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Thomas T. Veblen

Keith S. Hadley

Elizabeth M. Nel

Thomas Kitzberger

Marion Reid

Ricardo Villalba

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Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest

THOMAS T. VEBLEN, KEITH S. HADLEY,* ELIZABETH M. NEL, THOMAS KITZBERGER, MARION REID and RICARDO VILLALBA

Department of Geography, University of Colorado, Boulder, CO 80309, USA

Summary

1 The spatial and temporal patterns of fire, snow avalanches and spruce beetle outbreaks were investigated in Marvine Lakes Valley in the Colorado Rocky Mountains in forests of *Picea engelmannii, Abies lasiocarpa, Pseudotsuga menziesii* and *Populus tremuloides*. Dates and locations of disturbances were determined by dendrochronological techniques. A geographic information system (GIS) was used to calculate areas affected by the different disturbance agents and to examine the spatial relationships of the different disturbances.

2 In the Marvine Lakes Valley, major disturbance was caused by fire in the 1470s, the 1630s and the 1870s and by spruce beetle outbreak in *c.* 1716, 1827 and 1949.

3 Since *c.* 1633, 9% of the Marvine Lakes Valley has been affected by snow avalanches, 38.6% by spruce beetle outbreak and 59.1% by fire. At sites susceptible to avalanches, avalanches occur at a near-annual frequency. The mean return intervals for fire and spruce beetle outbreaks are 202 and 116.5 years, respectively. Turnover times for fire and spruce beetle outbreaks are 521 and 259 years, respectively.

4 Several types of disturbance interaction were identified. For example, large and severe snow avalanches influence the spread of fire. Similarly, following a stand-devastating fire or avalanche, *Picea* populations will not support a spruce beetle outbreak until individual trees reach a minimum diameter which represents at least 70 years' growth. Thus, recent fires and beetle outbreaks have nonoverlapping distributions.

Keywords: dendrochronology, fire, geographic information system, landscape, Rocky Mountain forests, snow avalanche, spruce beetle

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Introduction

The patchiness, or spatial heterogeneity, of a landscape is at least partially due to the history of disturbances affecting that landscape. This patchiness is believed to fundamentally influence present and future patterns of disturbance in that landscape, but rarely has this hypothesized influence been investigated (Turner 1987; Urban *et al.* 1987). Although interactions among disturbances such as fire, blow-down and insect outbreaks appear widespread in the coniferous forests of western North America, quantitative data describing these interactions are scarce (Knight 1987). In the present paper we examine how heterogeneity imparted in the landscape by past disturbances influences the subsequent pattern and consequences of disturbance. Specifically, we quantify some of the parameters of the disturbance regime (*sensu* White & Pickett 1985) and

examine interactions among the most important types of disturbance for a subalpine valley in the Colorado Rocky Mountains.

In the subalpine forests of Colorado (i.e. above *c.* 2750 m a.s.l.), characterized by *Picea engelmannii* (Parry) Engelm. (Engelmann spruce), *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir), *Populus tremuloides* Michx. (quaking aspen), *Pinus contorta* Dougl. var. *latifolia* Engelm. (lodgepole pine) and *Pinus flexilis* James (limber pine), fire is believed to have been historically the most important form of natural disturbance (Romme & Knight 1981; Peet 1988). Fires in the subalpine zone are characteristically infrequent but stand-devastating rather than frequent, light surface or patchy fires (Peet 1988; Baker & Veblen 1990).

In the subalpine zone of the Colorado Rockies, fire history studies based on fire-scar dates on remnant trees have not been conducted because the two dominant species, *Picea* and *Abies*, are both fire-sensitive and fire-scarred residual trees are therefore rare

(Romme & Knight 1981). However, fire return intervals of at least 300 years have been estimated by the less precise method of frequency distributions of even-aged postfire stands (Clagg 1975; Romme & Knight 1981; Romme 1982).

Spruce beetle (*Dendroctonus rufipennis* Kirby) is clearly the most damaging insect of the subalpine zone of the southern Rockies (Furniss & Carolin 1977; Alexander 1987). Endemic spruce beetle populations infest fallen trees and scattered live trees but during outbreaks can kill most canopy *Picea* over extensive areas. Small individuals of *Picea* (< 10 cm in diameter) are not usually attacked, nor is *Abies*. Spruce beetle outbreaks may be triggered by a combination of climatic conditions (e.g. mild winters) and blow-downs or logging (Dyer 1969; Frye *et al.* 1974; Schmid & Frye 1977). Single outbreaks of spruce beetle, such as those that occurred in the mid-1800s and the 1940s in western Colorado, can kill nearly all the mature spruce over areas of several 100 000 ha (Schmid & Frye 1977; Baker & Veblen 1990). The predominant response to beetle outbreak is the release of previously suppressed subcanopy trees of *Picea* and *Abies* as opposed to the dominant response to wildfire where seedling establishment results in even-aged postfire stands (Veblen *et al.* 1991a). With the death of canopy trees, previously suppressed subcanopy *Abies* and *Picea* show dramatic releases and sustain high growth rates for 40 to 100 or more years.

Beetle-disturbed stands are easily distinguished from postfire stands by patterns of tree growth (i.e. frequencies of trees released and the shapes of ring-width chronologies) and stand structure (Veblen *et al.* 1991a,b). The oldest individuals of postfire stands have initially rapid growth rates which decline exponentially as the stand ages. In contrast, live *Picea* trees in beetle-disturbed stands have slow initial growth until these suppressed subcanopy trees are dramatically released by the death of canopy trees killed by beetles. The coincidence of releases among trees in scattered stands of different topographic positions identifies the disturbance as a regionally extensive beetle outbreak rather than a small blow-down. Tree population age and size structures can also be used to identify prior disturbance by beetles or fire. Whereas old-growth *Picea–Abies* forests are typically characterized by larger and older *Picea*, *Abies* is the more abundant species in the larger size classes and older age classes after a beetle outbreak (Veblen *et al.* 1991a). In post-fire stands, age frequencies of both species are broadly bell-shaped whereas in stands disturbed by beetle they are all-aged.

Methods

STUDY AREA

Marvine Lakes Valley (107°22′W, 39°55′N) is located in the White River National Forest in north-western Colorado (Fig. 1). This east-west oriented valley is cut into a *c.* 3000-m-high basaltic plateau. The area included for mapping measured *c.* 5 km × 7 km. Upper and Lower Marvine Lake occupy the bottom of a glacial valley eroded in basalts and tuffs. The valley sides are steep and show evidence of recent rock falls as well as ancient mass movements that have resulted in extensive areas of hummocky topography, particularly in the south-western part of the study area. Talus and block streams are also common.

