FIRE INFLUENCES ON CENTRAL ROCKY MOUNTAIN LODGEPOLE PINE STAND STRUCTURE AND COMPOSITION

Tamara L. Franklin
Richard D. Laven

ABSTRACT

The effects of both crown and surface fire on lodgepole pine forest structure and species composition were examined in the central Rocky Mountains of Colorado. Three types of plots were established: 1) crown fire plots where regeneration initiated following high intensity stand destroying fire in 1890; 2) surface fire plots where lodgepole stands were burned by low intensity surface fire in 1890; and 3) residual plots containing no evidence of previous surface fire. Surface fire effects on size and age structures were determined by comparing residual and surface fire plots. Lodgepole pine regeneration was significantly greater in surface fire plots than in residual plots. Subalpine fir regeneration was significantly lower in surface fire plots than in residual plots. Successional development was inferred by comparing the crown fire plots (~100 years old) with the surface fire and residual plots (~300 years old). The differences between plot types suggest that surface fire may initiate alternate successional sequences and that achievement of climax forests dominated by spruce and fir be delayed or prevented.

INTRODUCTION

Succession in upper elevation lodgepole pine forests of the Colorado Rocky Mountains is usually considered a process in which stands of post-disturbance lodgepole pine (*Pinus contorta* Dougl. var latifolia Engelm.) are gradually replaced by spruce (*Picea engelmannii* [Parry] Engelm.) and fir (*Abies lasiocarpa* [Hook] Nutt.) forming a spruce-fir steady state (Stahelin 1943, Oosting and Reed 1952). However, this model of structural and compositional change in lodgepole pine forests does not always apply, especially where abiotic influences significantly impact successional development. Subalpine forest development is affected by many factors that can alter successional dynamics (Whipple and Dix 1979, Peet 1981, Romme and Knight 1981). Consequently, a direct sequence from dense post-fire lodgepole to steady state spruce-fir does not always occur.

High intensity crown fire initiates lodgepole pine regeneration in the Rocky Mountains (Clements 1910, Romme 1982, Lotan and Perry 1983). Successional processes in these forests are often considered to follow a model where postcrown fire seedling establishment pathways all eventually lead to a "spruce-fir climax" (Stahelin 1943). Subsequent crown fires are viewed as an interruption of this successional process, that delays the attainment of a spruce-fir climax and return the system to the starting point (Brown 1973). Self-perpetuating or climax lodgepole stands, are exceptions to the model and are usually located at sites with environments too xeric, too exposed, or otherwise too extreme for spruce or fir to successfully establish (Moir 1967, Whipple and Dix 1979).

Low intensity surface fires also occur throughout many Rocky Mountain subalpine forests (Brown 1973, Arno 1976, Perry and Lotan 1979) and may significantly influence the vegetation development of these forests. Vegetation patterns have been altered by surface fires in lodgepole pine stands of Alberta, Canada (Tande 1979), and in species other than lodgepole (Wooldridge and Weaver 1965, Kilgore and Taylor 1979, Harmon 1984, Henderson and Long 1984). Surface fire effects on Rocky Mountain subalpine tree species, however, have not been widely reported. The first objective of this study was to compare the effects of surface fire with the effects of crown fire and the effects of no fire on successional lodgepole stand structure and species composition. The second objective was to assess the impacts of these differing fire histories on succession.

METHODS

Study Area

The study area is within and immediately adjacent to the boundaries of a 2000-hectare crown fire that occurred in 1890. Sites are located in the Chambers Lake area of the Roosevelt National Forest, on the east side of the Rocky Mountains in northern Colorado. Elevations range from 2840 to 2990 meters. Mean annual temperature for this area is ~ 3.3 °C (Peet 1981). Aspects are north-facing and east-facing and slopes range from 10-60 percent. These forests are classified by Peet (1981) as the *Pinus contorta* community mosaic, bordering on the *Picea-Abies* community mosaic. Understory species include *Vaccinium scoparium* Leiburg, and *Vaccinium myrtillus* L. ssp. *oreophilum* (Rydb.) Love, Love, Kapoor. *Juniperus communis* L. ssp. *alpina* Celakovski, and *Rosa woodsii* Lindl. also occur frequently in the area.

