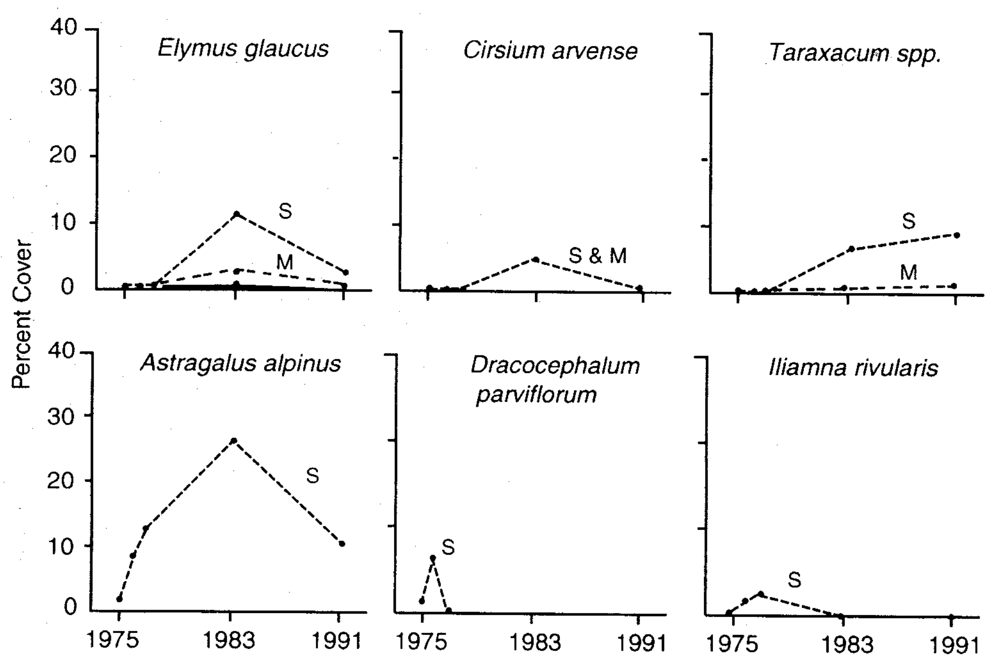

Figure 5. Mean percent cover of transient species in the unburned (U), moderately burned (M) and severely burned (S) stands.

and Stickney 1976, Armour et al. 1984, Stickney 1986, Anderson and Romme 1991, Turner et al. 1997), lending support to Egler's (1954) initial floristic composition hypothesis.

Life history traits

Many late seral (persistent) species establish soon after fire by sprouting from surviving plant structures (Lyon and Stickney 1976). For example, sprouting from underground rhizomes is an important means of surviving fire for *Carex geyeri* (Stickney 1986) and *Calamagrostis rubescens* (Bradley et al. 1992). Both species rapidly increased in abundance in the severe and moderate burns of our study area.

Late-seral shrub species differ in their below-ground morphology and ability to survive fire. *Spiraea betulifolia* var. *lucida* was the shrub species most resistant to fire, probably because of deep rhizomes (Mclean 1969, Bradley 1984). In contrast, *Lonicera utahensis*, *Chimaphila umbellata* and *Vaccinium globulare* have more shallow roots and rhizomes, which may explain why they were less successful in the burned stands. Notably, all three shrubs were more successful in the moderate burn than in the severe burn.

Combining the ability to sprout and produce numerous seeds is an effective adaptation to fire for some herbaceous plants. *Epilobium angustifolium* persists in unburned forests, sprouts vigorously from rhizomes after fire, and then produces numerous flowering stalks and light, wind- dispersed seeds. This species was most abundant during the third year after fire, as it was following the 1988 fires in Yellowstone National Park (Turner et al. 1997). *Calamagrostis rubescens* also increased dramatically over time in both burned stands. *Arnica cordifolia* and *Hieracium albiflorum* are susceptible to fire because their root systems are shallow (McLean 1969, Bradley et al. 1992), but they may reinvade because many wind-borne seeds are produced. Notably, Romme et al. (1995) found that *A. cordifolia* seeds were essentially nonviable in Yellowstone National Park, suggesting that sprouting is the primary mechanism for the persistence of this species after fire.

Long-term seed viability (Rowe 1983) may be an important adaptation for plants lacking mechanisms for sprouting and long distance dispersal. Three shade- intolerant, transient species, namely, *Iliamna rivularis, Ceanothus velutinus* and *Dracocephalum parviflorum*, have been documented as having long-term seed viability and high postfire germination rates (Lyon and Stickney 1976, Kramer 1984, Stickney 1986, Anderson and Romme 1991, Bradley et al. 1992).