The nearest climate station is the Marvine Ranch at 2380 m a.s.l. and *c.* 10 km north-west of the study area. At Marvine Ranch, mean annual precipitation and temperature are 564 mm and 19 °C, respectively. Precipitation is relatively evenly distributed throughout the year. It falls primarily as snow except during the summer months. The forest types of the Valley are forests dominated by *Pseudotsuga menziesii* (Mirbel) Franco (Douglas fir), *Picea engelmannii*, *Abies lasiocarpa* and/or *Populus tremuloides*. *Pseudotsuga*-dominated forests occur primarily in the north-western sector of the Valley on dry south-facing block-fields (Fig. 1). Mixed stands of *Picea* and *Abies* dominate the more mesic north-facing slopes. The western end of the study area, where the Valley broadens out, is occupied by a patchy mosaic of *Picea–Abies* clumps, *Populus* and subalpine meadow. Meadow is also prominent on the north-eastern side of Upper Marvine Lake on a south-facing slope. *Populus* occurs mainly on drier south-facing aspects and on basaltic block streams.

VEGETATION/DISTURBANCE MAPPING AND GIS ANALYSES

Cover types were initially mapped from 1:15 000 aerial photographs and plotted on enlarged USGS topographic maps to produce a cover type map at a scale of 1:12 000. This map was corrected on the basis of on-site inspection. On the aerial photographs, it was feasible to distinguish vegetation types according to physiognomy (forest versus meadow), tree species composition, and age (i.e. young postdisturbance stands versus old-growth stands). Seven vegetation and three ground surface types were recognized (Fig. 1).

A raster-based geographic information system (GIS) was used to calculate the area of each cover type and the area affected by each disturbance agent (IDRISI; Eastman, 1990). The photointerpreted vegetation map was digitized and converted to a raster format by assigning a separate text value to each of a total of 88 polygons. The digitized vegetation map was registered to a USGS digital elevation model (DEM). The Universal Transverse Mercator co-ordinates specified for the USGS 7.5-minute quadrangles were the same as those of the DEM which facilitated registration of the vegetation map. As a final check of the accuracy of the registration, the UTM co-ordi-
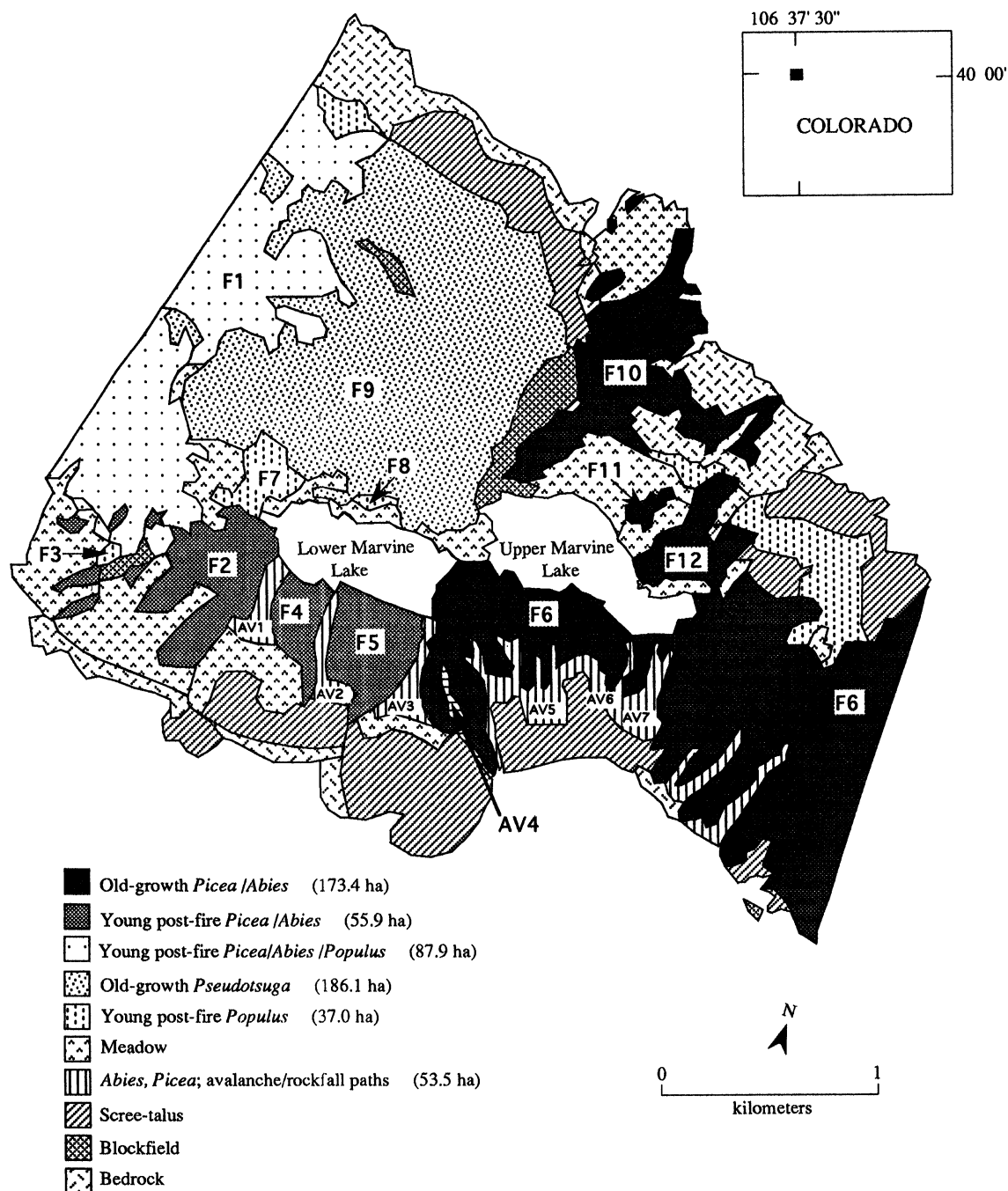
Fig. 1 Map of the Marvine Lakes Valley, Colorado, USA, showing the principal vegetation and surface types; total areas of each forest type are given in parentheses.

nates of five ground control points were determined in the field using the global positioning system (GPS). The percentage of forested area affected by each disturbance agent was determined by combining GIS images of the forested units and images of each disturbance agent.

The areas of the most recent stand-destroying fires and spruce beetle outbreaks could be determined with a high level of certainty because the evidence of these events is still obvious in the landscape. However, for earlier events the areas had to be estimated from dendroecological evidence (described below), presence of fire breaks, and the probable

extent of stands of susceptible structure for a beetle outbreak.

