

Methods of detecting past spruce beetle outbreaks in Rocky Mountain subalpine forests

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We examined the use of dendrochronological techniques and stand age structure for detecting past outbreaks of spruce beetle (*Dendroctonus rufipennis* Kirby) in subalpine forests in the Colorado Rocky Mountains. The methods were based on the observation that following beetle-caused mortality of canopy trees, growth rates of subcanopy Engelmann spruce (*Picea engelmannii* (Parry) Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) increase severalfold and remain high for several decades or more. Although inspection of unstandardized individual tree ring-width chronologies is useful for detecting past disturbance, standardized mean chronologies based on ≥ 20 cores assure adequate sample sizes and improve interpretability. Standardization of ring-width series by fitting the observed data to a horizontal line passing through the mean ring width facilitates detection of past outbreaks better than other standardization models such as polynomial or cubic spline functions. The incorporation of samples from dead-standing trees increases sample sizes and reveals patterns in the early history of a stand that may not be detectable if samples only from live trees are used. Patterns of release frequencies based on nearly all the trees in a stand were helpful in confirming interpretations not always clear from the chronologies alone. Variations in tree population age structures were related to the history of disturbance by beetle outbreak, but age structure alone was not a reliable means of detecting past outbreaks.

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Nous avons examiné l'utilisation des techniques dendrochronologiques et de la structure d'âge des peuplements pour retracer les épidémies antérieures du Dendroctone de l'épinette, *Dendroctonus rufipennis* (Kirby), dans les forêts subalpines des montagnes Rocheuses du Colorado. Les méthodes reposaient sur l'observation selon laquelle la croissance des épinettes d'Engelmann, *Picea engelmannii* (Parry) Engelm., et des sapins subalpins, *Abies lasiocarpa* (Hook.) Nutt., poussant en sous étage, augmente considérablement et se maintient à des niveaux élevés pendant plusieurs décennies suite à la mort des arbres de la strate supérieure causée par les attaques du dendroctone. Bien que les chronoséquences des cernes d'arbre individuel peuvent s'avérer utiles pour détecter les perturbations antérieures, les moyennes standardisées des chronoséquences basées sur au moins 20 carottes de croissance assurent une taille d'échantillonnage adéquate et améliorent l'interprétation. La standardisation des séries de largeur de cernes à l'aide des données observées et d'une droite horizontale passant par la moyenne des largeurs de cernes facilite la détection des épidémies antérieures et s'est avérée être supérieure aux autres modèles de standardisation telles que les fonctions polynomiales et les fonctions cubiques segmentées (cubic spline functions). L'ajout d'échantillons provenant d'arbres morts sur pied augmente la taille d'échantillonnage et révèle une information propre aux premiers stades de développement du peuplement laquelle peut passer inaperçue lorsque seuls les arbres vivants sont utilisés. L'allure des fréquences de relâchement basées sur la presque totalité des arbres du peuplement fut utile pour confirmer les interprétations parfois ambiguës lorsque basées seulement sur les chronoséquences. Les variations de structure d'âge des peuplements furent reliées à l'historique des perturbations causées par les épidémies de dendroctones quoiqu'elles ne constituaient pas à elles seules un moyen fiable pour retracer les épidémies antérieures.

[Traduit par la Rédaction]

Introduction

A major research goal in contemporary plant ecology is the quantification of spatial and temporal variations in disturbances, which are important influences on community composition and structure (Sousa 1984; Pickett and White 1985; Turner 1987). The "disturbance regime" concept has emerged as a framework for organizing this type of information and for directing research towards disturbance *per se* (Paine and Levin 1981; White and Pickett 1985). Typical parameters of a disturbance regime include frequency, return interval, predictability, magnitude or intensity, area, and spatial distribution of disturbances (White and Pickett 1985).

Quantitative data on disturbance regimes are available for only a few community types and typically for only one of the several kinds of disturbances that are important in each community type. Fire and small-scale tree falls are the most commonly quantified disturbances for most temperate forest communities (e.g., Martin 1982; Runkle 1985; Johnson and Fryer 1987; Denslow 1987). For other types of disturbances,

such as mass movements, large-scale blowdowns, volcanic events, and insect outbreaks, quantitative data are scarce (White 1979; Pickett and White 1985). Episodic outbreaks of insects lethal to particular tree species characterize the disturbance regimes of many temperate forests (Morris 1963; Furniss and Carolin 1977; Schowalter 1985; Knight 1987). The objective of our research is to develop techniques, based primarily on dendrochronology and age structure analysis, for detecting past occurrence and severity of spruce beetle (*Dendroctonus rufipennis* Kirby) outbreaks.

Dendrochronological techniques have long been applied to the study of the effects of defoliating insects on tree radial growth and detection of past outbreaks (e.g., Mott *et al.* 1957; Brubaker and Greene 1979; Swetnam and Lynch 1989). In these studies, past episodes of defoliation are reflected by periods of growth suppression in the host species. Methods developed for the detection of past outbreaks of defoliators are not appropriate for spruce beetles and most other *Dendroctonus* beetles because the host trees

TABLE 1. Site factors for the stands sampled

Stand	Elevation (m)	Aspect	Slope (degrees)	Severity of the 1940s outbreaks
Roosevelt National Forest				
Cameron Pass (C1)	3040	South	0-14	None
Blue Lake (C2)	3020	South	0-2	None
White River National Forest				
Trappers Lake (W1)	3000	North	11-27	High
Lily Pond (W2)	2970	Variable	0-14	High
Ripple Creek (W3)	3150	Northwest	0-5	High
Marvine Lakes (W4)	2870	North	34-35	None
Routt National Forest				
Walton Creek (R1)	3050	Northeast	2-10	Low
Grand Mesa National Forest				
Cottonwood Lake (G1)	3300	Northwest	0-17	None*
Big Creek (G2)	3080	Northeast	2-17	Moderate

*Although a spruce beetle epidemic was reported for this general area (Schmid and Hinds 1974), this stand was not significantly affected.

are usually killed by the beetle attack. Small-diameter trees of the host species and trees of all sizes of nonhost species, however, are not attacked during outbreaks of *Dendroctonus*, and are likely to accelerate their growth rates following the massive mortality of the dominant trees (Amman 1977; Stuart *et al.* 1989). Our approach to detection of past spruce beetle outbreaks is based on the observation that mortality of dominant spruce during an outbreak results in increased growth rates of surviving fir and spruce (Veblen *et al.* 1990). Thus, past spruce beetle outbreaks should be reflected in coincident releases of trees over extensive areas. We examine a variety of measurements, sampling intensities, and analytical procedures for detecting past spruce beetle outbreaks. We also describe criteria by which past spruce beetle outbreaks may be distinguished from fire, which is believed to have been historically the most important form of natural disturbance in these forests.

Spruce beetles in the southern Rocky Mountains

Widespread spruce beetle outbreaks are well documented for the southern Rockies since the mid-nineteenth century (Schmid and Hinds 1974; Schmid and Frye 1977). Spruce beetle outbreaks may be as significant as fire in the development of these forests (Baker and Veblen 1990), but in comparison with the numerous studies of post-fire stand development (e.g., Whipple and Dix 1979; Romme and Knight 1981; Peet 1981; Romme 1982; Veblen 1986; Aplet *et al.* 1988), knowledge of the effects of spruce beetle outbreaks on forest community properties is limited. Further understanding of stand responses to spruce beetle outbreaks depends on availability of methods for detecting spruce beetle outbreaks that occurred prior to the period of historical documentation (i.e., pre-1900 for the southern Rocky Mountains).