Field Sampling

Five sites were selected along the 1890 burn boundary. The burn boundary was distinguished by a marked change in forest structure between the 100-year-old forest burned by crown fire and the 300-year-old forest unburned by crown fire. Three types of ten-by-fifty-meter plots were established: 1) crown fire plots located within the boundary of the 1890 crown fire; 2) surface fire plots established in adjacent areas containing fire scarred trees, charred logs, and charred wood pieces; and 3) residual plots established in adjacent areas where no evidence of surface fire or crown fire was apparent.

Twenty-one crown fire plots, eleven residual plots, and ten surface fire plots were established over the five sites. All residual plots are considered successional lodgepole (sensu Whipple and Dix 1979) based on the presence of understory spruce and fir.

All plots were located at midslope positions and plot size was adjusted to a horizontal projection on the slope. The number of plots that could be established at each site was based on the clarity of the fire history and the absence of past logging activity.

Fire history was assessed for all plots. Partial cross-sections were removed from up to four fire-scarred trees in each surface fire plot, using the method described by McBride and Laven (1976). Fire-scarred trees outside the boundaries but within 10 m of each plot, were also examined to determine variability in fire history. Date of fire was determined on sanded cross-sections by annual growth ring counts beginning from the sampling year to the most recent fire scar. An historical record of fire for the Chambers Lake area confirms the date of occurrence (Crandall 1901).

Fire-scarred trees were considered primary evidence of surface fire. Plots with fire-scarred trees almost invariably contained adjacent charred logs and wood pieces, considered secondary evidence. Plots were classified as surface fire burned when 25% to 100% of the plot was covered by fire-scarred trees with corresponding charred logs or wood pieces in plot. Residual plots had no primary or secondary evidence of surface fire.

All trees in a plot that were ≥ five cm dbh were tagged, mapped and measured for diameter at breast height. Twenty-five percent of the live trees of each species in each five-cm size class were randomly selected for coring. Trees were cored as close to ground level as possible, usually within ten cm. Tree heights and distance to live crown were also measured for each tree in the subsample. The sample minimum for a size class was five trees, all were sampled if less than five trees were present in the size class. Consequently, the actual sampling frequency averaged 83.4% for lodgepole pine, 91.9% for Engelmann spruce and 66.1% for subalpine fir. Trees not included in the size class sample were later randomly assigned ages from the ages of trees in the same five-cm size class.

Live stems less than five cm dbh were mapped and aged in a 1 x 50 meter subsection of each plot. All seedlings and saplings within this section were measured for height and basal diameter. Each tree was assigned an approximate age by node scars count. The accuracy of this method was field tested by counting node scars for ten seedlings/saplings of representative sizes for each species at locations adjacent to the plots. Seedlings/saplings were then cut at ground level and aged by annual ring count. The correlation between the node scars age and the annual ring count age was $r^2 = 89.8$, indicating close correspondence between each method.

Fuels were sampled from transect lines set up along each plot boundary using the method described by Brown (1974). Amount of bare ground also was assessed along these transect lines by measuring the area not covered by aerial projections of shrubs and herb canopies.

Data Analysis

Site index was calculated with corrections for density to assess variation in site quality (Alexander et al. 1967). Differences in regeneration for each species on the surface fire and residual plots were assessed using a Students t-test. Regeneration since last fire in the surface fire plots was compared with regeneration in the residual plots over the equivalent time span (100 years). Differences in fuels and stand characteristics by fire history stand type also were assessed using t-tests.

Quantile-quantile plots were constructed for detailed comparisons of species regeneration distributions between residual and surface fire plots. If the ordered distributions of species regeneration are identical for the surface fire and residual stands being compared then all points would fall exactly on the line $x = y$. Departure from this line gives detailed information about how the distributions differ (Chambers et al. 1983).