SAMPLING METHODS

Eighteen of the mapped vegetation units (AV1-7 and F2-12 in Fig. 1) covering > 90% of the area mapped were selected for sampling of forest composition, structure and disturbance history. Each unit was subdivided into two to six equal-area elevation belts in which several 50–375-m^2 rectangular quadrats were randomly located. The size and number of quadrats varied (from 2 to 6) according to the extent of the unit and tree den-

sity to assure a sample of at least 50 tree ages in the small units and at least 100 tree ages in the larger units. In each quadrat, we measured the diameters at breast height (d.b.h.) of all live and dead trees ≥ 4 cm d.b.h., counted tree seedlings (< 1.4 m tall) and saplings (> 1.4 m tall but < 4 cm d.b.h.), and recorded the d.b.h. and species for all logs ≥ 15 cm d.b.h.. Field data were collected in 1988, 1991 and 1992.

In each quadrat, increment core samples for tree ageing were extracted at a height of *c*. 30 cm above the ground from all live trees > 4 cm d.b.h.. To estimate the ages of uncored seedlings and saplings, ten 80-cm-tall seedlings and ten 2-cm-d.b.h. saplings of each species were cut at the base in an old-growth stand, a young postfire stand and a young post-avalanche stand. This sampling procedure was not appropriate for stand F1 which consisted of *Picea–Abies* interspersed with small meadows and clumps of *Populus*. Here, 15 of the largest trees in this map unit were selected for coring to determine the age of this patchy postfire cohort. In addition to the cores taken from all trees in the quadrats in each stand, two cores were extracted at a height of 1.1 m from the largest, and presumably oldest, live and dead-standing trees of *Pseudotsuga* (17 trees) and *Picea* (43 trees) in four extensive old-growth stands. These cores were used for developing long ring-width chronologies from which information about disturbance history and climate variation was inferred.

Scars, caused by rock falls, avalanches, or fires, were sampled opportunistically as they were encountered. Since the study area is designated as wilderness, only nondestructive increment core samples (Barrett & Arno 1988) and wedges (McBride & Laven 1976) were taken of disturbance scars.

DENDROCHRONOLOGICAL ANALYSES

All cores were processed following standard dendrochronological procedures (Stokes & Smiley 1968). For determining tree ages, in cases where the pith could not be intercepted, 1–4 years were added for rings missing near the centre (as judged by the curvature of the rings; Duncan 1989). For samples that did not reach to within 4 years of the centre minimum ages were recorded but these data were not included in the age frequency distributions of the sampled stands. Also, because of rotten centres, a few trees in each stand could not be aged. Eighty-five per cent of the live trees ≥ 4 cm d.b.h. were successfully aged (89% in postfire stands, 78% in old-growth stands and 97% in postavalanche stands). The 80-cm-tall seedlings of *Picea* and *Abies* which were aged ranged in age from 17 to 87 years, implying age ranges at the 30-cm coring height of *c*. 5–30 years. Thus, because of the variable periods required for trees to reach coring height, tree ages are given as age at coring height.

Dendrochronological methods of detecting past spruce beetle outbreaks followed Veblen *et al.*

(1991a). Growth releases (i.e. periods of accelerated growth) were used to identify periods of past canopy disturbances. On all cores taken for age determination, years were recorded in which growth releases were initiated. A growth release was defined as a 250% increase in mean ring width when consecutive groups of five years were compared. The outermost ring of the trees cored in 1988 was 1987; thus, releases more recent than 1982 were not included. For simplicity, release frequencies were plotted until 1980. Trees which experienced initially rapid growth, reflecting establishment under relatively open conditions, were also counted as 'releases'. Such trees were identified by their consistently wide rings over the initial 10–20 years of growth. Release data are summarized as the percentage of those trees surviving to 1988 that showed a release in a given year. Release frequencies were only plotted if the total of sampled trees alive in a given year exceeded 20.

Ring-width chronologies were constructed from the 15 oldest trees of each species sampled for age structure in three old-growth and three postfire stands, and from all of the subjectively sampled older trees occurring outside of quadrats. Cores used for ring-width chronologies were visually and quantitatively cross-dated (Stokes & Smiley 1968; Holmes 1983). The chronologies from the subjectively sampled trees were extended by incorporating the cores from dead trees. The computer program COFECHA (Holmes 1983) was used to cross-date the cores from the dead trees against the master chronologies developed from the live trees in each stand. Ring-width chronologies were standardized to reduce ring-width variances among and within cores (Fritts 1976; Graybill 1979). For interpreting disturbance history, a horizontal straight line passing through the mean ring width of the entire core was used as the standardization procedure. This facilitates the detection of deviations from the average growth rate, thereby identifying periods of release such as those expected after a major canopy disturbance (Veblen *et al.* 1991a). We also used standard dendroclimatic standardization procedures (Fritts 1976) to detrend ring-width series and produced ratios of ring-width chronologies for stands potentially affected by beetle outbreaks and a control stand lacking *Picea*.

Results and interpretation

STAND DESCRIPTIONS

The two old-growth forest types, *Picea–Abies* and *Pseudotsuga*, accounted for about two-thirds of the total forested area of 593.8 ha (Fig. 1). Most of the remaining forest area consisted of postfire stands of *Picea–Abies* and/or *Populus*. The remaining forest type consisted of sites frequently disturbed by snow avalanches (and associated rock falls) that were dominated by *Picea* and *Abies*.

Table 1 Site factors and tree basal areas for sampled stands. Each site factor is given as a range of values for quadrats in each stand. Due to its large size, stand F6 was subdivided into eastern (F6e), middle (F6m) and western (F6w) sectors for characterization of site factors. Species codes are: *Pien, Picea engelmannii; Abla, Abies lasiocarpa; Psme, Pseudotsuga menziesii;* and *Potr, Populus tremuloides*

