

Albert J. Parker

Geography Department
University of Georgia
Athens, Georgia 30602

A Comparison of Structural Properties and Compositional Trends in Conifer Forests of Yosemite and Glacier National Parks, USA

Abstract

Structural properties (density, stand basal area, and mean diameter) are compared between forests of Yosemite National Park, California, and Glacier National Park, Montana, as well as among forest types within regions. Forest types within Glacier display markedly disparate structures, whereas those within Yosemite possess similar structures. Furthermore, two of the three Glacier forest types are characterized by pronounced compositional differences between small and large size classes. In Yosemite, each forest type has a similar composition in both the small and large size classes. These geographic differences in forest structure and compositional trend are attributed to distinctive fire patterns in each region. In Yosemite, the strength and consistency of summer drought stress favor a surface fire regime in all forest types sampled, promoting uniformity of structure and compositional dynamics among Yosemite forests. In Glacier, site microclimates mitigate or exacerbate occasional dry summers, resulting in a broader spectrum of disturbance regimes among forest types, ranging from frequent surface fires on dry, open flats, through crown fires on intermediate settings, to infrequent fires on mesic, sheltered slopes. The diversity of disturbance regimes promotes heterogeneity of structure and complex patterns of compositional dynamics among Glacier forests.

Introduction

Forest structure can be characterized in several ways, each with a different type of data. One approach is to examine the morphology of the species of which the community is composed (Knight and Loucks 1969). A second involves analyzing gross structural features of the entire community, such as density, stand basal area, and mean diameter, and comparing these features among sampling units (Goff and Zedler 1968). A third approach uses size/age class data to infer population trends (Whipple and Dix 1979). The writer has used the species-morphology approach previously to examine the structural dissimilarities of conifer forest of Yosemite National Park, California, in the central Sierra Nevada, and of Glacier National Park, Montana, in the northern Rocky Mountains (Parker 1982). He found that the variability of morphological features within Yosemite forests corresponds to an environmental gradient dominated by elevation. In Glacier, on the other hand, temporal differences among stands related to distinctive fire regimes obscure the direct expression of environmental influence on forest morphology. In this paper, forest structures in the two areas are compared in terms of density, basal area, and mean diameter among stands, as well as by compositional trends across size classes.

Three forest types are recognized in each region based on patterns of canopy dominance among individual stands (Table 1; cf. Parker 1982). In Yosemite, *Pinus ponderosa*/*Calocedrus decurrens* (ponderosa pine/incense-cedar) forests occur on xeric, lower elevation (1200-1900 m) sites; *Abies concolor*/*Calocedrus decurrens* (white fir/incense-cedar) forests occupy mesic, lower elevation sites; and *Abies magnifica*/*Abies concolor* (red fir/white fir) forests, with locally important *Pinus jeffreyi* (Jeffrey pine)

TABLE 1. Tree species composition by forest type.

YOSEMITE

Pinus ponderosa/Calocedrus decurrens:

- Pinus ponderosa Laws.
- Calocedrus decurrens (Torr.) Florin
- Pinus lambertiana Dougl.
- Quercus kelloggii Newb.
- Abies concolor (Gord. and Glend.) Lindl.

Abies concolor/Calocedrus decurrens:

- Abies concolor
- Calocedrus decurrens
- Pinus lambertiana
- Pinus ponderosa
- Quercus kelloggii
- Abies magnifica A. Murr.
- Cornus nuttallii Aud.

Abies magnifica/Abies concolor:

- Abies magnifica
- Abies concolor
- Pinus contorta ssp. murrayana (Engelm. ex Wats.) Critchfield
- Pinus jeffreyi Grev. and Balf.
- Pinus monticola Dougl.
- Pinus lambertiana

GLACIER

Pinus ponderosa/Pseudotsuga menziesii

- Pinus ponderosa
- Pseudotsuga menziesii (Mirb.) Franco
- Pinus contorta ssp. latifolia (Balf.) Critchfield
- Larix occidentalis Nutt.
- Picea engelmannii/glauca complex (see Habeck and Weaver 1969, Daubenmire 1974)

Pinus contorta/Larix occidentalis:

- Pinus contorta ssp. latifolia
- Larix occidentalis
- Pseudotsuga menziesii
- Picea engelmannii/glauca
- Betula papyrifera Marsh.
- Populus tremuloides Michx.