Stand structure and composition were determined by construction of ten-year age class sequences for each plot type. Successional sequence was inferred by comparing the 100-year-old crown fire plot with adjacent residual (300-year) or surface fire (300-year) age class structures. Substitution of space for time is commonly used in this way if plots cannot be monitored over a very long time (Laven 1982). Crown fire plots (100 years old) would be presumed to eventually reach species composition and structure similar to the adjacent residual plots (300 years old) given sufficient time without fire. We do not have a complete chronosequence encompassing many stand ages but are making indirect inferences about change from one time period to the next. Successional sequences are based on cumulative (for all plots with the same burn history) age class data adjusted to trees per hectare. Plots in 100- and 300-year chronosequences are directly across the crown fire burn border from one another, thereby maximizing between site homogeneity that is prerequisite to the use of substitution of space for time (Laven 1982).

RESULTS

Residual and surface fire stand ages of origin (maximum tree ages) all were approximately equal, ranging from 250 to 320 years. Site indices ranged from 61 to 68, denoting similar site quality for the study plots. Multiple fire scars were not apparent on any of the scar wedges from surface fire plots, which indicated that only one surface fire occurred over the age span of each current stand. Fire-scarred trees were rare in all of the burn plots, indicating a relatively complete, high intensity burn.

Lodgepole pine regeneration was significantly greater ($p \leq .05$) in surface fire plots than in residual plots, both in density (trees per hectare) and as a percentage of the total species composition (relative density) (Table 1). Engelmann spruce composition and density were variable, within and between surface fire and residual plot types (Table 1). Subalpine fir density and relative density were both significantly less ($p \leq .05$) in surface fire plots than in residual plots (Table 1). Tree density for all species combined was not significantly different between the two plot types (Table 2).

Quantile-quantile plots illustrate the differences in range of species regeneration for residual and surface fire stands (Figure 1). The range of lodgepole

Table 1a. Mean density (trees per hectare) for the ten surface fire plots compared to the eleven plots without surface fire. * indicates significant differences ($p \leq = .05$) between surface fire and residual plots for lodgepole pine and also between surface fire and residual plots for subalpine fir.

SPECIES	MEAN DENSITY (TPH) Surface Fire (std.err)	Residual (std.err)
lodgepole pine	2330 * (689)	600 * (174)
Engelmann spruce	728 (254)	1058 (459)
subalpine fir	2486 * (522)	9578 * (2932)

Table 1b. Percent of total species composition (relative density) for the ten surface fire plots compared to the eleven plots without surface fire. * indicates significant differences ($p \leq = .05$) between surface fire and residual plots for lodgepole pine and also between surface fire and residual plots for subalpine fir.

SPECIES	% OF SPECIES COMPOSITION (RD) Surface Fire (std.err)	Residual (std.err)
lodgepole pine	41 * (7.6)	15 * (5.6)
Engelmann spruce	12 (2.9)	8 (2.7)
subalpine fir	47 * (8.4)	77 * (5.6)

Table 2. Stand averages for five characteristics from each of the three stand types. Only trees ≥ = five cm dbh are represented. Two age groups are presented for comparison between characteristics of younger and older trees in each of the fire history stand types. Dbh, tree height and distance to live crown were similar for trees < 100 years old in all three stand types. Stand density index (all tree ages) and trees per hectare (trees < 100 years old) were both significantly lower (* indicates p ≤ = .05) in the surface fire burned areas than in crown fire burned areas. Significant differences were not found between residual and surface fire stand densities, however the trend of both types of density measurements is towards lower densities in surface fire plots.