Forest type/stand	Site factors Elevation (m)	Aspect	Slope (°)	Basal area (m² ha⁻¹) Live trees Pien	Abla	Psme	Potr	Standing dead trees Pien	Abla	Psme	Potr
Old-growth forests											
Picea–Abies											
F-6w	2840–2880	NNW	2–20								
F-6m	2840–2880	N	10–26								
F-6e	2850–2890	N	12–30								
F-6				8.51	46.41			15.59	5.88		
F-10	2850–2890	S	3–29	2.17	48.46	9.00	1.03		7.82	3.86	2.13
F-11	2860–2880	SW	14–17	4.76	41.80				19.76		
F-12	2850–2890	SW	11–17	18.54	39.00			23.17	30.75		
Pseudotsuga											
F-9	2860–2870	S	2–15	2.35	18.63	44.68	1.26	0.44	4.97		
Young post-fire forests											
Populus											
F-3	2930	E	32–40				40.13				0.25
F-7	2850	knoll	3–14	2.16	18.00	2.90	14.81				0.86
F-8	2850	knoll	1–10	0.65	1.15		39.23				1.65
Picea–Abies											
F-1	2850–2870	variable	5–35	ND							
F-2	2840–2880	N	34–37	60.62	33.94			0.67	0.13		
F-4	2850–2930	N	19–32	21.55	34.95			0.05	0.91		
F-5	2850–2960	N	17–27	20.57	42.19			0.19			
Avalanche *Picea–Abies* forests											
AV–1	2870–2930	N	26–33	5.74	18.50				0.07		
AV–2	2870–2930	N	24–35	9.55	3.06			0.33	0.43		
AV–3	2870–2930	N	22–42	4.59	14.85						
AV–4	2880–2970	N	24–31	0.95	8.60				0.14		
AV–5	2880–2980	N	15–30	12.74	6.79			0.79	0.92		
AV–6	2890–2930	N	25–32	1.36	4.94				0.44		
AV–7	2880–2980	N	22–33	6.36	10.19			0.20	3.41		

The old-growth *Picea–Abies* forests occurred primarily in the eastern half of the study area (Fig. 1). They ranged in composition from pure *Picea–Abies* (e.g. stands F-6, F-11 and F-12) to mixtures with *Pseudotsuga* and *Populus* in more open stands on drier slopes (e.g. stand F-10; Table 1). In stands F-6 and F-12, the basal area of dead *Picea* was greater than that for live trees, as is typical of stands affected recently by a spruce beetle outbreak (Table 1).

The young postfire stands occurred in the southwestern quarter and along the western edge of the study area (Fig. 1). The postfire *Populus* stands ranged from pure stands (e.g. stand F-3) to mixtures with conifers (e.g. stands F-7 and F-8). postfire stand F-1 was a heterogeneous mixture of mostly *Picea–Abies* patches interspersed with small meadow openings and clumps of *Populus*. Stands F-2, F-4 and F-5 were dense, pure *Picea–Abies* forests with low basal areas of dead-standing trees, as expected for young postfire stands (Table 1). The frequently disturbed forests occupying avalanche paths consisted exclusively of *Picea* and *Abies*, and as expected had the lowest basal areas of any forest type (Table 1). They occurred on the steepest forested slopes and were limited to north-facing slopes (Table 1; Fig. 1). These sites contained numerous large boulders near the bottom of their slopes as well as rock fragments inserted into trees 1–3 m above the ground surface indicating disturbance by rock fall as well as snow avalanche.

DETECTION OF PAST DISTURBANCE EVENTS

Avalanches

Age frequency distributions of the *Picea* and *Abies* populations occupying avalanche paths were relatively broad and generally young (Fig. 2). Maximum tree ages ranged from 88 to 140 years. Although the scar dates indicate that most sites experience frequent severe disturbances (several per decade at most sites), many trees survive each event. The high frequencies of releases (Fig. 3) at these sites suggest that snow avalanches and/or rock falls occur nearly annually at each site. Avalanche scars were also dated and yielded much lower avalanche frequencies, but the high frequency of releases at all sites indicated that
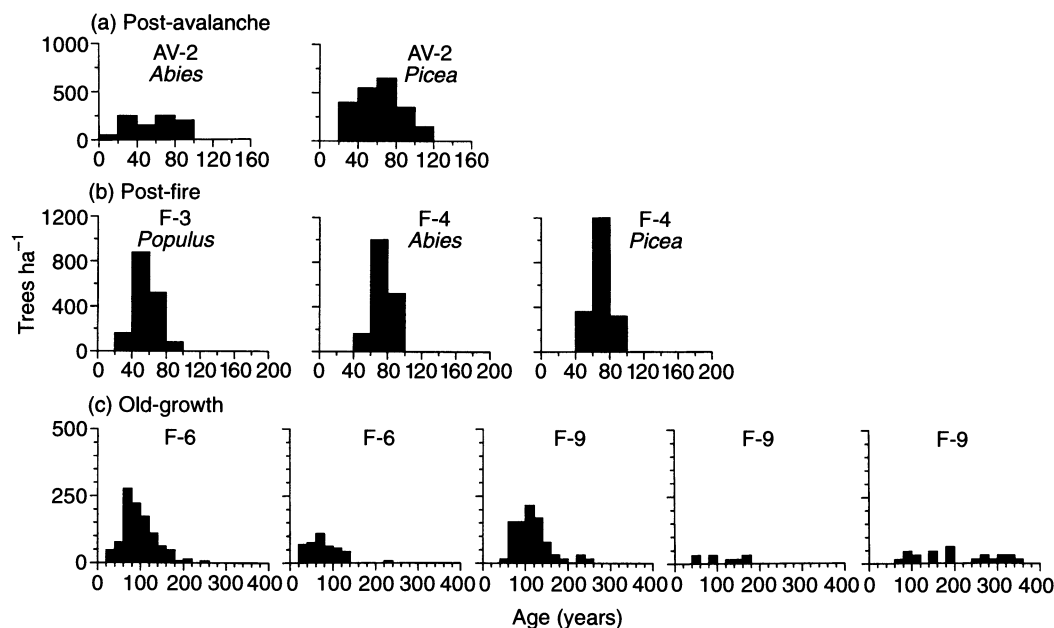
Fig. 2 Numbers of trees per ha in 20-year age classes in typical (a) post-avalanche stands, (b) post-fire stands and (c) old-growth stands.

scar-based estimates were underestimates due to the probable destruction of older trees by more-recent avalanches. For example, at stand AV-5, where only a single scar was found, release frequencies imply disturbances nearly every year over the last *c*. 50 years.

For avalanches, release frequencies appear to be the best measure of disturbance frequency. Tree age frequencies were not useful in detecting past avalanches, because the response to this type of disturbance is primarily one of accelerated growth of survivors rather than establishment of new trees. Snow cover protects seedlings and saplings from damage from all but basal slide avalanches. Thus, this type of disturbance generally does not result in pulses in the age frequency distributions. Although release frequencies are the best indicators of past avalanches, the record does not include dates more recent than 1980 because of the criteria used in identifying releases (i.e. comparison of 5-year means).