Outbreaks of spruce beetle, which is the most damaging insect in Engelmann spruce (*Picea engelmannii* (Parry) Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests, are triggered by blowdowns or the accumulation of logging debris (Schmid and Frye 1977; Furniss and Carolin 1977; Alexander 1987). Endemic spruce beetle populations infest fallen trees and scattered live trees, but during outbreaks they can kill most canopy spruce over extensive areas (Schmid and Frye 1977). Stands at highest risk have average diameters >41 cm, basal areas >35 m²/ha, and a

spruce composition accounting for at least 65% of the canopy (Schmid and Frye 1977). Spruce <10 cm in diameter at breast height (dbh) are not usually attacked. In unusually severe outbreaks, spruce beetles attack and kill lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) as well as spruce (Schmid and Hinds 1974).

In 1939 a strong windstorm blew down extensive patches of subalpine forest in western Colorado, thus promoting endemic spruce beetle populations to grow into the largest recorded epidemic of this century (Hinds *et al.* 1965). By 1952, when the epidemic subsided following an exceptionally cold winter, 4.3 billion board ft (1 board ft = 2.36 dm³) of timber had been killed (Massey and Wygant 1954). Most beetle-killed spruce remain standing for many years, so the severity of the outbreak was still evident at the time of our sampling over 40 years later.

Study sites

For sampling, we selected nine sites in subalpine forests located both on the western and eastern slopes of the northern Colorado Rocky Mountains (Fig. 1 and Table 1). Four sites are in White River, two in Grand Mesa, one in Routt, and two in Roosevelt national forests. The sites are on various aspects at elevations from ca. 2970 to 3300 m (Table 1), but elevation, degree of tree mortality, and stand structure were relatively uniform within each stand over an area >4 ha. All sites are characterized by Engelmann spruce and subalpine fir, and two of the drier sites (C1 and W1) also have lodgepole pine (Table 2). Stands W4 and C1 were selected to represent young (ca. 100 years) and older (ca. 230 years), respectively, first-generation post-fire stands (Table 3). Neither showed any sign of recent disturbance by spruce beetle or other agents. Stand C1 contains a remnant population of lodgepole pine, while stand W4 is purely spruce and fir. Stand C2 was selected to represent an old-growth (i.e., >300 years) spruce-fir stand in an area where no spruce beetle outbreaks had been reported. No spruce beetle outbreaks were reported for the areas sampled in Roosevelt National Forest, and thus they served as controls.

During the 1940s outbreak, at least 50% of the merchantable volume of spruce in Grand Mesa National Forest and over 90% in White River National Forest were killed (Schmid and Hinds 1974; Fig. 1). Near our sampling site in Routt National Forest, 43% of the spruce >20 cm dbh was killed (Hinds *et al.* 1965). The abundance of dead-standing spruce at our sites generally agreed with the historical documentation. In stands W1, W2, and W3 (White River National Forest), basal areas of dead-standing spruce were at least 30% greater than those for live spruce (Table 2). Stand

TABLE 2. Tree composition of the stands sampled

Stand and species	Basal area (m ² /ha)		Density (no./ha)	
	Live	Dead standing	Live	Dead standing
Cameron Pass (C1)				
<i>Pinus contorta</i>	18.1	2.1	175	31
<i>Abies lasiocarpa</i>	13.1	5.4	888	187
<i>Picea engelmannii</i>	24.7	0.3	600	19
Blue Lake (C2)				
<i>Abies lasiocarpa</i>	11.2	8.2	943	129
<i>Picea engelmannii</i>	30.9	8.8	1079	85
Trappers Lake (W1)				
<i>Pinus contorta</i>	3.9	14.1	59	208
<i>Abies lasiocarpa</i>	13.5	2.0	1105	87
<i>Picea engelmannii</i>	2.5	8.2	418	132
Lily Pond (W2)				
<i>Abies lasiocarpa</i>	20.5	3.9	1155	85
<i>Picea engelmannii</i>	11.6	15.3	485	80
Ripple Creek Pass (W3)				
<i>Abies lasiocarpa</i>	30.3	6.4	1650	100
<i>Picea engelmannii</i>	6.4	8.9	515	80
Marvine Lakes (W4)				
<i>Abies lasiocarpa</i>	33.4	0.1	1200	80
<i>Picea engelmannii</i>	36.1	0.6	1600	80
Walton Creek (R1)				
<i>Abies lasiocarpa</i>	35.9	3.8	952	171
<i>Picea engelmannii</i>	10.3	9.2	348	71
Cottonwood Lake (G1)				
<i>Abies lasiocarpa</i>	22.3	8.5	1015	305
<i>Picea engelmannii</i>	35.0	0.5	695	60
Big Creek Reservoir (G2)				
<i>Abies lasiocarpa</i>	24.9	11.3	727	195
<i>Picea engelmannii</i>	21.8	2.1	441	32

W4 (White River National Forest), however, was not attacked because it was a relatively young post-fire stand in the 1940s. Much smaller basal areas of dead-standing spruce indicate a moderate outbreak in stand G2 (Grand Mesa National Forest) and only a slight outbreak in stand R1 (Routt National Forest). There were relatively few dead-standing spruce in stands G1 (Grand Mesa National Forest), C1, and C2 (Roosevelt National Forest) indicating they were unaffected by the 1940s outbreak. Major outbreaks during the latter half of the nineteenth century were also reported for the White River and Grand Mesa national forests (Schmid and Hinds 1974).

Methods

Field methods

Each stand, except stand W4, was sampled in 1987 with 10 plots systematically located at 20-m intervals along a 300-m long transect running upslope. This plot placement assured that the samples were not too localized. Plot size varied from 10 by 10 to 10 by 30 m according to the density of live trees, so that each plot contained approximately 20 live trees. Species and dbh were recorded for all trees ≥ 4 cm dbh, both live and dead-standing. All saplings (< 4 cm dbh and > 1.4 m tall) were counted by species. We recorded the species and dbh of all logs ≥ 15 cm dbh that intercepted the transect tape that bisected each plot. Marvine Lakes (W4) was sampled with five randomly located, 5 by 10 m plots.

Increment core samples for tree aging were extracted at a height of ca. 30 cm above the ground from all live trees ≥ 4 cm dbh in all plots for each stand. Trees were cored parallel to the contour. For basal ring counts approximately 10 short seedlings (ca. 10 cm tall), tall seedlings (ca. 80 cm tall), and saplings of each species

were cut at the base. In addition, two cores were extracted at a height of 1.1 m from ca. 10 of the largest, and presumably oldest, live trees of each species and from ca. 10 of the largest dead-standing spruce in each stand. Ring-width chronologies from combined live and dead trees extended the time periods for which past change in radial growth patterns could be examined. Owing to their scarcity, no dead trees were cored in stands G1 or W4.

Dendrochronological analyses

All cores were mounted and sanded following the procedures of Stokes and Smiley (1968), and annual rings were counted with the aid of a stereomicroscope. Because of rotten centers, a few trees in each stand could not be aged. The percentages of trees in each stand successfully aged are given in Table 3. Owing to the variable periods required for trees to reach coring height, tree ages are given as age at coring height. Years were recorded in which growth releases were initiated. A growth release was defined as a 250% increase in mean ring width when means for consecutive groups of 5 years were compared. Trees that experienced initially rapid growth, presumably 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 1987 that showed a release in a given year. Cross-dating of 60 randomly selected cores indicated that most did not have false or missing rings over the past 100 years and only rarely did dating errors exceed 1 or 2 years. Thus, data on releases are given in single year age classes, despite the probability that some of the dates are not precise (Lorimer 1985).