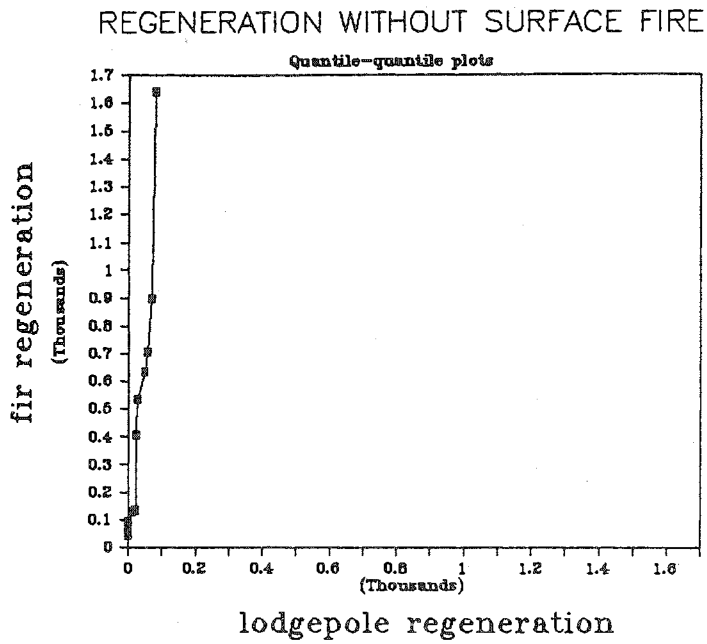
STAND CHARACTERISTICS	FIRE HISTORY TYPE					
	Residual		Surface Fire		Crown Fire	
	TREE AGE < 100	TREE AGE > 100	TREE AGE < 100	TREE AGE > 100	TREE AGE < 100	TREE AGE > 100
Stand Density Index mean (s.d.)	969 (391)		751 * (40.4)		1098 * (192)	
Trees Per Hectare mean (s.d.)	2475 (1902)	1000 (475)	1670 * (1741)	702 (157)	2869 * (1031)	—
DBH (cm) mean (s.d.)	11.3 (4.9)	18.1 (9.6)	11.4 (5.2)	22.8 (9.5)	12.2 (5.1)	—
Tree Ht. (m) mean (s.d.)	10.3 (3.7)	12.6 (4.8)	9.6 (4.1)	13.2 (4.6)	10.9 (3.7)	—
Dist. (m) To Live Crown mean (s.d.)	3.6 (2.5)	3.6 (3.1)	3.7 (3.2)	4.7 (3.2)	4.6 (2.7)	—

regeneration densities is much greater for surface fire areas than for residual areas. The range of fir regeneration densities is much greater for residual areas than for surface fire areas.

Age class structures in residual plots were found to be markedly different (Figures 2Af and 2Bf). Data collected from crown fire plots are presented in the age 100 chronosequence and data collected from surface fire and residual plots are presented in the age 300 chronosequence.

Diameter, tree height, and distance to live crown for trees < 100 years old are relatively similar between the three stand types (Table 2). Surface fire affected areas are less dense than crown fire areas (p ≤ .05), as indicated by both stand density index and trees per hectare (Table 2). Fuels were not significantly different between stand types (Table 3). The amount of bare ground was significantly greater in surface fire stands than in crown fire or residual stands (Table 3).

Figure 1. Fir and lodgepole pine regeneration in surface-fire and residual stands.