Three other transient species, *Cirsium arvense* var. *horridum, Elymus glaucus* and *Taraxacum* spp., were not part of the initial postfire vegetation in either burn. In subsequent years, however, they were found in both the severely and moderately burned stands. These species have light, wind-dispersed seeds and probably dispersed long distances to the burns.

The three tree species that were dominant before the WCF, *Abies lasiocarpa, Picea engelmannii* and *Pinus contorta*, became established following the fire even though they do not sprout and they require a nearby seed source for successful postfire establishment (Lotan 1975, Alexander et al. 1990, Alexander and Shepperd 1990, Bradley et al. 1992). The three severely burned plots were within 75-120 m of surviving trees. In the moderate burn, surviving trees within each plot provided a more readily available seed source.

Our finding that *P. engelmannii* can be the predominant pioneer species is not inconsistent with the results of other studies in the Rocky Mountains (Stahelin 1943, Whipple and Dix 1979, Peet 1981, Romme and Knight 1981, Veblen 1986, Johnson and Fryer 1989, Bradley et al. 1992), though Loope and Gruell (1973) concluded that *P. engelmannii* regeneration is very slow in the Teton region. Establishment usually depends on adequate moisture and a mineral-soil seed bed (Noble and Alexander 1977, Knapp and Smith 1982). Bradley et al. (1992) concluded that the effective distance of *P. engelmannii* seed dispersal is 90 m, although Alexander and Shepperd (1990) found that many seeds could be dispersed up to 180 m into an opening.

A. lasiocarpa is generally a less successful postfire pioneer species than *P. engelmannii* and *P. contorta*, but, as we observed, establishment of *A. lasiocarpa* under certain conditions is coincident with *P. engelmannii* and *P. contorta* (Stahelin 1943, Whipple and Dix 1979, Aplet et al. 1988). Johnson (1992) noted that *Picea glauca, Pinus banksiana* and *Abies balsamea* could all be common within a few years after fire (the fire cohort) in the boreal forest.

P. contorta is often the most successful pioneer species in Rocky Mountain forests due to its ability to produce serotinous cones and release many seeds after fire, when a mineral soil seed bed is available and competition for resources is low. Moreover, faster growth and higher water use efficiency often give *P. contorta* a competitive advantage over *A. lasiocarpa* and *P. engelmannii* in early succession (Knapp and Smith 1981). However, the proportion of *P. contorta* with serotinous cones varies across the landscape (Tinker et al. 1994). When the density of serotinous *P. contorta* is low, the proximity to live trees is important for postfire establishment (Ellis et al. 1994). In the unburned forests near the severely and moderately burned stands, both percent serotiny and density of *P. contorta* were low. This suggests that low seed availability caused the relatively low density of P. contorta after the WCF.

Species responses to burn severity

Stickney (1982, 1990) predicted that fewer shrubs and forbs will sprout following severe fires because of higher fire-caused mortality, and that species establishment from seed will be favored when this happens. Stickney's prediction is consistent with our results and with several studies in Yellowstone National Park (Anderson and Romme 1991, Ellis et al. 1994, Turner et al. 1997). Transient understory species that developed from seed after fire were more abundant in severely burned areas, whereas more moderately burned sites had a greater percent cover of sprouting forbs and shrubs (persistent species).

For the WCF, total tree recruitment was lower in the severely burn stand than in the moderately burned stand (where surviving trees provided a larger seed source). Similar results were found after the 1988 fires in Yellowstone National Park (Ellis et al. 1994, Turner et al. 1997). Unlike the WCF, however, seedlings of *P. contorta* were far more common than any other tree species, a reflection of the abundance of *P. contorta* on the Yellowstone plateau and the rarity there of *P. engelmannii* and *A. lasiocarpa*.

Plant species richness increased following the 1988 fires on the Yellowstone plateau (Turner et al. 1997), although species richness declines later in succession, probably due to canopy closure (Taylor 1971). Total cover increased for the first 9 years and species richness increased for 17 years after the WCF. Both cover and richness were highest in the severe burn. In contrast, Turner et al. (1997) found a higher richness and percent cover of understory plants in the less intensively burned areas of YNP. Notably, species richness during the initial postfire years was considerably greater in the WCF severely burned stand than in any of YNP stands studied by Turner et al. (21-26 species and 6-16 species, respectively).