Cores used for ring-width chronologies were visually cross-dated using the techniques of Stokes and Smiley (1968). Ring widths were measured to the nearest 0.01 mm with a Henson computer-compatible incremental measuring machine. The computer program COFECHA (Holmes 1983) was used to detect measurement and cross-dating errors, and cores containing such errors were corrected or removed from the data set. COFECHA tests for errors by computing correlation coefficients between individual series and the master chronology for each species in a stand. The master dating series was derived by fitting the visually cross-dated ring-width series to a 20-year cubic spline function and removing low-frequency variance by dividing the series values by the corresponding spline curve values. Series values were then log-transformed and the mean values were computed. Mean ring-width chronologies were developed for live trees of each species in each stand and were based on 15–20 cores. For spruce, these chronologies were extended by incorporating the cores from dead trees. COFECHA was used to cross-date the cores from the dead trees against the master chronologies developed from the live trees in each stand. The cross-dating by COFECHA was checked by visually cross-dating each sample. Cross-dating of the samples from the dead trees allowed determination of their approximate dates of death. For dead-standing trees lacking bark, loss of the outermost rings as a result of weathering may prevent precise dating of tree death. However, 47% of the cores from dead trees still had bark remnants attached, and the presence of beetle engravings on the other trees indicates that only a few millimetres of the outer wood may have disappeared because of weathering.

Ring-width chronologies were standardized with the programs INDEX and SUMAC to reduce ring-width variances among and within cores (Fritts 1976; Graybill 1979). Standardization involves fitting the observed ring-width series to a curve or straight line and computing an index of the observed ring widths divided by the expected value. This reduces variances among cores and transforms ring widths into dimensionless index values. Thus, standardization permits computation of average tree-ring chronologies without the average being dominated solely by the faster growing trees with large ring widths. In dendroclimatic studies, an important objective of standardization is the removal of trends in ring-width series which may be attributed to the age of the tree (Fritts 1976). In our

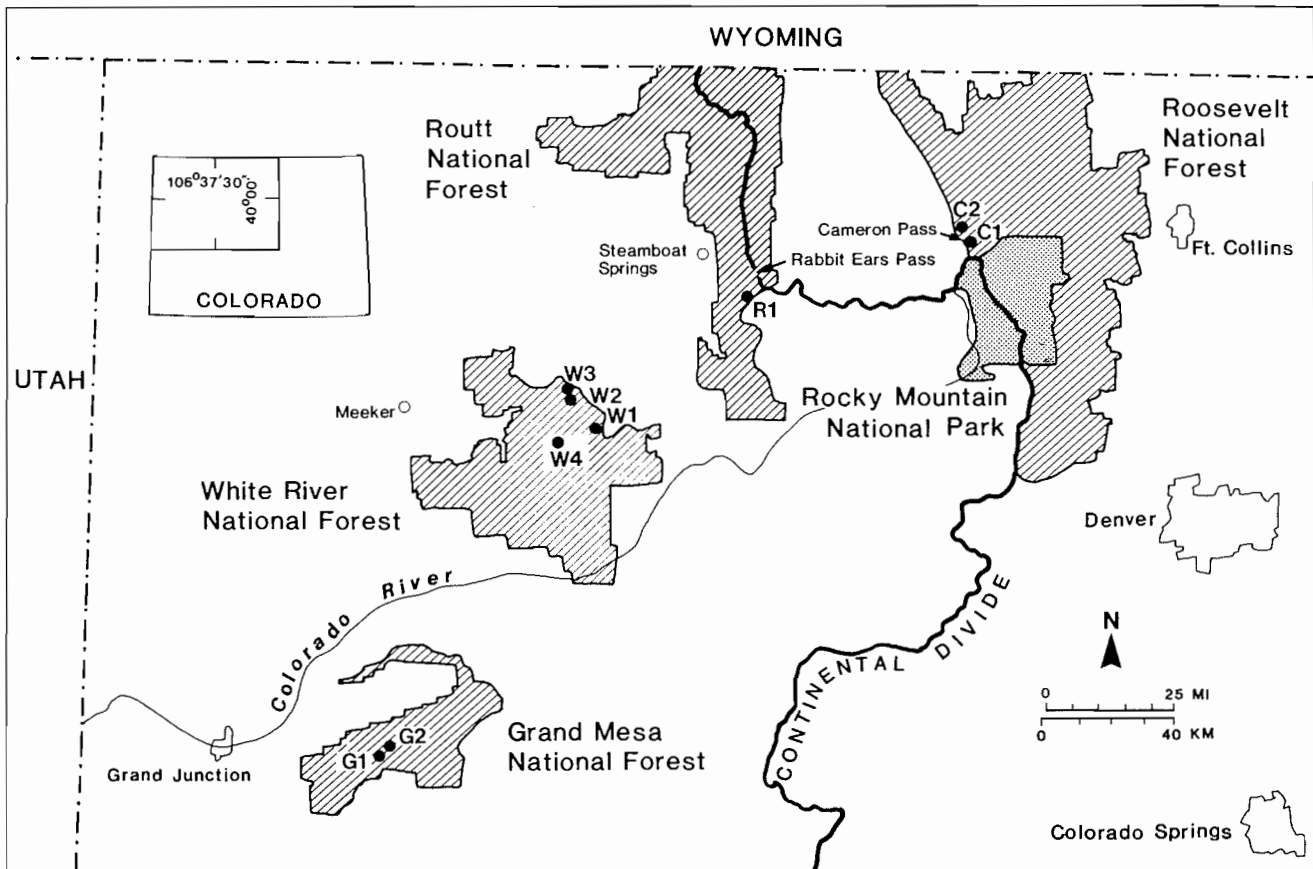


FIG. 1. Map of northwestern Colorado showing the locations of stands sampled. C1, Cameron Pass; C2, Blue Lake; R1, Walton Creek; W1, Trappers Lake; W2, Lily Pond; W3, Ripple Creek Pass; W4, Marvine Lakes; G1, Cottonwood Lake; and G2, Big Creek Reservoir.

study, however, such removal of the age-related growth trend was not an objective. We evaluated all the common alternatives used in standardization: horizontal or inclined straight lines, cubic spline functions, and exponential or polynomial curves (Fritts 1976; Cook and Peters 1981).

Results

Comparisons of different methods of constructing chronologies *Individual tree ring-width chronologies*

For conciseness, ring-width chronologies from only two stands are used to compare the usefulness of individual tree versus mean stand chronologies, standardization options, and total chronologies (live and dead trees) versus chronologies based only on live trees. Since radial growth patterns of spruce and fir following beetle outbreak were similar (Veblén *et al.* 1990), only those of spruce, the longer-lived species, are presented.

Chronologies for an individual tree are ring widths plotted against time and indicate actual radial growth for that tree. Examination of individual ring-width chronologies allows consideration of variation among trees in the timing and degree of growth responses to beetle-caused mortality of canopy trees. Examples of individual tree ring-width chronologies from stands W1 and G2 illustrate tree responses to the 1850s and 1940s outbreak (Fig. 2). The 1940s outbreak had a severe impact on stand W1, as indicated by the high dead-standing basal area of spruce (Table 2). The 2.1 m²/ha of dead-standing basal area of spruce in stand

G2 implies that it was only moderately affected by the 1940s outbreak. In stand W1, spruce that survived the 1940s outbreak typically show dramatic and sustained increases in radial increment (Fig. 2). In contrast, in stand G2 the response to the 1940s outbreak, while evident in some trees, is much less dramatic. This reflects the lower mortality of canopy trees in G2, and to a lesser extent, the larger sizes of the trees sampled. At the time of the 1940s outbreak, the trees from stand W1 were mainly small-diameter subcanopy trees which benefited more from the death of canopy trees than the larger trees illustrated for stand G2. In stand G2, however, the 1850s outbreak is very conspicuous in the selected individual trees, which would have been small subcanopy trees at that time (Fig. 2). There is no evidence of a nineteenth century outbreak in stand W1.

Among the surviving trees at both sites there is substantial variation in the timing and magnitude of growth increases. In most cases there is a severalfold increase in ring width and in some cases ring width increases 15–20 times. For most trees, the releases have been sustained for at least 40 years following the 1940s outbreak and for >100 years following the 1850s outbreak. Both the magnitude and the duration of these growth increases suggest release from competition rather than from climate fluctuation.