Thuja plicata/Tsuga heterophylla:

- Thuja plicata Donn
- Tsuga heterophylla (Raf.) Sarg.
- Larix occidentalis
- Pinus monticola
- Picea engelmannii/glauca
- Populus trichocarpa Torr. and Gray
- Betula papyrifera

Species are listed in order of importance by forest type.

and *Pinus contorta* ssp. *murrayana* (lodgepole pine) populations, are found at higher elevations (1900-2400 m) (cf. Rundel *et al.* 1977). In Glacier, upland forest types are arranged along a locally-controlled moisture/fire frequency gradient, with *Pinus ponderosa*/*Pseudotsuga menziesii* (ponderosa pine/Douglas-fir) forests on somewhat xeric sites, *Pinus contorta* ssp. *latifolia*/*Larix occidentalis* (lodgepole pine/western larch) forests on intermediate settings, and *Thuja plicata*/*Tsuga heterophylla* (western redcedar/western hemlock) forests on mesic sites (cf. Pfister *et al.* 1977, Kessell 1976). (See Table 1 for taxonomic authorities.)

Strong seasonality of precipitation on the western flank of the Sierra Nevada contrasts with the weak seasonality of precipitation west of the Continental Divide in Glacier (Fig. 1). Greater than one-half of the annual precipitation in Yosemite falls