Fires

The young postfire populations of *Populus* (stand F-3) and *Picea–Abies* (stands F-2, F-4, F-5, F-7 and F-8) have bell-shaped distributions typical of postfire tree populations in Colorado subalpine forests (Fig. 2; Whipple & Dix 1979). The maximum age (108 years) of these postfire cohorts indicate that the fire occurred prior to 1880. Scars on three *Pseudotsuga* in adjacent stands date from *c*. 1874. These dates, plus the maximum age of postfire stems of *Populus* in stand F-7 (108 years plus *c*. 5 years to reach the coring height of 30 cm) suggest that these intermediate-aged postfire stands burned in *c*. 1874.

In a few stands (F-5, F-7 and F-8) small numbers of *Abies* survived the fire resulting in bimodal frequency distributions. The lack of surviving *Picea* older than *c*. 100 years, however, does not necessarily imply that none survived the late-19th-century fire
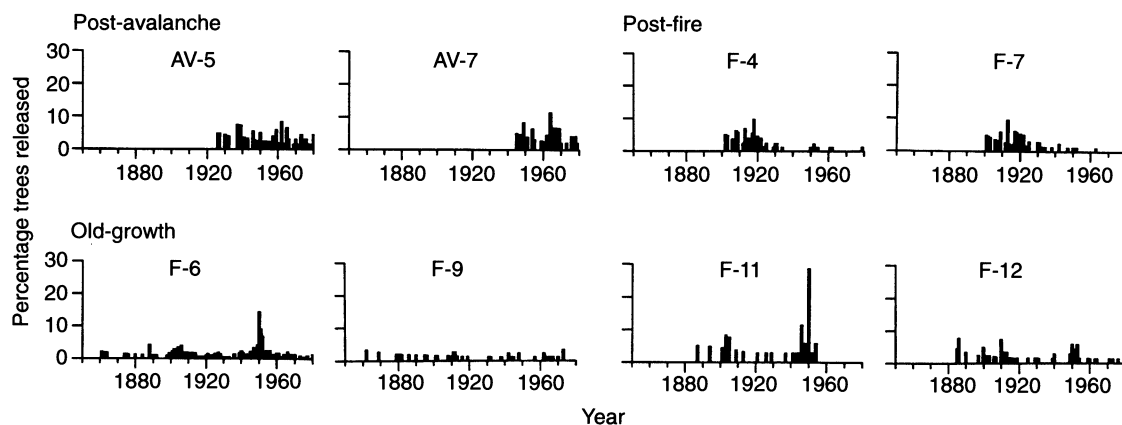
Fig. 3 Percentage of live trees released in typical post-avalanche, post-fire and old-growth stands. A release is an increase in mean ring width of ≥ 250% when adjacent groups of five rings are compared. Releases are not shown where the number of live trees was ≤ 20.

because any survivors would probably have been killed in the 1940s' spruce beetle outbreak.

In the postfire stands, the frequency of release is greatest during the early phases of stand initiation and low over the most recent *c*. 50 years of development (Fig. 3). The releases during the early part of stand development correspond to trees that experienced rapid initial growth. Such rapid initial growth is expected under the open conditions created by a stand-destroying fire.

The ages of fire-sensitive *Abies* in all the old-growth stands indicate that these stands have not been affected by a stand-destroying fire for at least 200 years (Fig. 2). Because *Abies* rarely live longer than *c*. 350 years, and in old unburned stands often have maximum ages of *c*. 250 years (Whipple & Dix 1979; Veblen 1986), the maximum ages of these populations are generally not helpful in estimating time since last stand-destroying fire for older stands. The maximum ages and growth patterns of *Pseudotsuga* are more useful in estimating fire dates In stand F-9 the *Pseudotsuga* chronology indicates initially rapid tree growth followed by a steep decline (Fig. 4) as is typical of subalpine postfire tree growth (Veblen *et al.* 1991a). The cores in the earliest *c*. 150 years of the stand chronology are from dead-standing *Pseudotsuga* which appear to be the remnants of a postfire population because of their initially rapid growth. Based on the earliest date of the innermost ring in this population, the date of the fire appears to have been in the

1470s (in Fig. 4 the chronology is not plotted for dates for which *n* is < 5). As only five individuals of such great age could be found, the dating of a fire affecting stand F-9 in the 1470s is only tentative.

The F-9 stand chronology also shows a large increase in both the ring-width index and the number of samples in the chronology beginning in the mid-17th century (Fig. 4). This pattern is indicative of a second cohort of rapidly growing postfire trees. The ages of the oldest trees in this cohort suggest the fire occurred *c*. 1633 (Figs. 2 and 4).

Spruce beetle outbreaks

Because the dominant response to spruce beetle outbreak is accelerated growth of established trees, including both the nonhost *Abies* and *Picea* too small to be colonized by beetles (Veblen *et al.* 1991a), age structures are not useful in dating past beetle outbreaks. Nevertheless, the scarcity or absence of *Picea* older than *c*. 140 years in all the *Picea–Abies* old-growth stands (Fig. 2) is strong evidence that an outbreak has occurred. Elsewhere, in the absence of spruce beetle outbreaks, old-growth *Picea–Abies* forests are characterized by numerous *Picea* 300 to over 500 years old (Veblen 1986; Peet 1988).

The dramatic increases in the frequencies of growth releases in the late 1940s in stands F-6 and F-11 reflect the historically documented 1940s spruce beetle outbreak, as does a slight increase in stand
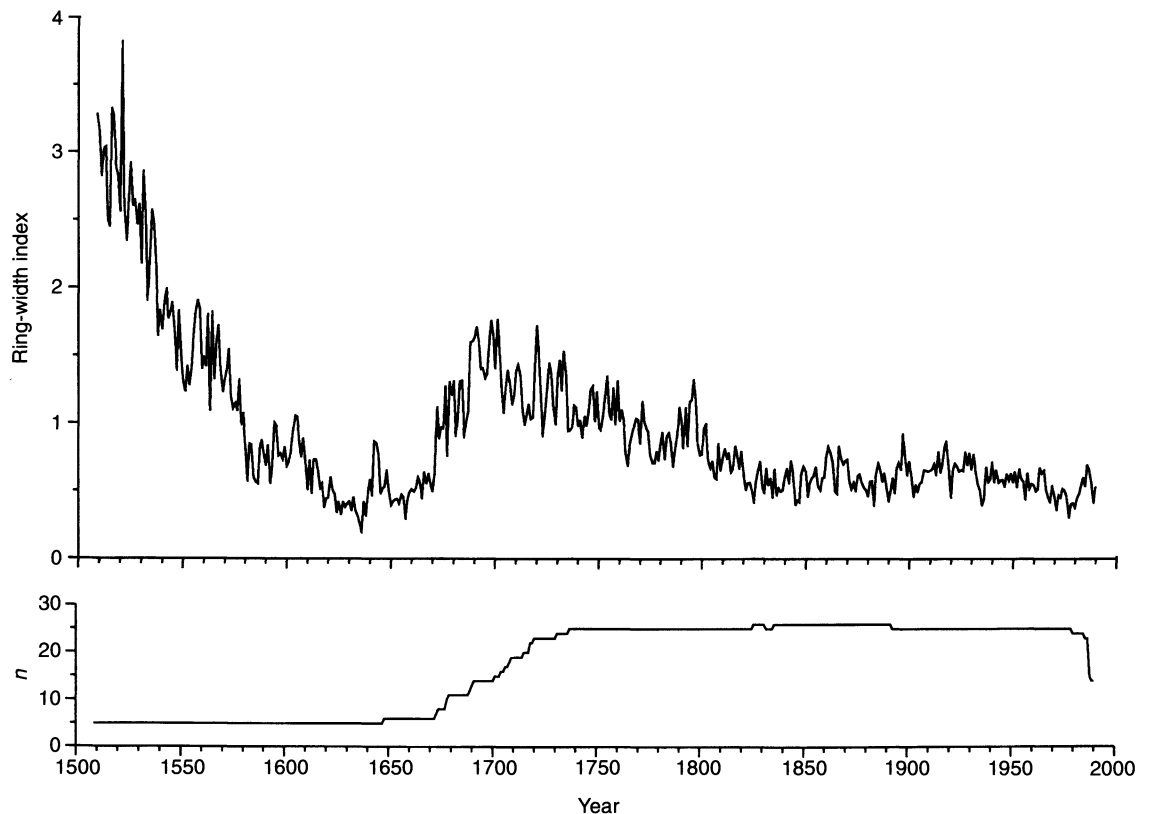