Initiation of releases by individual trees in the same stand may vary by several years following an outbreak (Fig. 2). This variation in the timing of releases may be the result of variation in the time of canopy tree death. In a severe

TABLE 3. Age and size characteristics of the stands sampled

Stand and species	No. of trees	Age (years)		dbh (cm)		% trees aged
		Range	Mean \pm SD	Range	Mean \pm SD	
Cameron Pass (C1)						
<i>Pinus contorta</i>	27	111-191	156 \pm 20	14-50	31 \pm 11	96
<i>Abies lasiocarpa</i>	136	63-193	130 \pm 27	4-32	11 \pm 7	97
<i>Picea engelmannii</i>	84	43-223	155 \pm 40	4-52	17 \pm 12	88
Blue Lake (C2)						
<i>Abies lasiocarpa</i>	117	43-315	110 \pm 51	4-30	9 \pm 5	88
<i>Picea engelmannii</i>	131	37-306	132 \pm 75	4-45	12 \pm 9	87
Trappers Lake (W1)						
<i>Pinus contorta</i>	11	216-261	238 \pm 16	16-43	28 \pm 9	85
<i>Abies lasiocarpa</i>	215	23-251	99 \pm 52	4-36	10 \pm 7	89
<i>Picea engelmannii</i>	87	16-220	57 \pm 32	4-21	8 \pm 3	95
Lily Pond (W2)						
<i>Abies lasiocarpa</i>	197	22-192	88 \pm 37	4-41	11 \pm 8	84
<i>Picea engelmannii</i>	93	25-234	74 \pm 49	4-49	14 \pm 10	97
Ripple Creek Pass (W3)						
<i>Abies lasiocarpa</i>	274	29-222	91 \pm 32	4-38	10 \pm 7	83
<i>Picea engelmannii</i>	94	22-204	81 \pm 35	4-28	10 \pm 5	90
Marvine Lakes (W4)						
<i>Abies lasiocarpa</i>	25	55-95	78 \pm 11	4-28	16 \pm 8	83
<i>Picea engelmannii</i>	39	47-94	79 \pm 10	5-31	15 \pm 8	98
Walton Creek (R1)						
<i>Abies lasiocarpa</i>	161	35-309	116 \pm 41	4-47	14 \pm 10	80
<i>Picea engelmannii</i>	67	37-241	105 \pm 46	4-46	13 \pm 9	89
Cottonwood Lake (G1)						
<i>Abies lasiocarpa</i>	144	68-211	113 \pm 22	4-38	12 \pm 7	71
<i>Picea engelmannii</i>	108	55-261	128 \pm 35	5-49	21 \pm 10	77
Big Creek Reservoir (G2)						
<i>Abies lasiocarpa</i>	115	33-257	110 \pm 44	4-55	12 \pm 10	73
<i>Picea engelmannii</i>	83	41-310	119 \pm 14	4-54	20 \pm 14	86

outbreak, spruce beetles first attack and kill large diameter trees and gradually attack smaller diameter trees as the outbreak persists (Schmid and Frye 1977). Growth releases of small trees growing adjacent to dead-standing trees, but not near a fallen tree, indicate that death of a canopy tree, even if it remains standing, is sufficient to release subcanopy trees.

Standardization options

Two common standardization procedures used in dendroclimatic studies for revealing high frequency variation in ring-width series are cubic spline and polynomial functions (Fritts 1976; Cook and Peters 1981). The Tucson tree-ring programs (Graybill 1979) automatically accept a given order polynomial when the next two higher orders do not reduce the residual variance by 5% or more. The default for the cubic spline is based on a 50% frequency-response cutoff of 67% of the series length (moderately stiff fit).

The mean ring-width chronologies based on standardizations with polynomial and cubic spline functions are nearly identical in stands W1 and G2 (Fig. 3). The chronologies based on these functions exhibit an increase in index values for the 1850s (G2) and 1940s (W1) outbreaks. However, the increases are neither dramatic, unique, nor sustained.

Standardization with a horizontal straight line passing through the mean ring width value yields substantially different patterns. In stand W1, the dramatic and sustained release following the 1940s outbreak, which was evident in most of the individual tree chronologies, is also reflected by index values dramatically different from those of the preceding 100 years (Fig. 3). Similarly, in stand G2 the 1850s

outbreak is clearly distinguished and the 1940s outbreak is more evident than it was with either the polynomial or cubic spline standardizations.

The horizontal straight line standardization also reveals important differences in tree growth patterns during the early histories of each stand, which are not evident with the other standardizations. In stand W1, initial growth rates were high (Fig. 3), as expected for trees colonizing an open site following a large-scale disturbance such as fire. The presence of a remnant population of lodgepole pine (Table 3), fire scars, and abundant charcoal also indicates that stand W1 is a first-generation post-fire stand. In contrast, the uniformly low index values for spruce in stand G2 prior to the 1850s outbreak indicate that the oldest trees did not initially grow rapidly. Thus, stand G2 is not a first-generation post-fire stand.

Extension of chronologies by including dead trees

To assure that a chronology is representative of stand history rather than the idiosyncratic growth patterns of a few trees, it is desirable to include as many cores in the sample as possible. The numbers of cores included in chronologies generally decrease towards earlier dates, and no index values were plotted where the sample size was less than five. Since beetles kill the largest and oldest trees, samples from live trees were often insufficient for the early periods of stand histories. To extend chronologies to earlier dates, cross-dated series from dead spruce were combined with those of live spruce trees.

