

Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range

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The montane forests (i.e., below ca. 2900 m) of the Colorado Front Range have experienced repeated outbreaks of western spruce budworm (*Choristoneura occidentalis* Free.) and Douglas-fir bark beetle (*Dendroctonus pseudotsugae* Hopk.), both of which locally attack Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). In this study we examine the effects of historically documented outbreaks of these insects on succession, stand structure, and radial growth of host and nonhost species in Rocky Mountain National Park. The most recent budworm (1974–1985) and bark beetle (1984–present) outbreaks resulted in the most severe and widespread disturbance of these forests since the late 1800s. Stand response to these outbreaks is primarily a function of stand structure and age characteristics of Douglas-fir prior to an outbreak. Young, vigorous postfire stands show minimal budworm defoliation, and in these stands only remnant trees from the prefire generation appear susceptible to beetle-caused mortality. Dense stands exhibit higher budworm-induced mortality, which hastens the natural thinning process and shifts dominance towards the nonhost species. The stands most severely disturbed by the combined insect agents are multistoried stands with high host densities and a wide range of stem sizes. The stand response to these disturbances include the growth release of shade-intolerant, seral species, and in some cases, a higher survivorship among mid-sized individuals of the host Douglas-fir. The net result of the combined insect outbreaks is the temporary slowing of the successional trend towards a steady-state Douglas-fir forest. Fire suppression, by increasing the density of suppressed Douglas-fir, has previously been shown to favor increased outbreak severity of western spruce budworm in the northern Rockies. However, in the Front Range, recent increases in outbreak severity and their synchronicity may also be the result of large areas of forest, burned during the late 19th century during European settlement, simultaneously entering structural stages susceptible to insect outbreak.

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Les forêts subalpines (c.-à.-d. au-dessous de ca. 2900 m) de la chaîne frontale du Colorado sont soumises à des épidémies répétées de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Free.) et du dendroctone du Douglas (*Dendroctonus pseudotsugae* Hopk.) qui attaquent localement le sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco). Cette étude porte sur les effets des épidémies documentées de ces insectes sur la succession forestière, la structure des peuplements et la croissance radiale d'espèces hôtes et nonhotes situées dans le parc national des montagnes rocheuses. Les plus récentes épidémies de tordeuses (1974–1985) et de rongeurs de l'écorce (1984 à aujourd'hui) ont causé les plus fortes perturbations en incidence et en sévérité dans ces forêts depuis la fin des années 1800. La réponse des peuplements à ces épidémies est principalement fonction de leur structure et des caractéristiques d'âge du sapin de Douglas avant le début de l'épidémie. Les peuplements jeunes et vigoureux établis après feu ont été très peu défoliés par la tordeuse et seuls les arbres présents avant feu semblent être vulnérables aux rongeurs de l'écorce. Les peuplements denses ont subi les plus forts niveaux de mortalité induite par la tordeuse. L'éclaircie naturelle induite par l'insecte dans ce type de peuplement a favorisé une dominance en espèces non hôtes. Les peuplements les plus sévèrement touchés par les effets combinés des deux insectes sont ceux à strates multiples, ayant de fortes densités et possédant une large gamme de dimensions de tige. La réaction à ces perturbations comprend le dégagement des espèces intolérantes sériales et, dans certains cas, une plus grande survie des sapins de Douglas de taille intermédiaire. Le résultat final des épidémies combinées des deux espèces d'insecte étudiées consiste en un ralentissement temporaire de la succession forestière vers une forêt stable de sapins de Douglas. En augmentant la densité des sapins de Douglas supprimés, la lutte contre les incendies de forêt est reconnue pour favoriser la sévérité des épidémies de tordeuses dans la partie nordique des montagnes rocheuses. Toutefois, dans la chaîne frontale, les augmentations récentes de sévérité et leur synchronisme pourraient être le résultat de la présence de vastes superficies de forêts, brûlées vers la fin du 19^e siècle par les colons européens, atteignant de façon simultanée des stades de structure susceptibles aux épidémies d'insectes.