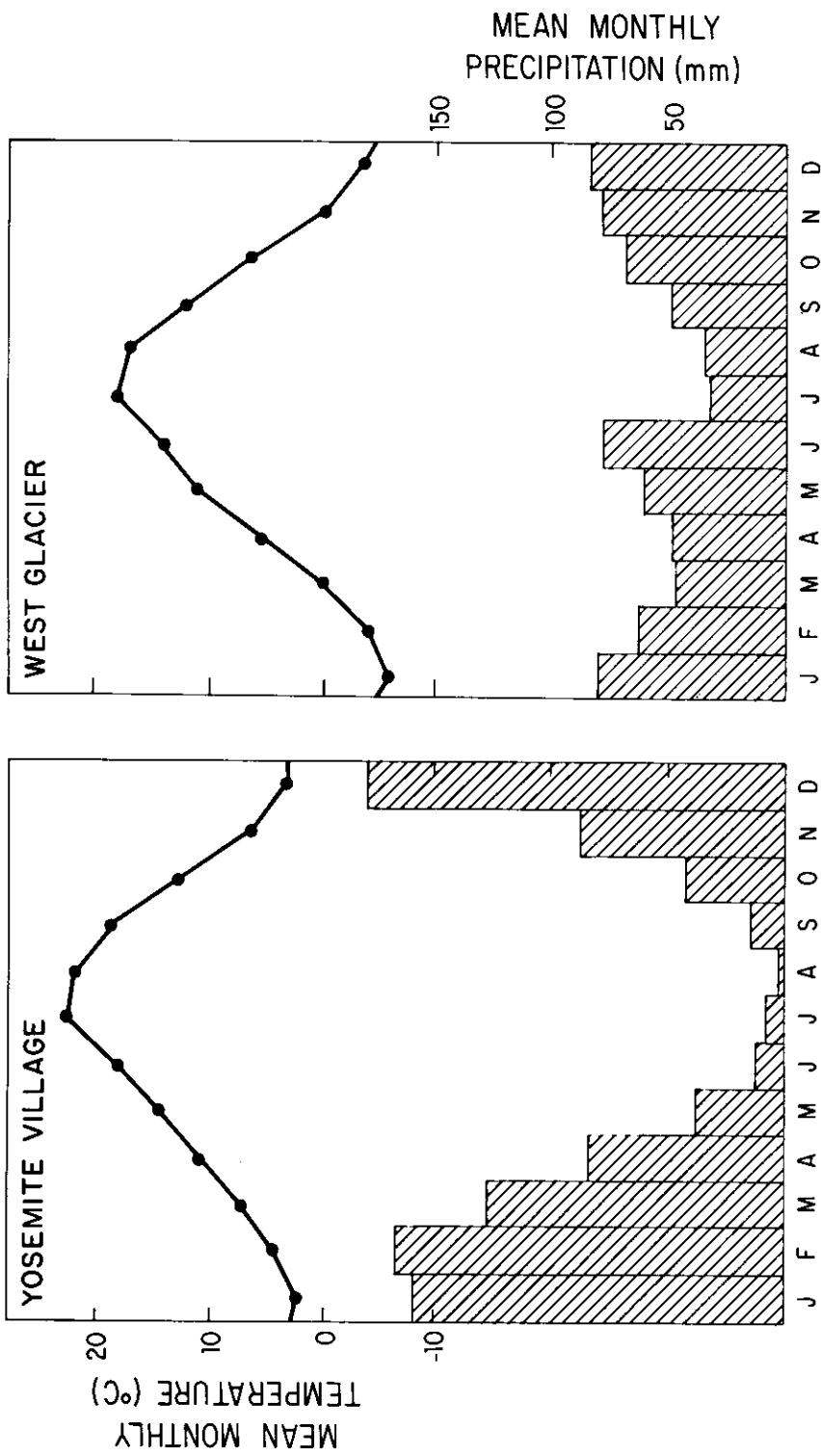


Figure 1. Thirty year means of monthly temperature and precipitation for Yosemite Village, California, and West Glacier, Montana. Source: National Oceanic and Atmospheric Administration, 1978.

from January through March, when upper level westerly flow induces frequent passage of cyclonic storms. Summers are characterized by chronic drought, because of the persistent anchoring of the North Pacific subtropical high pressure cell off the coast of California. Conversely, the year-round penetration of cyclonic systems inland from the North Pacific provides Glacier with a more uniform precipitation regime. The July/August precipitation minimum reflects occasional dry years when the subtropical anticyclone is either atypically strong or displaced poleward.

Chronic summer drought in Yosemite favors a surface fire regime throughout montane and lower subalpine forests; the recurrence interval of these surface fires in pre-settlement times apparently lengthened with increasing elevation. In spite of interruption by fire suppression, the prevalence of surface fires appears to have promoted structural similarity among Yosemite forests types. In Glacier, occasional summer drought can be reinforced or mitigated by site microclimates, allowing a greater variety of characteristic disturbance regimes among forest types. On drier, open sites (whether induced by aspect, sandy substrates, or grazing history) surface fires are common. On somewhat more mesic slopes and flats, stand-destroying crown fires are more common. On sheltered mesic slopes (often exhibiting a local-scale lake-influence) fires are uncommon events. This diversity of fire regimes manifests itself in structural dissimilarities among Glacier forest types.

Methods

In Yosemite, 30 stands were sampled within the 1220 to 2440 m elevation range, whereas in Glacier 18 stands between 910 and 1370 m elevation were sampled. In both regions, attempts were made to collect samples from a variety of slope aspects and gradients. Criteria employed to select stands included gross environmental and compositional homogeneity as assessed by field inspection, uniformity of the canopy, dominance by conifers, and exclusion of riparian sites. Samples in each stand consisted of twenty circular quadrats (5.64 m radius) located within a 60 x 75 m grid system by a stratified systematic unaligned sampling technique (Berry and Baker 1968). Within each 1/100 ha quadrat, the species and basal area at breast height (1.4 m) were recorded for all trees with stems 10.2 cm or greater in basal diameter. These data were summarized to yield structural properties, including tree density, total basal area, and mean tree diameter for each stand.