Fig. 4 Mean ring-width index (horizontal line standardization) for the oldest live and dead *Pseudotsuga* in stand F-9. Indices are plotted only for the period when *n* ≥ 5. The varying number of cores contained in each chronology is indicated by the graph of *n*.
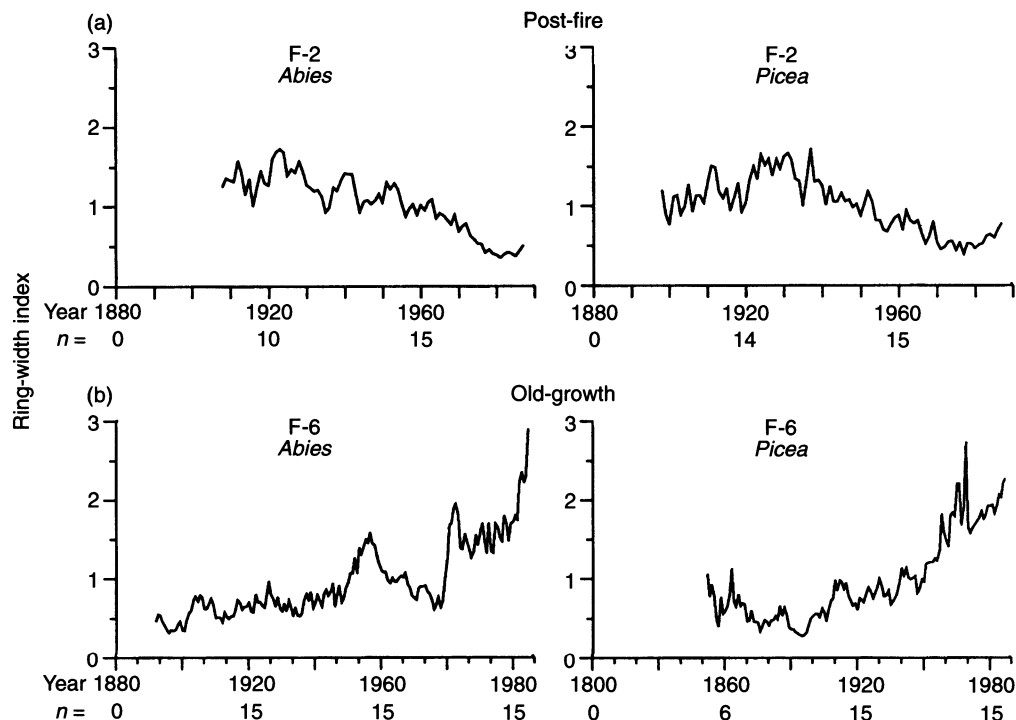
Fig. 5 Mean ring-width indices (horizontal line standardization) for the oldest 15 trees of each species in typical post-fire and old-growth stands. The varying number of cores contained in each chronology at the beginning of every other decade is given by n. Indices are plotted only for periods when $n \geq 5$.

F-12 (Fig. 3). Stands F-9 and F-10, occurring on drier sites and having only a minor *Picea* component, do not appear to have been affected by the 1940s outbreak. In these stands, *Picea* was apparently too small and scarce to support the beetle outbreak as reflected by the scarcity of dead-standing *Picea* (Table 1). Stand F-12 shows only a modest increase in the frequency of releases in 1949, but given the large amount of dead-standing *Picea* (Table 1) it also must have been affected by the beetle outbreak.

The growth patterns of the 15 oldest trees from the quadrat samples of old-growth (Fig. 5) contrast sharply with those from the postfire stands (Fig. 5). In the postfire stands, maximum growth rates are attained during the first c. 60 years of stand development and growth rates decline during the 1950s through 1980s. In contrast, in the old-growth stands affected by the late-1940s' spruce beetle outbreak growth rates abruptly increase during the 1950s through 1980s (Fig. 5a). The chronology based on the subjectively selected older *Picea* in stands F-6, F-11 and F-12 also shows a sharp increase in ring-width index in the 1950s (Fig. 6a). Furthermore, the sudden decline in the sample depth curve for this chronology clearly reflects the coincident mortality of many *Picea* in the late 1940s.

The chronology based on the subjectively selected older *Picea* also shows a sharp increase in ring-width index in c. 1716 and a less-pronounced increase in the 1830s (Fig. 6a). This increase in the 1830s, however, is not necessarily greater than increases in the 1790s, 1860s or early 1900s. Because the horizontal

straight line standardization did not clearly date the 19th-century outbreak an alternative technique was used. The same *Picea* data set and the *Pseudotsuga* data set (from stand F-9 with no history of insect outbreak) were standardized using standard dendroclimatic techniques to detrend both series (Holmes 1983). The ratios of their index values better identify the periods of accelerated growth initiated in c. 1716 and 1827 (Fig. 6b). Thus, two prehistoric spruce beetle outbreaks are tentatively identified as initiating in 1716 and 1827.