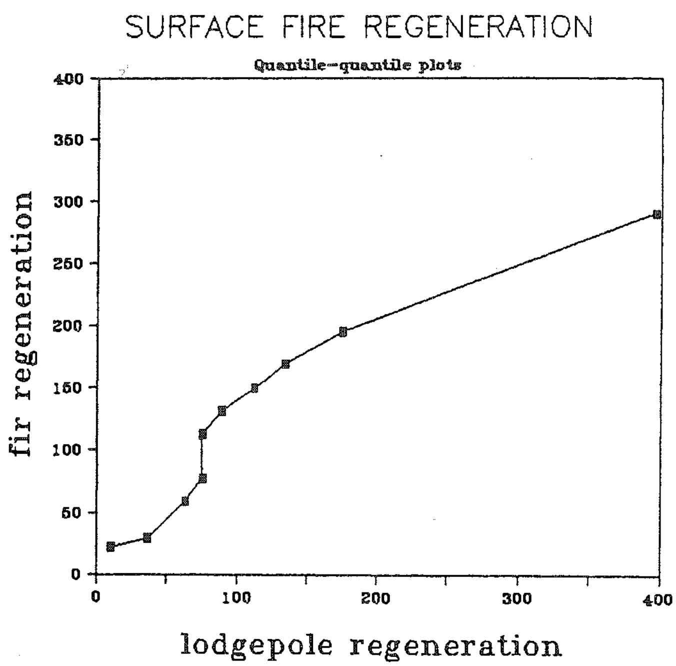
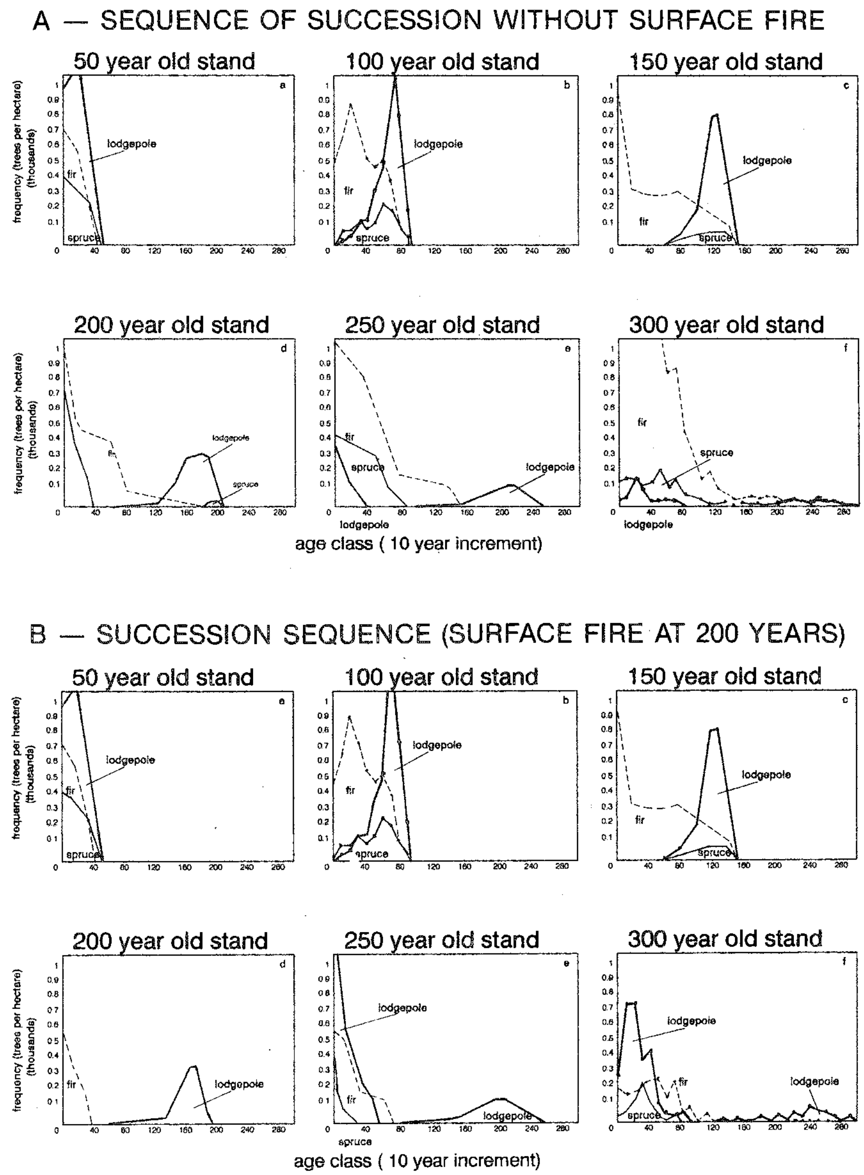


Figure 2. Projected successional sequences of stands with and without surface-fire.



DISCUSSION

Fire history in lodgepole pine forests is variable. Many uneven-aged lodgepole pine stands result from low intensity surface fires (Brown 1973). While the surface fire in this study is burned as part of an 1890 crown fire, low intensity fire also may occur in islands within crown fire, or over extensive areas without becoming a crown fire. Arno (1976) found evidence of low intensity surface fires over widespread areas in lodgepole pine forests of the Bitterroot National Forest, Montana. Loope and Gruell (1973) found similar evidence in northwestern Wyoming lodgepole pine. Surface fires were documented at 20- to 40-year intervals in part of the Bob Marshall Wilderness Area, Montana (Gabriel 1976). Gabriel also found clusters of fire scarred trees within large areas burned by stand destroying fires. Whether or not a surface fire becomes a crown fire is to some extent a stochastic process; the probability of eventual crown fire should increase with time since last fire due to fuels build-up (Romme 1982). Alternatively, frequent surface fires will promote uneven-aged stand structures, increasing ladder fuels which also may increase the probability of crown fire. Differences in dead and downed fuels or distances to the live canopy were not observed between stands of different fire histories. However, variability was high for both fuels and canopy distances between plots of the same fire history.