[Traduit par la rédaction]

Introduction

Defoliating insects of the genus *Choristoneura* are the most destructive forest pests in North America (Fellin *et al.* 1983). Cambial-feeding bark beetles (*Dendroctonus* spp.) hold a similar distinction as the most destructive insects found in western coniferous forests (Furniss and Carolin 1980). During the past 50 years, singular, overlapping, and repeated outbreaks of western spruce budworm (*Choristoneura occiden-*

talis Free.) and Douglas-fir bark beetle (*Dendroctonus pseudotsugae* Hopk.) have greatly altered the structure and composition of montane forests (i.e., below ca. 2900 m) of the Colorado Front Range. Both insects preferentially attack Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), one of the dominant tree species in these forests.

Although forest disturbances often involve multiple and interacting agents such as fire, blowdown, pathogens, and parasites (Knight 1987), empirical studies focusing on the interactions of two or more disturbance agents and their

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effects on succession are rare (Franklin *et al.* 1987). Nonetheless, empirical investigations of the interdependence and synergism of disturbances are important to describing disturbance regimes and understanding relationships between pattern and process. In this study, we use stand structural and dendroecological data and documentation of recent insect outbreaks to examine the effects of independent and overlapping western spruce budworm and Douglas-fir bark beetle outbreaks on forest structure and succession in the montane forests of Rocky Mountain National Park.

Spruce budworm, bark beetles, and fire as disturbance agents

Spruce budworm alters stand structure by increasing mortality among defoliated understory trees, by predisposing larger trees to bark beetle attack, and by diminishing seed sources for the host species. Spruce budworm feeds on both cones and seeds of Douglas-fir (Dewey 1970) and may consume up to 100% of the local seed production during an outbreak (Fellin *et al.* 1983). Budworm defoliation can also cause fine-root mortality (Swaine and Craighead 1924; Redmond 1959) and predispose host trees to subsequent pathogen (Stillwell 1956) and bark beetle attack.

In general, budworm outbreaks are most severe in dense stands as smaller, suppressed trees are more susceptible to defoliation damage and suffer higher mortality rates (Blais 1958; Fellin *et al.* 1983). Also, understory trees are likely to be infested by large populations of budworm larva that have been intercepted as they disperse from overstory trees (Carlson *et al.* 1983; Fellin *et al.* 1983).

Bark beetle outbreaks generally follow the weakening of host trees by drought, fire, pollution, logging, lightning strikes, or prior insect defoliation (Furniss 1965; Cates and Alexander 1982; Christiansen *et al.* 1987). In contrast with spruce budworm, Douglas-fir bark beetles generally prefer larger diameter trees that possess thicker phloem, cambium, and outer sapwood in which adult beetles can construct egg galleries. Age may be a secondary factor determining the resistance of individual trees to bark beetle attack, as tree resistance initially increases with age in certain tree species but declines thereafter (Cates and Alexander 1982; Christiansen *et al.* 1987). Stands of evenly dispersed trees suffer more severe attacks because of decreased beetle mortality during host-search flights (Berryman 1982). Thus, outbreak severity would presumably be greatest in old, even-aged stands of evenly dispersed, weakened, large-diameter trees.

Fire may interact with insect disturbance in a synergistic fashion to alter forest succession (Geiszler *et al.* 1980; Gara *et al.* 1985). For example, several studies suggest that fire suppression in the Rocky Mountains since ca. 1900 may have led to increasingly severe and synchronous recurrences of spruce budworm by promoting dense, multistoried stands (Carlson *et al.* 1983; McCune 1983; Anderson *et al.* 1987; Swetnam and Lynch 1989). Prior to fire suppression, small trees, seedlings, and saplings were eliminated by frequent, low-intensity fires, thus decreasing the abundance of available hosts.