Results

Density-Basal Area-Diameter Relationships. The forests of Yosemite (Y) are less dense than those of Glacier (G), yet they generally support a greater standing biomass and are composed of individuals of larger girth (Table 2). In both regions, as expected, mean diameter and tree density exhibit a strong negative correlation ($r_Y = -0.848$, $p < 0.01$; $r_G = -0.741$, $p < 0.01$). This is because within closed forests, as individual trees grow, they progressively utilize or assimilate a greater proportion of the available nutrient, light, and water resources. Hence, biomass becomes concentrated in a few, large individuals (cf. Waring and Franklin 1979). In addition, the correlation between mean diameter and stand basal area is positive among both Yosemite and Glacier stands, although the correlation coefficient for Glacier is weak ($r_Y = 0.639$, $p < 0.01$; $r_G = 0.331$, $p < 0.2$).

The relationship among density, basal area, and diameter within each forest type clarifies comparisons between regions based on collective data; averaged values of these properties are presented for the six forest types (Table 2). A comparison of averaged values for each forest type in Yosemite (using the Mann-Whitney U-test) indicated

TABLE 2. Structural properties of Yosemite and Glacier forests.

	Tree Density (stems. ha ⁻¹)	Basal Area (dm ² . ha ⁻¹)	Mean Diameter (cm)
YOSEMITE:			
All stands	544 ± 90*	7802 ± 773	45.9 ± 4.7
Forest types:			
<i>Pinus ponderosa</i> /Calocedrus (n = 8)	714 ± 290	6564 ± 913	38.5 ± 12.0
<i>Abies concolor</i> /Calocedrus (n = 9)	563 ± 191	7883 ± 1381	44.5 ± 7.9
<i>Abies magnifica</i> / <i>Abies concolor</i> (n = 13)	425 ± 79	8508 ± 1442	51.5 ± 6.0
GLACIER:			
All stands	667 ± 124	4857 ± 825	32.0 ± 4.2
Forest types:			
<i>Pinus contorta</i> / <i>Larix</i> (n = 8)	766 ± 171	3766 ± 673	25.3 ± 1.8**
<i>Thuja</i> / <i>Tsuga</i> (n = 6)	764 ± 137	6665 ± 1326**	33.6 ± 4.9
<i>Pinus ponderosa</i> / <i>Pseudotsuga</i> (n = 4)	323 ± 180**	4327 ± 1357	43.9 ± 12.2

*95% confidence limits based on Student's t distribution are shown.

**Among Glacier forest types, the mean for this type is significantly different ($p < 0.05$, Mann-Whitney U-test) from the other two forest types. There are no significant differences among means of structural properties in Yosemite forests.

that no significant differences in tree density, basal area, or mean diameter existed among types. Hence, gross structural features of Yosemite forests in the montane zone are similar, even among diverse forest types. In Glacier forests, statistically significant differences in average values among forest types were apparent (Table 2). First, the density of the *Pinus ponderosa*/*Pseudotsuga* type on somewhat xeric sites was significantly lower than forest types on more mesic sites. The open grown character of these stands appears to have been maintained by a presettlement surface fire regime (Lunan and Habeck 1973). Second, basal area was significantly greater in mesic *Thuja*/*Tsuga* forests than in the other forest types. On the sheltered, northwest facing slopes of the Lake McDonald drainage, local climate and topographic features mitigate the drought conditions associated with periods of low precipitation; fires are thus infrequent, and allow a large accumulation of biomass (Kessell 1976, Anderson 1968). Third, mean diameter was significantly lower in *Pinus contorta*/*Larix* forests than in the other two forest types. These forests, on dry/mesic sites, appear to represent typical conditions at lower elevations throughout much of the northwestern sector of Glacier. On these sites, stand-destroying crown fires occur episodically, resulting in smaller tree size when compared to the other two Glacier forest types.

Correlations among tree density, basal area, and mean diameter within forest types underscore the patterns described above (Table 3). Small sample sizes for each forest type diminish the likelihood of statistically significant correlations between structural properties within forest types. In view of this observation, only the general pattern of

TABLE 3. Correlation values among structural properties and values of the index of compositional change by forest type.