DISTURBANCE REGIME DESCRIPTORS

Areas

Because the late-15th-century fire was only tentatively dated, and because it was not possible to determine its area, it is not included in the estimation of areas disturbed. The occurrence of the 1633 fire was inferred from the growth pattern of numerous trees dispersed throughout stand F-9. Consequently, all of the area now occupied by stand F-9 was judged to have burned (Fig. 7a). In addition, a fire of that size was assumed to have spread to most of the area west of stand F-9, but was stopped by the patches of meadows at the western end of Lower Marvine Lake; its eastward spread was stopped by a large block field just north of the western end of Upper Marvine Lake (Fig. 1).

For the 1716 and 1827 spruce beetle outbreaks, it was assumed that all the mesic *Picea–Abies* forests
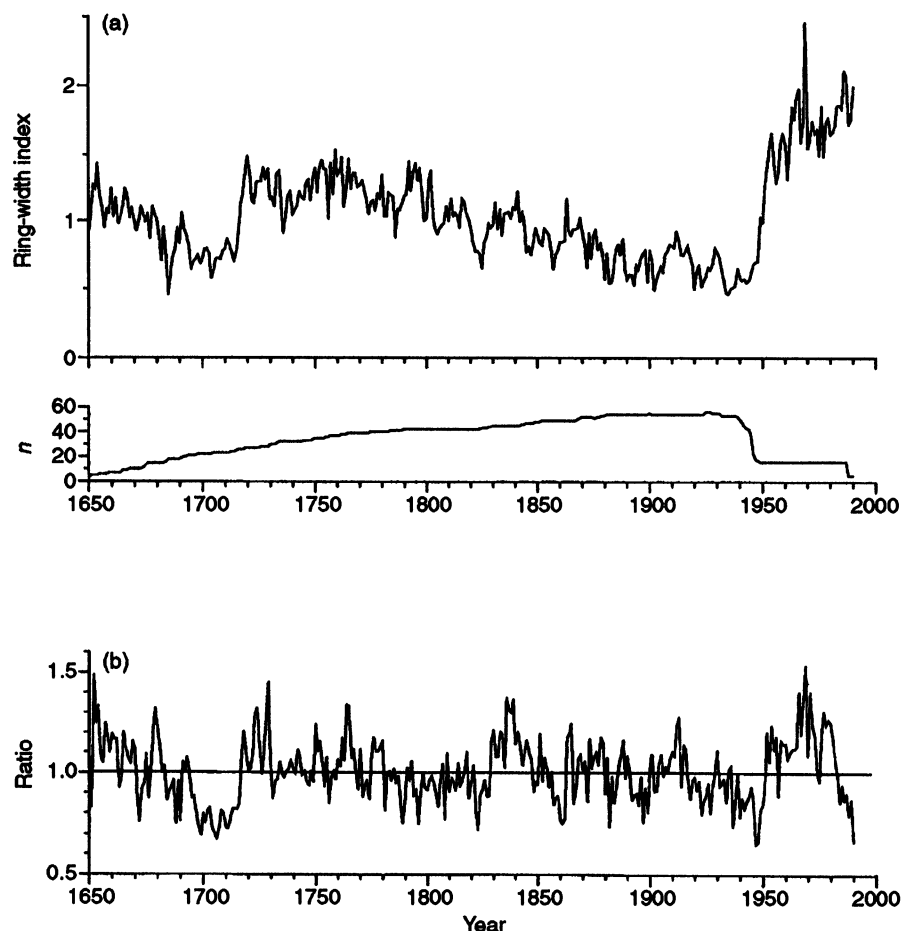
Fig. 6 Mean ring-width indices for (a) *Picea* and (b) ratios of mean ring-width indices for *Picea* and *Pseudotsuga*. The standardization procedures were a horizontal straight line passing through the mean ring width in (a) and complete detrending with inclined straight lines, negative exponential curves and cubic spline functions in (b). Indices are plotted only for the period when $n \geq 5$. The varying number of *Picea* cores contained in each chronology is indicated by the graph of n. For the sample-depth curve of *Pseudotsuga* see Fig. 4.

were affected (Fig. 7b). This included the area affected by the 1949 spruce beetle outbreak as well as the area affected by the 1874 fire. The larger extent of the prehistoric spruce beetle outbreaks is also indicated by the presence of a salt-and-pepper pattern of tree mortality above the area affected by the 1874 fire in a historical photograph taken c. 1900. The area of the prehistoric spruce beetle outbreaks did not include stands F-9 and F-10 which are too dry to support a population of large *Picea*. Thus, during the c. 359 year (1633–1992) record of mapped disturbance events, 38.6% and 59.1% of the total forested area were affected by at least one major beetle outbreak or fire, respectively (Table 2). When only *Picea–Abies* forests are considered, the area affected by beetle outbreaks is substantially greater than that affected by fire.

Snow avalanches and/or rock falls occur in topographically susceptible sites nearly every year (Fig. 3). Thus, in the 9% of the forested area susceptible to this disturbance type, snow avalanches (sometimes in combination with rock falls) are regarded as a chronic disturbance. The data available on the occurrence of snow avalanches did not permit the mapping of the extent of individual events and

there is no reason to assume that each event affected the entire avalanche path. Consequently, additional descriptors (other than frequency) of this disturbance type cannot be computed.

Mean return intervals and turnover times

The mean return intervals for major spruce beetle outbreaks and stand-destroying fires (including the tentatively dated 1470s' fire) are 116.5 and 202 years,

Table 2 Areas affected by disturbances and the percentage of the total forest area affected ($\%_{tot}$)

	Area (ha)	$\%_{tot}$
Individual events		
1633 fire	241.3	40.6
1716 spruce beetle outbreak	229.2	38.6
1827 spruce beetle outbreak	229.2	38.6
1874 fire	167.8	28.3
1949 spruce beetle outbreak	173.4	29.2
Areas affected by each disturbance type		
Fire	350.9	59.1
Spruce beetle outbreak	229.2	38.6
Avalanche	53.5	9.0

(a)

(b)