Swetnam and Lynch (1989), working in Colorado and New Mexico, used tree-ring chronologies to reconstruct the timing, duration, and radial growth impacts of budworm outbreaks from 1700 to 1983. Their results show that at a regional scale, a long period of reduced budworm activity during the early decades of this century was followed by increased outbreak synchronicity. They hypothesize that such increased synchronicity

is the result of changes in forest structure following anthropogenic disturbance and fire suppression since the late 1800s and early 1900s (Swetnam and Lynch 1989).

Few studies have attempted to define the direct influence of fire on insect outbreaks. However, in Idaho and Oregon, the incidence of bark beetle attacks increases with defoliation and cambium injury due to fire (Furniss 1965; Geiszler *et al.* 1980; Gara *et al.* 1985).

Succession and disturbance in the montane forests of the Colorado Front Range

The montane forests of the Colorado Front Range are part of a complex landscape-mosaic shaped by steep environmental gradients and natural and human disturbance (Peet 1978, 1981, 1988; Veblen and Lorenz 1991). The dominant trees in these forests include Douglas-fir, ponderosa pine (*Pinus ponderosa* Laws. var. *scopulorum* Engelm.), lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), and limber pine (*Pinus flexilis* James). Aspen (*Populus tremuloides* Michx.) and blue spruce (*Picea pungens* Engelm.) are common among mesic sites. Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and sparse subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) are present at higher elevations. Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) is present at lower and more xeric sites.

Succession in these forests has been described by Peet (1978, 1981, 1988), Parker and Parker (1983), and Veblen and Lorenz (1986, 1991). In general, successional patterns vary according to topographic position, edaphic conditions, and propagule availability following disturbance (Peet 1981). Post-disturbance succession primarily follows an "initial floristics" pattern (*sensu* Egler 1954), where late-successional species establish synchronously with early successional species (Veblen and Lorenz 1986). Stand structures consistent with facilitation (*sensu* Connell and Slatyer 1977) are less common and limited to environmentally stressed sites (Veblen and Lorenz 1986).

In this study we examine the responses of 11 stands to repeated budworm and bark beetle outbreaks during 1938–1986. Specifically, we sought answers to the following questions: What was the role of stand structure in determining outbreak severity and recurrence? What was the tree growth response to these disturbances? How has fire suppression altered stand structure and what is its relationship to the increasing severity and synchronicity of budworm outbreaks in these forests? Finally, did outbreaks retard successional replacement of shade-intolerant trees by permitting increased growth rates among established individuals or by permitting new establishment?

Study sites

Rocky Mountain National Park is located along the crest of the Front Range in northeastern Colorado (Fig. 1). Park Service records (Anonymous 1934–1986) document epidemics of western spruce budworm and Douglas-fir bark beetle outbreaks in or near the Park since the late 1930s. Western spruce budworm outbreaks occurred during 1938–1945, 1958–1965, and 1976–1985. Douglas-fir bark beetle outbreaks developed during 1950–1951 and again from 1984 to the present. Termination of the earlier budworm and bark beetle outbreaks was associated with several factors, including extremely low summer and winter temperatures, lower insect parasite populations, and foliage reduction due to defoliation.

Eleven stands, selected to represent a wide range of environmental conditions present in the middle to upper elevational range of the