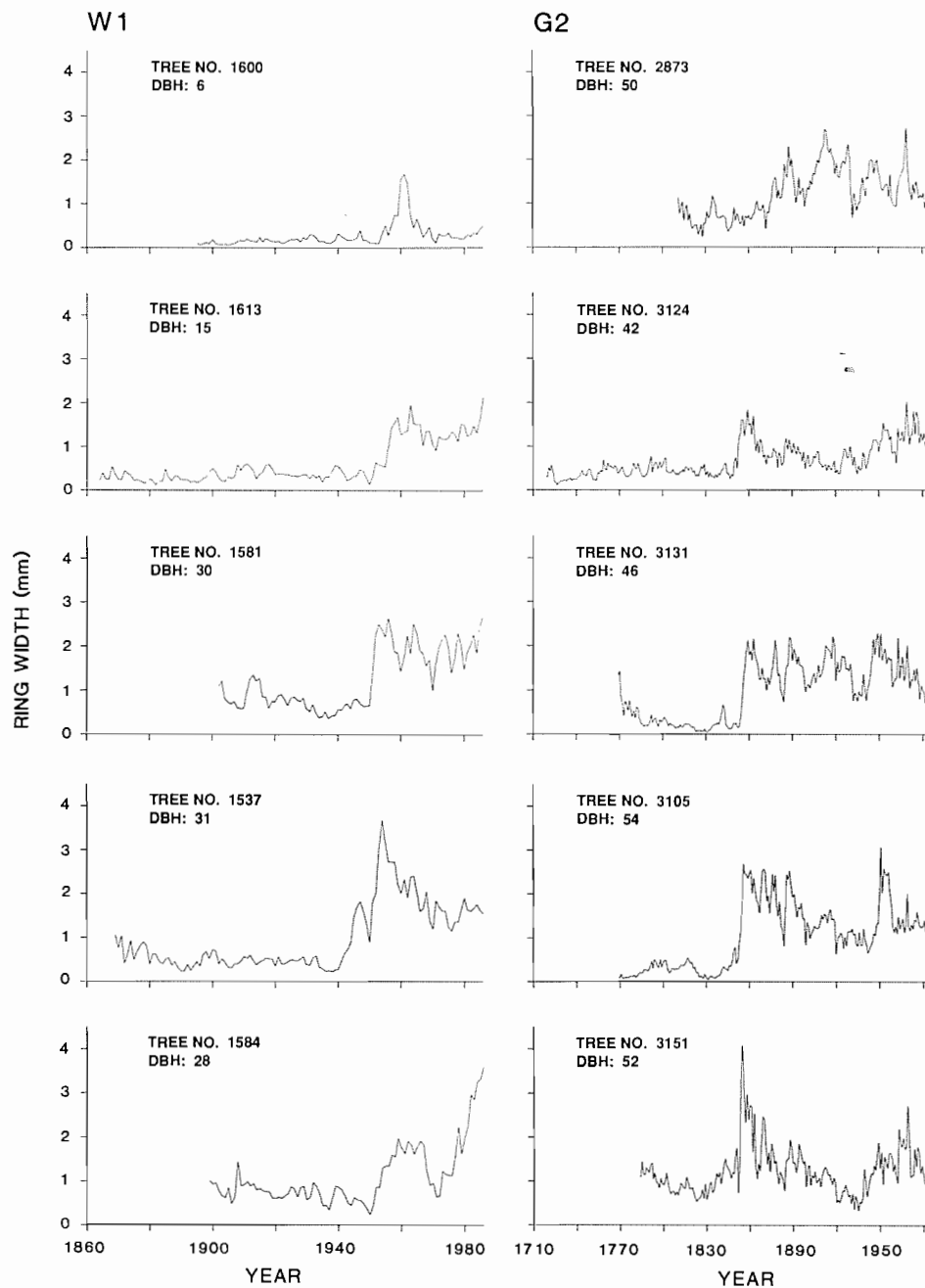


FIG. 2. Selected ring-width series for individual spruce trees in stands W1 (Trappers Lake) and G2 (Big Creek Reservoir). Note the different scales of the x-axes for each stand. The dbh is given in centimetres.

For the seven stands where dead-standing trees were abundant enough to permit this procedure, starting dates of chronologies were extended backwards by an average of 94 years (range, 17–186 years). Inclusion of dead trees is particularly useful where a recent spruce beetle outbreak has killed most of the larger and older trees. By substantially increasing the sample size during the early history of most stands, this procedure strengthened the interpretability of the ring-width chronologies and revealed patterns that were not obvious when the chronologies from live trees were considered. For example, in stand W1, the live tree chronology did not begin early enough to clarify the post-fire origin of this stand (Fig. 3).

Stand histories

Stand chronologies

For the reasons given above, ring-width chronologies from combined dead and live spruce using a horizontal straight line standardization were constructed for each stand. Dead-standing spruce were scarce in stand G1, and consequently, only live trees were included in the chronology for this stand. Dramatic and sustained increases in index values clearly indicate severe disturbance in the 1940s for stands W2, W1, and W3 (Figs. 3 and 4). Sharp declines in sample sizes in these chronologies indicate that most of the dead trees sampled probably died during the 1940s outbreak. In stands G2 and R1, the 1940s outbreak is not clearly reflected by

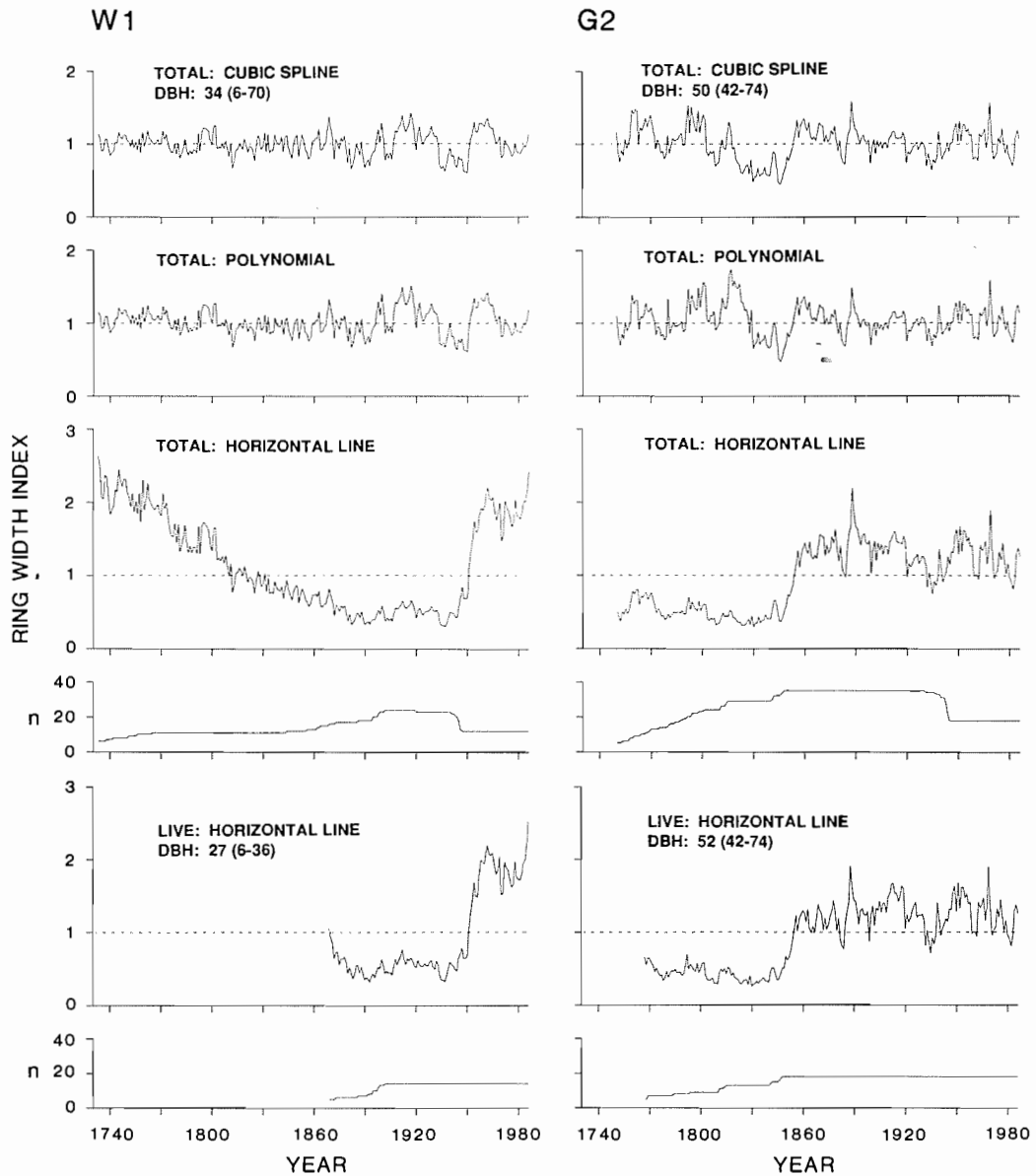


FIG. 3. Mean spruce ring-width chronologies illustrating different standardization procedures and total chronologies (i.e., live combined with dead trees) versus live only chronologies. Median and ranges of dbh (cm) are given. Graphs of core sample sizes (n) appear below chronologies. Abbreviations as in Fig. 1.

increased index values, but the abrupt decline in sample sizes in the 1940s confirms that these stands were also affected by this outbreak (Figs. 3 and 4). In contrast, stand G1 and control stands C1 and C2 show no sustained increases in index values suggestive of recent large-scale canopy disturbance. Nor are there sharp declines in sample sizes for the chronologies in stands C1 and C2, as expected if extensive mortality had occurred in the 1940s (dead trees were not included in the chronology for stand G1). The 1850s outbreak is clearly indicated by the chronologies for stands G1, G2, and R1 (Figs. 3 and 4).