	Correlation values			Index of Compositional Change
	DENS/DIAM	BA/DIAM	DENS/BA	
YOSEMITE				
All stands	-0.848**	0.639**	-0.271	
Forest types				
Pinus ponderosa/Calocedrus (n = 8)	-0.889**	0.477	-0.136	0.746
Abies concolor/Calocedrus (n = 9)	-0.870**	0.745*	-0.437	0.634
Abies magnifica/Abies concolor (n = 13)	-0.686**	0.624*	-0.123	0.756
GLACIER				
All stands	-0.741**	0.331	0.246	
Forest types:				
Thuja/Tsuga (n = 6)	-0.805	0.729	-0.189	0.764
Pinus contorta/Larix (n = 8)	-0.649	0.181	0.618	0.550
Pinus ponderosa/Pseudotsuga (n = 4)	-0.753	0.032	0.630	0.300

* p < 0.05.

** p < 0.01

structural correlations in each forest type is emphasized here. In Yosemite forests, where no significant differences were found in inter-type structural comparisons of averaged stands properties, no strong differences in patterns of correlation among these stand properties are apparent. In Glacier forests, however, correlation of structural properties within forest types displays distinctive patterns. *Thuja/Tsuga* forests show a correlation pattern similar to that of Yosemite forests (i.e., a strong positive correlation between basal area and mean diameter coupled with a weak negative correlation between density and basal area). All of the Yosemite forest types and Glacier's *Thuja/Tsuga* forest type seem to display the influence of competitive thinning on forest structure, with standing crop being maximized in forests with relatively few, but large trees. Glacier's *Pinus ponderosa/Pseudotsuga* and *Pinus contorta/Larix* forest types exhibit correlation patterns unlike Yosemite forests. Both show a rather strong positive correlation between density and basal area, indicating that in these forest types, high density (presumably related to initial stocking levels) accompanies large stand basal area values (cf. Goff and Zedler 1968).

Compositional change within forest types. In order to assess the compositional change within forest types, I developed an index, patterned after the Dynamic Adaptation Values of Peet and Loucks (1977), but altered to provide a single value for each forest type (See Table 3). To determine compositional change index values, trees in each stand were stratified into 10 cm diameter class intervals by species. For all species in each stand with a relative density exceeding five percent, the species' relative density in the smallest tree diameter class (RD_s : 10-20 cm) and species relative density for all larger diameter classes (RD_l : > 20 cm) were computed. Stand index values are based on the ratio of RD_s to RD_l . RD_s/RD_l values of about 1.0 identify species that are comparably represented in both small and large diameter classes; values range toward zero for declining species and toward positive infinity for invading species. Thus,

variation of RD_s/RD_L values from 1.0 in either direction reflects species compositional shifts across diameter classes in the stand. Next, values of RD_s/RD_L exceeding 1.0, representing species apparently increasing in importance, were converted to reciprocals. Consequently, the ratio value will approach zero for any species showing marked differences in representation between small and large size classes, irrespective of the species trend. Index values for entire stands were then calculated by multiplying the RD_s/RD_L value (or its reciprocal) for each species by that species' relative density (thus weighing each species contribution to the index by its commonness in the stand), and summing the resultant values for all species. The final index values for a stand, therefore, range from 1.0 in stands of constant composition across size classes to a hypothetical extreme of 0.0 in stands where there are no shared species in small and large size classes. Compositional change index values reported for each forest type are arithmetic means of index values from each stand in the forest type.

Compositional change index values for Yosemite and Glacier forest types (Table 3) suggest that all Yosemite forest types plus Glacier's *Thuja/Tsuga* forest type (with index values exceeding 0.600 for each type) exhibit less compositional alteration than either the *Pinus ponderosa/Pseudotsuga* or *Pinus contorta/Larix* forest types in Glacier.

Discussion

Although Yosemite forests show compositional and morphological changes with elevation and topographic conditions (Parker 1982), average values of tree density, basal area, and mean diameter for each forest type are similar. Additionally, correlation patterns among these same structural properties are comparable among forest types, suggesting that structural development is similar for all forests sampled. The structural similarity among Yosemite forest types may be, in part, a consequence of the severity of summer drought in the montane zone in Yosemite, which induces pronounced soil moisture deficit (Arkley 1981) and thereby intensifies competitive stress among trees.