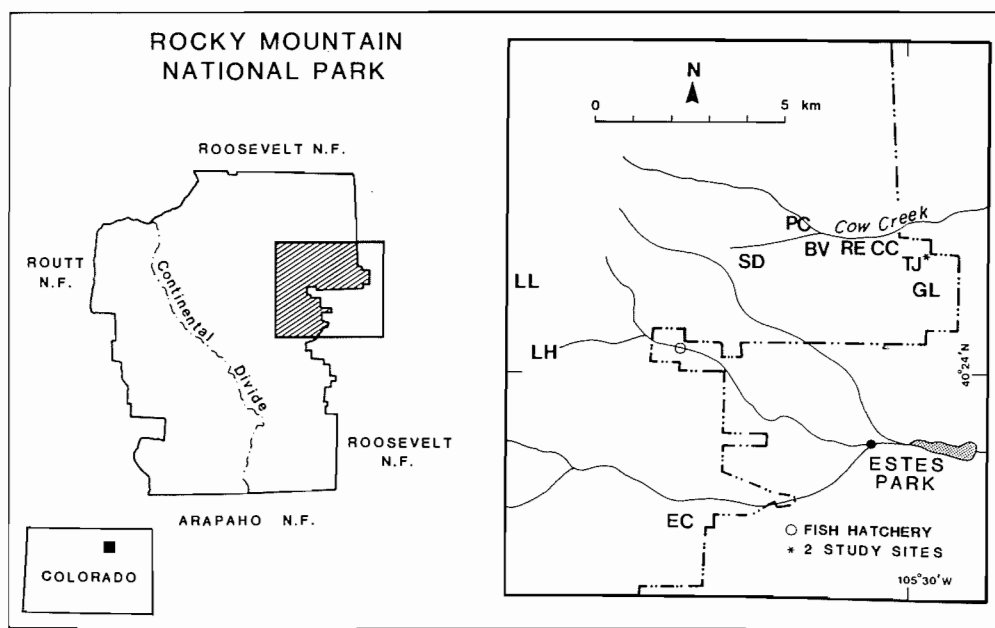


FIG. 1. Index map of Rocky Mountain National Park showing the locations of study sites. Abbreviations are as follows: BV, Bridal Veil Junction; CC, Cow Canyon Meadows; EC, Eagle Cliff Mountain; GL, Gem Lake Trail; LH, Little Horseshoe Park; LL, Lawn Lake Trail; PC, Peregrine Campground; RE, Rabbit Ears Campground; SD, Sundance Butte; TJ represents two adjacent stands: TJL, Trail Junction Lower and TJU, Trail Junction Upper.

montane forest within the Park, were studied during 1987 and 1988 (Fig. 1, Table 1). Each of the stands falls within the "*Pinus ponderosa*. *Pseudotsuga* forest series" as delineated by Peet (1981, p. 20). These forests are composed of a mixture of old (>250 years) stands with relatively open understories and young (<130 years) dense, even-aged, postfire stands with small trees. Evidence of recent anthropogenic disturbance was absent in all stands.

The mean annual precipitation for the combined records of the Fall River Fish Hatchery (2444 m) for 1910 to 1929, and Estes Park (2316 m) for 1930 to 1984, was 41.17 cm (National Park Service 1984). These stations are located 100–600 m lower than the sampled stands but within 10 km distance (Table 1; Fig. 1). The annual precipitation regime of the Front Range is characterized by pronounced May maximum and winter minimum (Barry 1973).

Methods

Field methods

Each stand was sampled using contiguous 10 × 20 to 10 × 50 m plots along transects running upslope. This sampling strategy assured that the plots represented a range of stand conditions that might be associated with changes in elevation or topography. Transect lengths (50–170 m) and plot size varied to ensure the sampling of a minimum number of live Douglas-fir trees (>45) at each site.

Data collected in each plot included counts of live and dead seedlings (<1.4 m tall) and saplings (>1.4 m tall but <4 cm diameter at breast height; DBH) and DBH measurements of all live and dead standing trees (>4 cm DBH). The presence of small branches on dead seedlings, saplings, and trees suggests that most of the dead Douglas-fir in the sampled stands died within the past several years.

Size structure analyses included a numerical comparison of live versus dead Douglas-fir seedlings and saplings in each stand as a measure of budworm-induced mortality during the 1976–1985 outbreak. This measure is based on the results of previous studies that suggest that budworm-induced mortality is greatest among suppressed seedlings, saplings, and small trees (Blais 1958; Carlson *et al.* 1983; Fellin *et al.* 1983). We also assume that the number of live versus dead large (>10 cm DBH) subcanopy and canopy Douglas-fir trees provides a measure of beetle-induced mortality and hence, distur-

bance severity (Cates and Alexander 1982). Based on these assumptions, survivorship would, hypothetically, vary according to the size structure of the respective stands and the severity of the respective outbreaks. For example, among populations having a wide range of stem sizes and mortality caused by both insects, survivorship would be the greatest in intermediate size classes (Fig. 2). Peak survivorship would predictably shift according to changes in disturbance severity by the respective insect agents and stand structure.