Data from this study indicate that while overall tree density may not be significantly different between plots with different types of fire histories, statistically significant compositional shifts are present that are not reflected by total tree densities. Differing life history strategies of lodgepole pine, spruce, and fir are apparent in the comparisons of species composition by plot type. Recruitment of lodgepole pine subsequent to surface fire is expected, given characteristics of both serotinous and nonserotinous cones and high tolerance of seedlings to direct sunlight. These characteristics are conducive to regeneration in gaps left by surface fires. Presence of these gaps may be supported

Table 3. Dead and downed woody fuels and bare ground averages for each of the three types of stand fire history. Fuels were not significantly different between stand types. The amount of bare ground was significantly greater ($p \leq .05$) in the surface fire affected areas than in the residual or crown fire areas. Letters in common (a or b) indicate significant differences between elements.

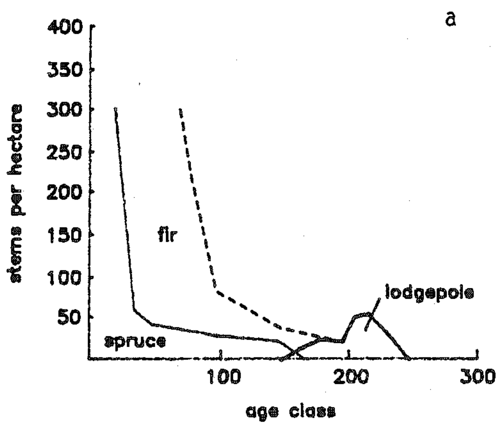
FUELS CHARACTERISTICS	FIRE HISTORY TYPE		
	Residual	**Surface Fire**	**Crown Fire**
Total Fuel (Kg/ha) mean (s.d.)	63643 (25581)	73802 (28866)	53396 (22931)
Fuel ≤ 2.5cm (Kg/ha) mean (s.d.)	1404 (849)	1318 (721)	1102 (739)
% Bare Ground mean (s.d.)	35.3 a (12.7)	57.2 a b (7.2)	41.4 b (17.0)

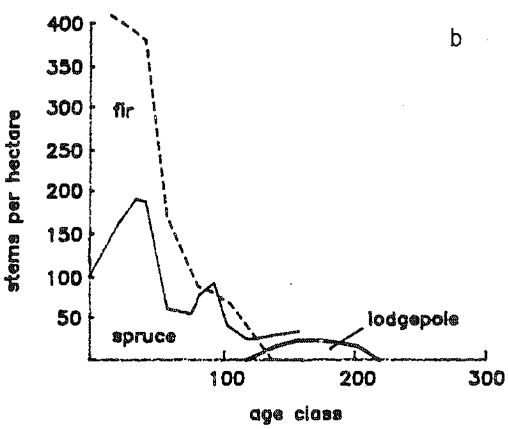
by lower stand density indices and lower number of trees per hectare found in surface fire stands compared to residual stands, however these trends were not statistically significant. Greater percentages of bare ground in surface fire stands than in residual stands also may indicate favorable conditions for lodgepole pine germination and growth in plots burned by surface fire. Elevated soil temperatures and lowered soil moisture may be present after surface fire, although to a lesser extent than found in crown fire burned areas. Amelioration of the microenvironment by lodgepole pine may be required before fir can regenerate in prefire densities. Models incorporating processes such as facilitation, tolerance, and inhibition (Connell and Slatyer 1977) have potential application here despite the absence of intermediate, low intensity disturbance in their model. If the amelioration process is slow or if the fire return interval is high, the classic spruce-fir stable state may not be approached as quickly or as frequently as is generally perceived.