The role of fire history in forest structure in the Sierras must also be considered. Many workers have found that the structure of Sierran conifer forests (particularly the "mixed" conifer forests, which are homologous to *Abies concolor/Calocedrus* forests here) has been changed from presettlement conditions (Bonnicksen and Stone 1981) by a decline in fire frequency associated with a decline in burning by native Indians (ca. 1875) and an aggressive fire suppression policy imposed by land management agencies (ca. 1900) (Kilgore and Taylor 1979). The index of compositional change value for *Abies concolor/Calocedrus* forests (0.634) is lower than for the other two forest types, reflecting the influence of fire frequency alteration on the composition of these mesic lower elevation forests. The virtual exclusion of surface fires has promoted an increase in stem density and an associated compositional shift toward increased dominance by the tolerant *Abies concolor* (Fig. 2) (Vankat and Major 1978). Nevertheless, the fire frequency reduction has existed for about 110 years, and many trees that invaded these stands in the late nineteenth century are dominants or co-dominants of the forest canopy today. Thus, the contrast between small and larger diameter classes reflected in the compositional change index, which was likely more pronounced several decades ago, has been reduced. The influence of fire frequency alteration on the composition of the other two Yosemite forest types has not been as pronounced, judging from their higher compositional change index values. In xeric, lower elevation

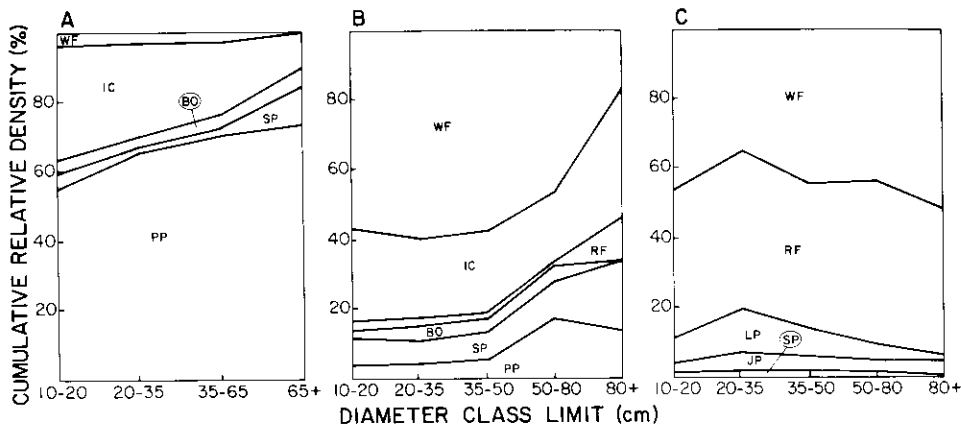


Figure 2. Composite size-class diagrams for forest types in Yosemite. (A) *Pinus ponderosa*/*Calocedrus*, (B) *Abies concolor*/*Calocedrus*, and (C) *Abies magnifica*/*Abies concolor*. species are arranged from most (first) to least (last) shade tolerant: WF—*Abies concolor*; IC—*Calocedrus decurrens*; RF—*Abies magnifica*; BO—*Quercus kelloggii*; LP—*Pinus contorta* ssp. *murrayana*; JP—*Pinus jeffreyi*; SP—*Pinus lambertiana*; PP—*Pinus ponderosa*.

forests, although the importance of the tolerant *Calocedrus decurrens* has increased with fire suppression (Fig. 2), drought stress appears to have allowed the intolerant *Pinus ponderosa* to remain an important element in all diameter classes. In the *Abies magnifica*/*Abies concolor* forest type at higher elevations, presettlement fires were apparently less common events (Kilgore 1971). Hence, the advent of fire suppression has not greatly influenced patterns of species importance among the codominants of this forest type (Fig. 2).

Glacier forest types exhibit greater dissimilarities in both structural properties and compositional trends than Yosemite forest types. Structural complexity is evident in the significant differences in averaged values of density, basal area, and mean diameter among forest types, as well as in differences in correlation pattern within types.