For stands W1, C1, and W2, the chronologies indicate rapid initial growth, implying that they are first-generation post-fire stands (Figs. 3 and 4). The pattern of tree growth in a young first-generation post-fire stand (ca. 100 years old) is illustrated by stand W4 (Fig. 4). Highest growth rates are attained under open conditions during the initial ca. 50 years of stand development, and subsequently growth declines as

stand density increases and resources become less available. However, maximum ring-width indices in stand W4 are ca. 1.6, in contrast to values of 2.5–3.0 during the early histories of stands C1, W1, and W2. As stand W4 continues to develop, future ring widths are likely to continue to decline and the mean ring width will be reduced. This will result in substantially higher ring-width indices for the initial decades, so the chronology from this stand in the future will be more similar to those for the older first-generation post-fire stands. The abrupt and severe suppression in stand C1 from 1758 to 1770 is also evident in the other Front Range stand, stand C2, which suggests that it was probably climatically induced.

Release frequencies

In contrast to the mean stand chronologies, which are derived from 20 to 36 samples each, the frequencies of release are derived from the total sample of aged trees

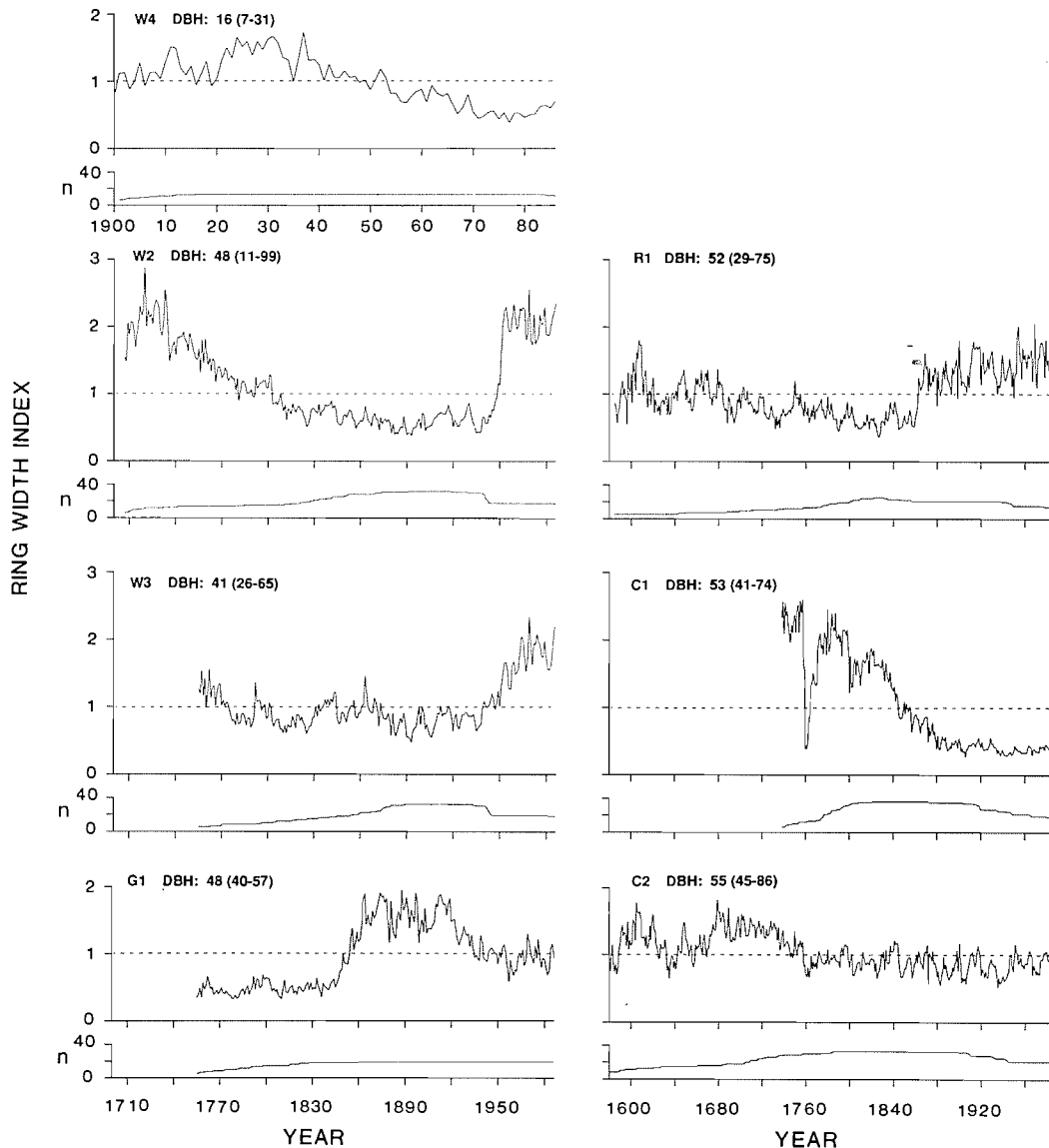


FIG. 4. Mean ring-width chronologies for live and dead spruce in each stand. Standardization was achieved by dividing observed ring widths by the mean ring-width value for each tree. Medians and ranges of dbh (cm) are given. Graphs of core sample sizes (n) appear below chronologies. Abbreviations as in Fig. 1.

(median of 248 per stand; range, 64–368). Frequencies of release are not plotted if the number of trees alive at that date were <20 .

Owing to their greater abundance, release frequencies of fir are more interpretable than those of spruce. Release frequency patterns in stands W1, W2, W3, and G2 clearly reflect the 1940s outbreak (Fig. 5). In stand R1, the 1940s outbreak is not clearly reflected by increased release frequency. In stand W3 a peak in release frequencies in 1940 is probably the direct response to the 1939 windstorm (see section on Spruce beetles in the southern Rocky Mountains) and is followed by another peak 8 years later because of the beetle outbreak. The 1850s outbreak is reflected by the patterns of release frequencies in stands G2, G1, and R1.

In control stands C1 and C2 there are periods of above average frequencies of release (e.g., 1885–1895 and 1949–1952). However, there are no sharp increases in frequencies comparable to the stands affected by the 1940s outbreak (Fig. 5). The abundance of releases in stand C1

between 1790 and 1830 is actually the fast initial growth of the colonizing trees in this post-fire stand. The scarcity of releases over the most recent 150 years of stand development in C1 reflects a low rate of tree falls for large canopy trees in this seral stand. The colonizing lodgepole pine and spruce are still relatively young and little mortality of canopy trees has occurred (Table 3).

Age structure

In stand W4, a young post-fire stand, age structures of spruce and fir are the typical bell-shaped distributions expected for stands that originate following a single large-scale disturbance which kills all former occupants of the site (Whipple and Dix 1979; Veblén 1986; Fig. 6). For both species, the frequency distributions are not significantly different from a normal distribution ($P < 0.05$; Kolmogorov-Smirnov goodness-of-fit procedure). Similarly, in the ca. 230-year-old post-fire stand C1, age frequency distributions of spruce and fir are not significantly different from