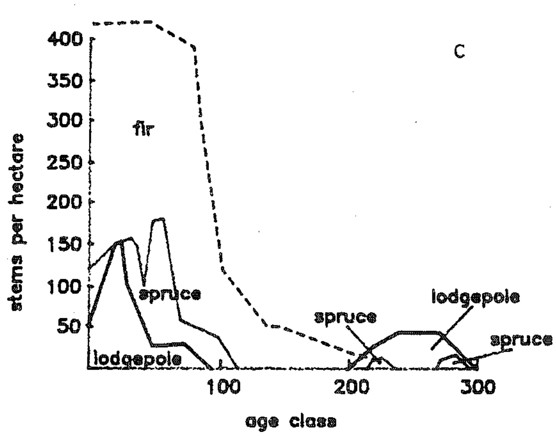
A variety of environmental stresses such as dwarf mistletoe and bark beetle infestation, as well as surface fire, may alter stand structure and composition patterns in successional lodgepole forests. In addition, variability in subalpine forest structure and composition caused by environmental and topographic gradients (Whipple and Dix 1979, Peet 1981, Romme and Knight 1981) may be increased by low intensity disturbance events (White 1987). Low intensity disturbance is considered a process which creates and maintains a multispecies compositional mixture (Whipple 1975, Romme and Knight 1981, Despain 1983). This view gives disturbance a role as an endogenous part of the system, not an exogenous force interrupting the natural successional sequence.

Age class data for lodgepole pine/spruce-fir forests are not commonly presented in the literature. The geographic range of structure and composition patterns for forests of a given age is therefore difficult to determine. Day (1972) described the successional sequence after fire in Alberta, Canada as a four phase process in which spruce is a more significant part of the 250- to 300-year-old forest than has been found for similar aged forests in the Rocky Mountains (Figure 3a). In the Colorado Rockies, Whipple and Dix (1979) characterized types of subalpine stands as climax lodgepole, successional lodgepole, or climax spruce-fir, based on stand age structures. The successional lodgepole age class structures presented by Whipple and Dix (Figure 3b) are supported by age class structures found in our residual plots, but not by age class structures in surface fire plots (Figure 3c). Striking similarities exist between age class structures determined by Whipple and Dix and those determined in this study, including the almost identical curve shapes for each species and bimodality of spruce regeneration. The recent lodgepole regeneration seen in our cumulative residual (age 300) graph (Figure 3c), but not represented by the age class curves of Whipple and Dix, may be attributable to some residual effects of the adjacent crown fire, such as opening of serotinous cones or creation of small gaps in the canopy. Lodgepole regeneration seen in surface fire plots, however, is much greater than the small amount of lodgepole regeneration noted in the residual plots of Figure 3c.

Figure 3. Stand structure designated as successional in previous studies compared with stands known to have been influenced by surface-fire.







Two different successional pathways over 300 years are conjectured based on differences in stand fire history (Figures 2a and 2b). Intermediate stand structures at fifty-year intervals are stylized based on the older and younger chronosequences at 100 and 300 years. Successional pathways are markedly changed in structure and composition when surface fire occurs during stand development.

Linear approaches to a spruce-fir steady state are often assumed (Stahelin 1943). However, surface fire may introduce cyclic processes or alternative pathways into the system in which the spruce-fir steady state may or may not eventually be reached. Species composition and stand structure cannot be exactly set back to earlier seral stages following surface fire, partly because of the presence of older age classes of trees still remaining in the stand. Reduction of fir seed sources along with increased lodgepole regeneration following surface fire also may alter stand structure and composition such that it is different than at any presurface fire stage. These differences may indicate that change induced by surface fire is not exactly cyclic, because the forest does not return to a previous stage. However change is not unidirectional either, as is commonly represented in models.

Succession is a function of species life histories, site and environmental conditions, along with disturbance and stochastic elements. These factors interact to produce lodgepole/spruce-fir forests of great variability, where succession may not be best represented by unidirectional models. Incorporation of surface fire and other non-stand-destroying disturbances into mechanistic models, or the development of new models, may increase understanding of stand dynamics in upper elevation Rocky Mountain subalpine forests.

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