▨	1633 fire
▧	1874 fire

N

0 _____ 1
kilometers

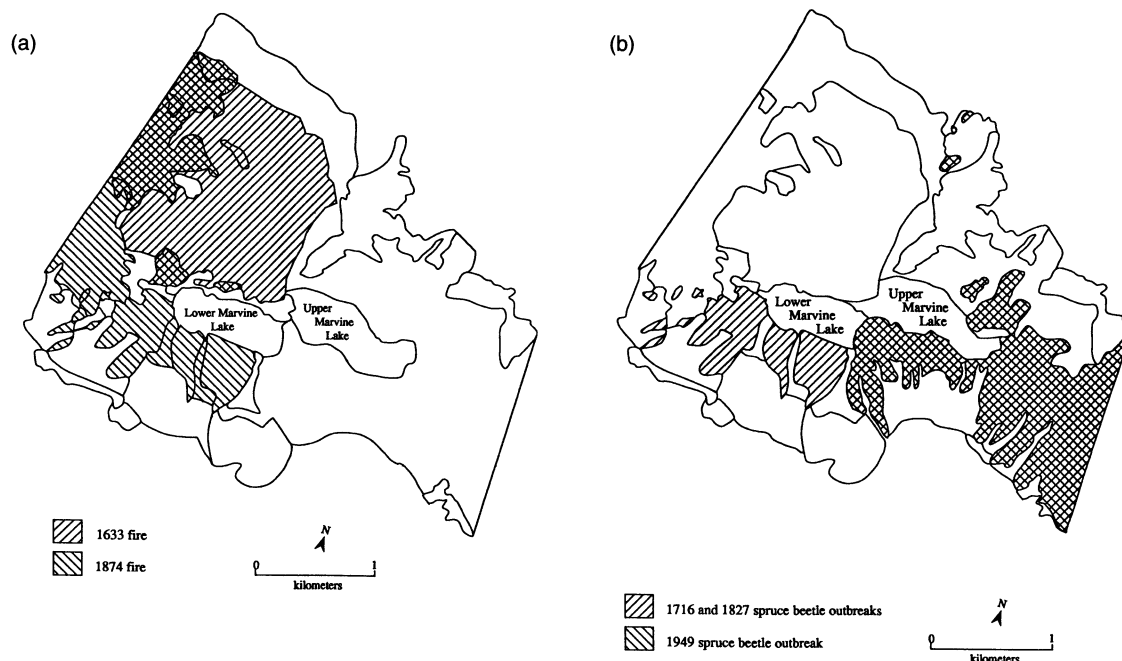|	
▨	1716 and 1827 spruce beetle outbreaks
▧	1949 spruce beetle outbreak

N

0 _____ 1
kilometers

Fig. 7 Areas (a) burned by the 1633 and 1874 fires and (b) disturbed by the 1716, 1827 and 1949 spruce beetle outbreaks.

respectively. If the 1470s' fire is not included, the fire return interval (based on only two events) is 241 years.

Turnover time is the time required for the entire study area to be affected by at least one event of a particular disturbance type. It is computed from the mean return interval and the total area affected by all disturbance events. The 1470s' burn was not included in the computation of turnover time because of the lack of evidence of the extent of this event. Even though the areas affected by the prehistoric beetle outbreaks are conservative estimates, and the areas of prehistoric burns were possibly overestimated, spruce beetle outbreaks have a substantially more rapid turnover period (259 vs. 521 years). If the parameters were computed only for *Picea–Abies* forests (i.e. excluding the large area of *Pseudotsuga*), the dominance of beetle outbreaks would be much greater.

DISTURBANCE INTERACTIONS

The spatial distributions of the 1874 fire and the 1949 spruce beetle outbreak are nonoverlapping (Fig. 7). This is explained by the young age, and therefore small size, of *Picea* in the burned area at the time of the 1949 outbreak. In the late 1940s there would have been few *Picea* older than *c.* 70 years in stands burned in 1874. Trees of this age growing under these site conditions would not have attained sufficient diameter to be susceptible to a spruce beetle outbreak. Even in 1988, the mean d.b.h. of the postfire cohorts of *Picea* in these stands was only 11–12 cm. Small diameter trees and stands lacking large diameter trees are not colonized by spruce beetle (Schmid & Frye 1977). Thus, prior occurrence of a stand-destroying fire provides immunity to spruce beetle outbreak for at least 70 years at these sites.

Sites frequently disturbed by snow avalanches are also unlikely to be affected by a spruce beetle outbreak due to the lack of large-diameter *Picea*. The spatial pattern of the 1874 fire suggests that avalanche paths may also serve as fire breaks; for example, the 1874 fire did not burn east of the large avalanche path (stand AV-3) at the south-eastern end of Lower Marvine Lake. This high frequency of disturbance by avalanches may prevent the development of sufficient biomass and appropriate fuel configuration to carry a fire.

Discussion

Most studies of disturbance regimes include only a single type of disturbance, but in the subalpine forests of the Colorado Rockies multiple types of disturbances are important. Complete quantification of such disturbance regimes is difficult due especially to the disappearance of evidence of older disturbances (cf. Fox 1989). Stand-devastating disturbances, such as fire and to lesser extent snow avalanches, may destroy most or all trees that survived or originated following earlier disturbances. Disappearance of evidence also means that areas of earlier disturbances, even when accurately dated, cannot be mapped with certainty. Thus, the estimation of areas of all but the most recent disturbances requires assumptions about the spread of the disturbance.

In quantitatively describing the disturbance regime of Marvine Lakes Valley the infrequent occurrence of fire and spruce beetle outbreaks also limits the general applicability of our results. For example, with only three dates for each fire and spruce beetle outbreak, the computed mean return intervals may or may not be representative of longer term patterns. Similarly, the small number of disturbance events means that

conclusions about the effects of climate variation on the occurrence of disturbance must be tentative. Additional studies of disturbance regimes in similar areas are required for assessing the general applicability of the results from Marvine Lakes Valley.

Despite these caveats, in the Marvine Lakes Valley, major disturbance by fire appears to have occurred in the 1470s, *c.* 1633 and *c.* 1874 and by spruce beetle outbreak in *c.* 1716, *c.* 1827 and *c.* 1949. Over the past *c.* 300 years spruce beetle outbreaks have occurred more frequently and have had a more rapid turnover period than stand-devastating fires. Thus, in the *Picea–Abies* forests, spruce beetle outbreaks have been the dominant disturbance. Approximately 9% of the forested area has been chronically disturbed by snow avalanches, occurring at a nearly annual frequency where the topography is suitable.

Our results suggest that there are predictable relationships in space and time among disturbances by fire, snow avalanche and beetle outbreak that help to explain the landscape-scale vegetation pattern in this subalpine valley. For example, large and frequent snow avalanches create areas of lower forest biomass which appear to serve as fire breaks. Avalanches and stand-devastating fires create young stands of *Picea* which even after 70 years of growth consist of trees too small to be susceptible to spruce beetle attack. Thus, the spatial distributions of recent avalanches and stand-devastating fires do not overlap with the recent spruce beetle outbreak. Eventually, however, as the spruce in the postfire stands attain sizes susceptible to spruce beetle attack, it is likely that the distributions will again overlap.

Analogous disturbance interactions may be important in explaining vegetation patterns in many landscapes.

Acknowledgements

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