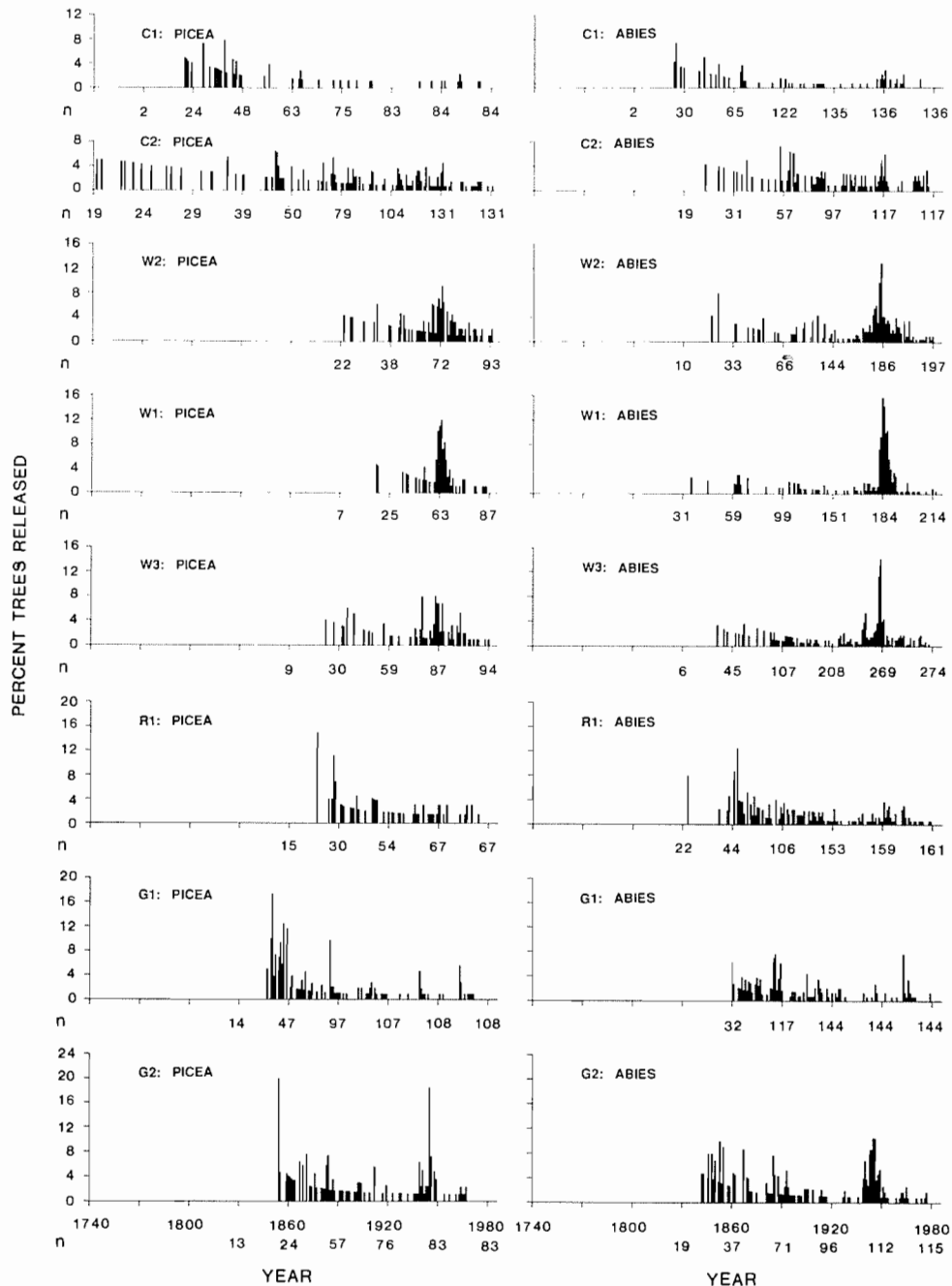


FIG. 5. Percentage of live trees released. A release is an increase in mean ring width $>250\%$ when adjacent groups of five rings are compared. The number of surviving trees alive at the beginning of indicated decades is given by n . Release frequencies are not shown for $n < 20$. Abbreviations as in Fig. 1.

a normal distribution ($P < 0.05$). The presence of a remnant lodgepole pine population further confirms that this older stand is a first-generation post-fire stand. Similarly, for stand W1 a remnant lodgepole pine population indicates that this is a post-fire stand (Fig. 6). Such remnant pine populations are a good indicator of fire origin because neither blowdown nor severe spruce beetle outbreak in mixed stands of lodgepole pine, fir, and spruce results in significant new establishment of pines (Veblen *et al.* 1989, 1990). In both stands C1 and W1 the frequency distributions of the remnant lodgepole pine populations do not differ significantly from normal distributions ($P < 0.05$).

Although establishment rates of spruce and fir might be expected to increase following severe disturbance by spruce beetle, based on the examination of stands affected by the 1940s outbreak we were unable to confirm any increases in establishment rates (Veblen *et al.* 1990). Nevertheless, our failure to detect any increases may have been due to the absence of data on seedling densities prior to the outbreak. Increases in establishment rates following past outbreaks might be reflected in age frequency distributions. In all stands severely affected by the 1940s outbreak (i.e., stands W1, W2, and W3) the number of spruce and fir in the <40 -year age class are greater than in stands unaffected or

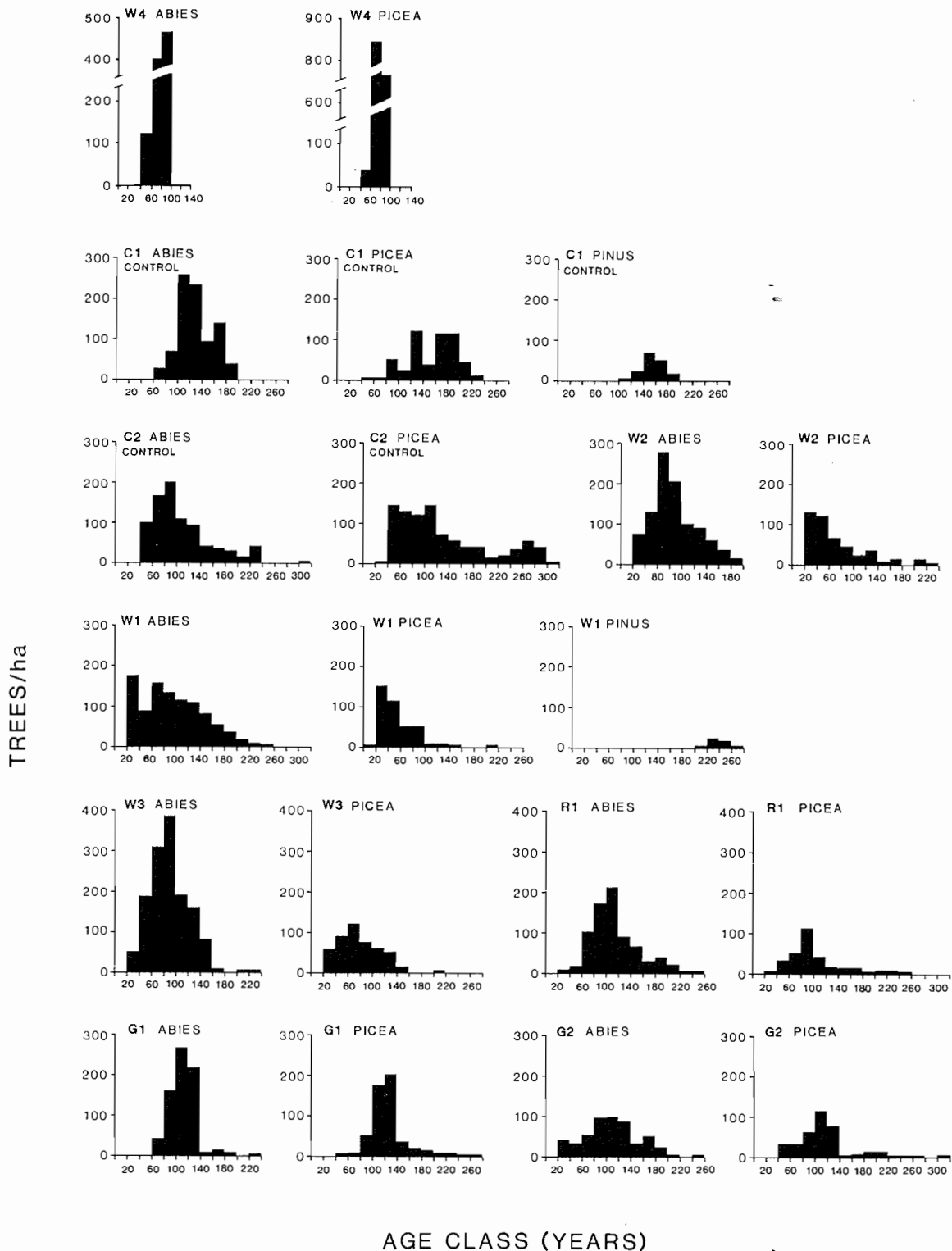


FIG. 6. Frequency distributions of trees in 20-year age classes. The percentages of trees in each sample which were successfully aged are given in Table 3. Abbreviations as in Fig. 1.