Regional variation in species composition and successional patterns should be expected. Fire severity undoubtedly affects the successional patterns that develop, due to the varying levels of seed and whole plant mortality caused by fires of different intensity (Stickney 1982, 1990). However, other factors are important as well, such as prefire community composition, density of serotinous trees, climate, substrate, and environmental characteristics (Turner et al. (1997). The study of a few permanent plots does not enable a thorough analysis of all the variables involved, but they do provide a documentation of successional patterns that is not readily available in any other way. Continued sampling of the WCF permanent plots, and others, will provide answers to questions about the persistence of differences that appear early in succession and the potential for the invasion of new species, if any. The results of the permanent plot studies in the Rocky Mountain region, despite their small size and number, already have enabled more confident statements than were previously possible about the nature of succession in fire-prone coniferous forest ecosystems.

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References

Alexander, R.R. and W.D. Shepperd. 1990. *Picea engelmannii* Parry ex Engelm. In: Silvics of North America, Vol. 1, conifers (edited by R.M. Burns and B.H. Honkala), U.S. For. Ser. Agriculture Handbook 654, Washington, DC, pages 187-203.

Alexander, R.R., R.C. Shearer, and W.D. Shepperd. 1990. *Abies lasiocarpa* (Hook.) Nutt. In: Silvics of North America, Vol. 1, conifers (edited by R.M. Burns and B.H. Honkala), U.S. For. Ser. Agriculture Handbook 654, Washington, DC, pages 187-203.

Anderson, J.E., and W.H. Romme. 1991. Initial floristics in lodgepole pine (*Pinus contorta*) forests following the 1988 Yellowstone fires. Int. J. Wild. Fire 1:119-124.

Aplet, G.H., R.D. Laven, and F.W. Smith. 1988. Patterns of community dynamics in Colorado Engelmann spruce- subalpine fir forest. Ecology 69:312-319.

Armour, C.D., S.C. Bunting, and L.F. Neuenschwander. 1984. Fire intensity effects on the understory in ponderosa pine forests. J. Range Mgmt. 37:44-49.

Barmore, W.J., D.L. Taylor, and P. Hayden. 1976. Ecological effects and biotic succession following the 1974 Waterfalls Canyon fire in Grand Teton National Park. Grand Teton National Park, unpublished report.

Bazzaz, F.A. 1979. The physiological ecology of plant succession. Annu. Rev. Ecol. Syst. 10:351-371.

Bradley, A.F. 1984. Rhizome morphology, soil distribution, and the potential fire survival of eight woody understory species in Western Montana. Thesis. University of Montana, Missoula, Montana, USA. Bradley, A.F., W.C. Fischer, and N.V. Noste. 1992. Fire ecology of the forest habitat types of eastern Idaho and western Wyoming. U.S. For. Ser. Gen. Tech. Rep. INT-290, Ogden, Utah. 92 pages.

Clark, D.L. 1991. The effect of fire on Yellowstone ecosystem seed banks. Thesis. Montana State University, Bozeman, Montana, USA.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northw. Sci. 33:43-64.

Dole N.E., M.H. Mitchell, H.E. Bailey, and W.D. Thomas. 1936. Vegetation type map of Grand Teton National Park. U.S. Department of the Interior, Grand Teton National Park. Unpublished map.

Dorn, R.D. 1992. Vascular plants of Wyoming. Mountain West Publishing, Cheyenne, Wyoming. 339 pages.

Doyle, K.M. 1994. Succession following the 1974 Waterfalls Canyon Fire, Grand Teton National Park, Wyoming. Thesis. University of Wyoming, Laramie, Wyoming, USA.

Egler, F.E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4:412-417.

Ellis, M., C.D. von Dohlen, J.E. Anderson, and W.H. Romme, 1994. Some important factors affecting density of lodgepole pine seedlings following the 1988 Yellowstone fires. In: Plants and their environments. Proceedings of the First Biennial Scientific Conference on the Greater Yellowstone Ecosystem (edited by D.G. Despain), Yellowstone National Park, Wyoming, September 16-17, 1991, pages 139-148.

Habeck, J.R., and R.W. Mutch. 1973. Fire-dependent forests in the Northern Rocky Mountains. Quaternary Res. 3:408- 424.

Halpern, C.B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70:704-720.

Johnson, E.A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge. 129 pages.

Johnson, E.A., and G.I. Fryer. 1989. Population dynamics in lodgepole pine-Engelmann spruce forests. Ecology 70:1335-1345.

Kilgore, B.M., and G.S. Briggs. 1972. Restoring fire to high elevation forests in California. Journal of Forestry 70:266-271.

Knapp, A.K., and W.K. Smith. 1981. Water relations and succession in subalpine conifers in southeastern Wyoming. Bot. Gaz. 142:502-511.

Knapp, A.K., and W.K. Smith. 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. Can. J. Bot. 60:2753- 2761.

Kramer, N.B. 1984. Mature forest seed banks on three habitat types in central Idaho. Thesis. University of Idaho, Moscow, Idaho, USA.