In the sheltered *Thuja*/*Tsuga* forests of Glacier, fires are apparently uncommon events. These stands have been free from fire for long periods (at least 150 years: Kessell 1976); disturbance of the forest canopy during this time has been limited to sporadic individual treefalls. The relatively undisturbed canopy configuration promotes progressive thinning of the trees. Both *Thuja plicata* and *Tsuga heterophylla* maintain self-replicating populations on these sites (Fig. 3). Hence, like the Yosemite forests studied, the *Thuja*/*Tsuga* forest type in Glacier displays both a high value of the compositional change index and a structural correlation pattern indicative of maximum standing crop in mature forests with relatively few, but large individuals.

Fires are more frequent in dry/mesic *Pinus contorta*/*Larix* forests than in *Thuja*/*Tsuga* forests (crown fire return interval is perhaps 50-100 years, Kessell 1976, cf. Arno 1980). Moreover, burns often occur as stand-killing crown fires. The frequency and intensity of crown fires in Glacier appears to have been increased by widespread mortality of *Pinus contorta* caused by periodic mountain pine beetle epidemics (Amman and Baker 1972). Following crown fires, open sites are soon recolonized by *Pinus contorta* and *Larix occidentalis*, producing an even-aged forest structure. With time, more tolerant species, such as *Pseudotsuga menziesii* and *Picea engelmannii*/*glauca*

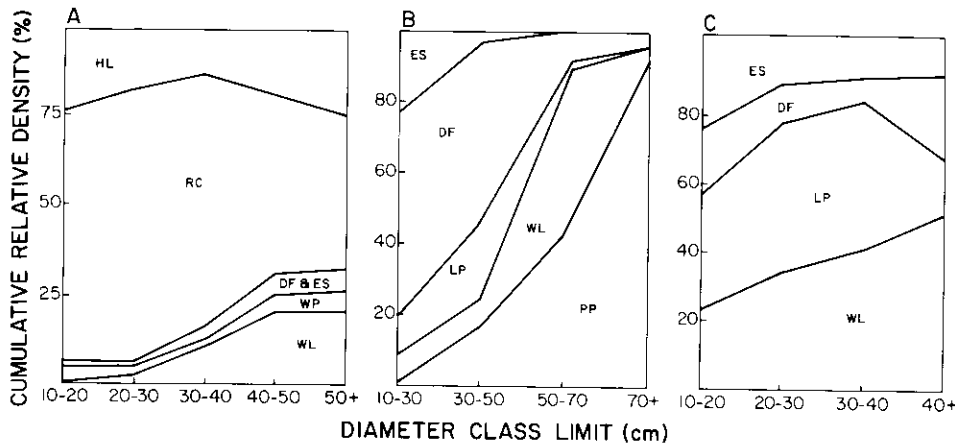


Figure 3. Composite size-class diagrams for forest types in Glacier: (A) *Thuja/Tsuga*, (B) *Pinus ponderosa/Pseudotsuga*, (C) *Pinus contorta/Larix*. Species are arranged from most (first) to least (last) shade tolerant: HL—*Tsuga heterophylla*; RC—*Thuja plicata*; ES—*Picea engelmannii/glauca*; DF—*Pseudotsuga menziesii*; WP—*Pinus monticola*; LP—*Pinus contorta* ssp. *latifolia*; WL—*Larix occidentalis*; PP—*Pinus ponderosa*.

invade the understory, thereby promoting compositional differences between canopy and understory (Fig. 3). In the absence of fire, eventual conversion to *Pseudotsuga menziesii* and *Picea*-complex dominance could be anticipated. Dominance by *Pinus contorta* and *Larix occidentalis* over large areas in Glacier, however, suggests that the fire recurrence interval is typically shorter than the life span of either of these colonizer species (i.e., a century or less). Hence, recurrent crown fires in this region appear to truncate ecosystem recovery during the gradual transition from intolerant to tolerant species dominance. The patchy distribution of crown fires produces a patterned mosaic of different-aged forest stands (Wright 1974) that are characterized, in general, by low compositional stability (the compositional change index value is 0.550). The correlation pattern within the *Pinus contorta/Larix* forests type differs from those of Yosemite or Glacier's *Thuja/Tsuga* forest type. The positive correlation between density and basal area suggests that in this ecosystem, initial density of established trees may play a greater role in dictating biomass accumulation than processes of competitive thinning. Goff and Zedler (1968) found a similar correlation pattern in boreal transition forests of the upper Midwest, which are periodically disturbed by canopy fires and spruce budworm outbreaks (Hett and Loucks 1976). The compositional changes within and structural traits of *Pinus contorta/Larix* forests are characteristic of periodic crown fire regimes.