slightly affected by the outbreak (Fig. 6). However, since ages are given as "age at coring height," many of these trees may have been seedlings in the 1940s that were released by the canopy disturbance. In stands G1 and G2 the age frequencies also imply substantial increases in rates of seedling establishment following the 1850s outbreak. Again, the

lack of data on total tree ages (versus age at coring height) is a possible confounding factor. For example, in the eight stands sampled for seedling and sapling ages, median ages of 10-cm tall seedlings ranged from 8 to 25 years and of 80-cm tall seedlings from 28 to 113 years. Although 20–35 years may be a reasonable estimate of the average time

required to grow to coring height, considerable caution is required in interpreting the age frequency data. Furthermore, since the age frequencies are only for trees ≥ 4 cm dbh and some of the smaller trees may be over 100 years old, the age structures are incomplete.

Discussion and conclusions

Widespread mortality of Engelmann spruce observed in western Colorado ca. 1900 has been attributed to one or more severe spruce beetle outbreaks during the nineteenth century (Schmid and Hinds 1974). However, documentation of the effects of spruce beetle during the nineteenth century is based largely on historical photographs and qualitative reports of forest mortality from which precise dates of outbreaks cannot be determined (Sudworth 1900; Hopkins 1909; Baker and Veblen 1990). The methods developed in the present paper reveal that ca. 1850 extensive areas of subalpine forest in western Colorado were severely affected by a widespread spruce beetle outbreak.

For detection of past spruce beetle outbreaks a combination of methods is desirable. Analyses of tree population age structures, frequencies of release, and stand chronologies are all useful in detecting past outbreaks and in distinguishing their effects from stand-replacing fires. Construction of stand chronologies based on ring-width measurements is the most time-consuming method but is also the most effective method of detecting past outbreaks. Inspection of individual tree ring-width chronologies is a simple and effective method of detecting releases from past disturbances. For the construction of a mean (or stand) ring-width chronology, adequate sample size is essential. In this study, patterns were usually evident with as few as 5 samples, but it is desirable to have at least 15–20 samples to assure adequate replication.

For the type of low frequency variation in radial growth associated with a beetle outbreak, the recommended standardization procedure is a horizontal line passing through the mean ring width. Other standardization procedures, such as fitting the observed data to a polynomial curve or a cubic spline function, failed to reveal the dramatic and sustained releases following a spruce beetle outbreak. These other standardization procedures, however, have been used successfully to detect past episodes of insect defoliation where the period of reduced ring width typically lasts fewer than 12 years (Brubaker and Green 1979; Swetnam and Lynch 1989). Standardization with stiffer splines might have distinguished the more sustained growth pattern of spruce beetle outbreaks. The horizontal straight line fit does not detrend the series and remove the "biological growth trend," which is a main purpose of standardization in dendroclimatic studies (Fritts 1976). Rather, the horizontal fit facilitates the detection of deviations from the average growth rate and is particularly useful in identifying long periods of release, such as those following a major canopy disturbance.

We found that in some stands the incorporation of cores taken from dead standing trees substantially improved the interpretability of a stand chronology. Determination of dates of tree death was also helpful in ascertaining if there had been a past period of massive tree death as expected for a spruce beetle outbreak. This is a particularly useful procedure for distinguishing an epidemic of spruce beetle, in which dates of tree death will be tightly clustered, from the effects of an endemic beetle population, which over many decades can cause substantial tree mortality.

Although stand chronologies provide information of the most precise resolution for detecting past beetle outbreaks, determination of the percentage of trees alive that were released (i.e., a 250% increase in mean ring width for at least 5 years) is also useful. This procedure has the advantage of large sample sizes (i.e., all the trees used in an age structure analysis) and requires little time additional to that required for counting the annual rings. In the case of the 1940s outbreak in stand G2, the ring-width chronology was ambiguous, but the data on release frequencies clearly indicated the outbreak. On the other hand, slight increases in the numbers of releases, such as in the 1890s and early 1950s in stand C2, are probably the result of increased windthrow without subsequent beetle outbreaks. For example, 1949 and 1951 are years of high windthrow rates generally in the Colorado Front Range (Veblen *et al.* 1989, 1990).

Analysis of age frequency distributions alone is not recommended as a method of detecting past spruce beetle outbreaks. Although increased rates of spruce and fir seedling establishment following an outbreak may be reflected in the age frequency distribution, variations in the time required for a tree to reach coring height will result in some error in estimating total tree ages. A small sample of ages of seedlings and saplings combined with their densities is sufficient for determining the regeneration status of each species (e.g., Veblen 1986). However, for the purpose of dating possible beetle outbreaks this procedure lacks the required accuracy.

To distinguish past beetle outbreaks from the effects of past fire, both chronologies and age structures are useful. In stands initiated following a stand-devastating fire, growth rates of the initial colonists will be high. In stand chronologies using a horizontal straight line standardization, a first-generation post-fire stand has declining index values. In some habitats, a stand-devastating fire results in establishment of lodgepole pine either prior to, or contemporaneously with spruce and fir (Peet 1988). As the stand develops, establishment of lodgepole pine declines and eventually ceases. Thus, remnant populations of this species, usually with bell-shaped age distributions, are clear evidence of a past stand-replacing fire. In the stands we have examined, neither spruce beetle outbreak nor blowdown resulted in new seedling establishment of lodgepole pine (Veblen *et al.* 1989, 1990). Apparently, without the destruction of the advance regeneration of spruce and fir, or the exposure of bare mineral soil, the seral species does not establish. The rapid initial growth of spruce in a post-fire stand contrasts with the slow growth of the oldest trees in stands affected by beetle outbreaks. Spruce that survive a beetle attack are likely to have been small, suppressed trees at the time of the attack, and therefore, would have been growing slowly.

Although stand-devastating wildfires are the most common type of fire in the subalpine zone of the southern Rocky Mountains (Peet 1988; Baker and Veblen 1990), light surface fires may occur in some habitats. We have observed evidence of such fires (in the form of fire scars) primarily in open spruce and fir stands near the timberline. A light surface fire may release the surviving trees from competition, resulting in growth patterns similar to those for trees released by a beetle outbreak. However, both spruce and fir are easily killed by fire because of their thin bark (Alexander 1987), so that a past light surface fire should be reflected in the age structure of the stand. Furthermore, the effects of a light surface fire are unlikely to be confused with

those of a beetle outbreak because of the presence of fire scars on the surviving spruce. Thus, in attempting to detect past spruce beetle outbreaks, it is important to record and date any fire scars present.

Although both fires and spruce beetle outbreaks are known to have been major disturbance agents in southern Rocky Mountain forests, the relative importance of these two disturbance agents is unknown (Baker and Veblen 1990). Application of the methods described here to more extensive areas of forest can allow comparison of their relative importance. Long-term records of the frequency and severity of spruce beetle outbreaks are also essential for evaluating the possible effects of management practices such as logging and fire suppression on insect outbreaks. Given the widespread importance of disturbance by lethal insect outbreaks in temperate forests in general, detection of past beetle outbreaks is essential for understanding present patterns of forest structure and composition, and the methods described here may have wide applicability.

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