Loope, L.L., and G.E. Gruell. 1973. The ecological role of fire in the Jackson Hole Area, Northwestern Wyoming. Quaternary Res. 3:425-443.

Lotan, J.E. 1975. Regeneration of lodgepole pine forests in the northern Rocky Mountains. In: Management of lodgepole pine ecosystems. Proceedings of symposium (edited by D.M. Baumgartner), Cooperative Extension Service, Washington State University, Pullman, Washington, pages 516-535.

Love, J.D., J.C. Reed, and A.C. Christiansen. 1992. Geologic map of Grand Teton National Park, Teton County, Wyoming. U.S. Department of the Interior, USGS. Miscellaneous Investigations Series Map I-2031.

Lyon, J.L. and P.F. Stickney. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. Proceedings of the Montana Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium 14:355-375.

Martner, B.E. 1986. Wyoming climate atlas. University of Nebraska Press, Lincoln, Nebraska. 432 pages.

McLean, A. 1969. Fire resistance of forest species as influenced by root systems. J. Range Mgmt. 22:120-122.

Noble, D.L., and R.R. Alexander. 1977. Environmental factors affecting natural regeneration of Engelmann spruce in the Central Rocky Mountains. For. Sci. 23:420-429.

Noble, I.R., and R.O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5-21.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range. Vegetatio 45:3-75.

Pickett, S.T.A., S.L Collins, and J.J. Armesto. 1987. Models, mechanisms and pathways of succession. Bot. Rev. 53:335-371.

Romme, W.H., L. Bohland, C. Persichetty, and T. Caruso. 1995. Germination ecology of some common forest herbs in Yellowstone National Park, Wyoming, U.S.A. Arct. Alp. Res. 27:407-412.

Romme, W.H., and D.H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62:319-326.

Rowe, J.S. 1983. Concepts of fire effects on plant species and individuals. In: The role of fire in northern circumpolar ecosystems (edited by R.W. Wein and D.A. MacLean), Wiley, New York, pages 135-154.

Stahelin, R. 1943. Factors influencing the natural restocking of high altitude burns by coniferous trees in the Central Rocky Mountains. Ecology 24:19-30.

Steele, R., S.V. Cooper, D.M. Ondov, D.W. Roberts, and R.D. Pfister. 1983. Forest habitat types of eastern Idaho-western Wyoming. U.S. For. Ser. Gen. Tech. Rep. INT-144, Intermountain Forest and Range Experiment Station, Ogden, Utah. 122 pages.

Stickney, P.R. 1980. Data base for post-fire succession, first 6 to 9 years, in Montana larch-fir forests. U.S. For. Ser. Gen. Tech. Rep. INT-62, Ogden, Utah. 133 pages.

Stickney, P.F. 1982. Vegetation response to clear-cutting and broadcast burning on north and south slopes at Newman Ridge. In: Site preparation and fuel management on steep terrain. Proceedings of a symposium (edited by D. M. Baumgartner), Washington State University, Cooperative Extension Service, Spokane, Washington, February 15-17, pages 159-165.

Stickney, P.F. 1986. First decade plant succession following the Sundance forest fire, Northern Idaho. U.S. For. Ser. Gen. Tech. Rep. INT-197, Ogden, Utah. 26 pages.

Stickney, P.F. 1990. Early development of vegetation following holocaustic fire in Northern Rocky Mountain forests. Northw. Sci. 64:243-246.

Taylor, D.L. 1971. Biotic succession of lodgepole pine forests of fire origin in Yellowstone National Park. Nat. Geog. Soc. Res. Rep. 12:693-702.

Taylor, D.L. 1973. Some ecological implications of forest fire control in Yellowstone National Park, Wyoming. Ecology 54:1394-1396.

Taylor, D.L. 1976. Waterfalls Canyon Forest Fire: A move toward nature's way of ecosystem management. Naturalist 27:36-39.

Tinker, D.B., W.H. Romme, W.W. Hargrove, R.H. Gardner, and M. G. Turner. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Can. J. For. Res. 24:897-903

Turner, M.G., W.H. Romme, R.H. Gardner, and W.W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67:411-433.

Veblen, T.T. 1986. Age and size structure of subalpine forests in the Colorado Front Range. Bull. Torr. Bot. Club 113:225-240.

Whipple, S.A., and R.L. Dix. 1979. Age structure and successional dynamics of a Colorado subalpine forest. Am. Midl. Nat. 101:142-158.

Young, J.F. 1982. Soil survey of Teton County, Wyoming, Grand Teton National Park area. Soil Conservation Service, USDA. 173 pages.