Pinus ponderosa/Pseudotsuga forests in Glacier were characterized by a presettlement surface fire regime similar in frequency to that of lower elevation Yosemite forests. However, because fire suppression in Glacier has been implemented more recently than in Yosemite (ca. 1910) and was not generally effective in the region until the 1930s (Arno 1980), these previously open-grown *Pinus ponderosa* woodlands still exhibit pronounced compositional alteration, as evidenced by the low index value for this forest type (0.300). Both *Pseudotsuga menziesii* and *Picea*-complex have become established under the *Pinus ponderosa* overstory (Fig. 3), apparently in response to fire suppression (Lunan and Habeck 1973, Habeck and Mutch 1973). *Pinus ponderosa*/

Pseudotsuga forests exhibit a structural correlation pattern similar to that of *Pinus contorta*/*Larix* forests of Glacier, in that density correlates positively with stand basal area.

In both *Pinus contorta*/*Larix* and *Pinus ponderosa*/*Pseudotsuga* forest types, compositional trends within the forest and associated structural properties reflect responses to ecosystem disruption. On the one hand, periodic crown fires in *Pinus contorta*/*Larix* forests interrupt successional recovery and promote a structure that is greatly influenced by the density of established trees in the post-burn forest. On the other hand, recent suppression of a surface fire regime in *Pinus ponderosa* woodlands has triggered a release of *Pseudotsuga menziesii* and *Picea*-complex populations, producing a pulse of invasive trees which accounts for both the compositional shifts and the increased importance of tree density on standing crop in this forest type. A similar response might be anticipated following exclusion of livestock grazing (Vale 1981), although Lunan and Habeck (1973), studying *P. ponderosa* woodlands in Glacier, never mention grazing as a contributing factor in the development or maintenance of these plant communities.

The differences in compositional trends within and structural characteristics between forest types in Glacier and Yosemite, then, reflect differences in climate, natural fire regimes, and the influence of fire suppression. The variety of structures among forest types in Glacier appears to be related to the differences in natural fire regimes allowed by the modification of regional climate by site factors. For example, on topographically dry sites (south-facing aspects; thin sandy substrates), recent suppression of surface fires has triggered invasion of more tolerant species (*Pseudotsuga menziesii* and *Picea*-complex). On dry-mesic sites covering most slopes in the montane zone of Glacier, sporadic crown fires periodically reinitiate vegetation recovery mechanisms, resulting in a forest type possessing intolerant species (*Pinus contorta* ssp. *latifolia* and *Larix occidentalis*) in the overstory, with varying representations of invasive tolerant species. Mesic, sheltered slopes rarely burn, so that *Thuja*/*Tsuga* forests in Glacier maintain a forest structure strongly influenced by gradual thinning, a structure more similar to Yosemite forests than to the other Glacier forest types. In Yosemite, more intense summer droughts, by exacerbating moisture stress, induce thinning on most sites. Hence, forest structures are similar throughout the montane zone of Yosemite, although subtle differences in compositional patterns among forest types suggest that the influence of suppression of surface fires has not been uniform.

Acknowledgments

I acknowledge Drs. Thomas R. Vale, Kathleen C. Parker, and Vernon Meentemeyer for advice and critical review of the manuscript. Furthermore, I thank Kathleen C. Parker for assistance in data collection. Funds in support of data collection, analysis, and publication have been provided by a National Science Foundation fellowship, a University of Wisconsin travel grant and fellowship, and the University of Georgia graduate school.

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Received October 8, 1982

Accepted for publication April 4, 1983