In addition to the collection of size data, all live trees >4 cm DBH were cored at ≈30 cm height to obtain tree ages at coring height. Age data for seedlings and saplings were not collected because of the destructive methods required to obtain these data. Relative estimates of defoliation by western spruce budworm were also noted for all live Douglas-fir present in the sample plots. Defoliation estimates were grouped using a scale of zero to three (zero indicating no defoliation and three indicating almost complete defoliation).

Dendroecological analyses

All cores were prepared following the procedures of Stokes and Smiley (1968) and were examined under stereomicroscopes. Dendroecological analyses included tree ring counts, calculations of ring-width suppression and release frequencies, and development of ring-width chronologies. Suppression and release frequencies and ring-width chronologies were used to determine the timing and relative growth response of trees following canopy changes due to defoliation or tree mortality.

Suppression and release frequencies

A growth suppression was defined as an abrupt reduction in mean ring width of >40% when sustained over a period of 5 years or more (Schweingruber 1986). A growth release was defined as an abrupt increase in mean ring width of >250% when compared with the mean ring width of the prior 5 years (Veblen *et al.* 1991).

Suppression and release data are summarized as percentages of live trees that were suppressed or released during earlier budworm and beetle outbreaks and were still alive at the time of sampling. These data are given in single-year classes to allow detection of short-term trends. Because defoliation often results in missing rings, exact dates of the onset of defoliation for each tree and years with missing

TABLE 1. Site and stand characteristics for 11 stands sampled in Rocky Mountain National Park

Stand*	Elevation (m)	Aspect	Slope angle (degrees)		Area sampled (ha)	Relative age	Canopy structure	Relative moisture
			Mean	Range				
BV	2591	NW	26	24–27	0.10	Very young	Single tiered	Intermediate
CC	2481	ENE	7	5–9	0.15	Mature	Two tiered	Mesic
EC	2500	N	24	15–27	0.34	Young	Two tiered	Intermediate
GL	2615	SE	2	2	0.32	Mature	Single tiered	Xeric
LH	2636	ESE	18	11–23	0.44	Mature	Two tiered	Intermediate
LL	2890	W	24	12–29	0.20	Mature	Two tiered	Intermediate
PC	2542	N	25	23–27	0.12	Young	Two tiered	Mesic
RE	2505	N	27	15–31	0.10	Very young	Two tiered	Mesic
SD	2798	WSW	20	17–24	0.28	Old	Single tiered	Xeric
TJL	2515	N	22	21–23	0.04	Young	Single tiered	Intermediate
TJU	2518	N	26	24–29	0.06	Old	Multitiered	Intermediate

*Abbreviations are defined in Fig. 1.

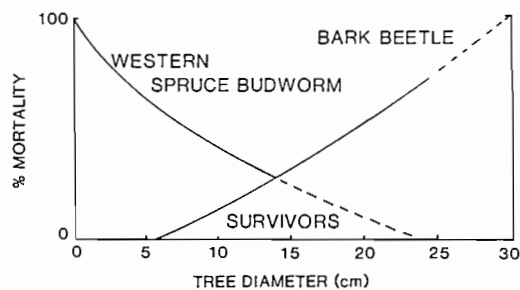


FIG. 2. Hypothetical survivorship curves for trees of varying size and attacked by either or both western spruce budworm and Douglas-fir bark beetle. The slope of the curves is a function of the host size frequency distribution and the severity of the respective budworm and bark beetle outbreaks.

rings are not known. Consequently, these data underestimate the severity of the budworm outbreaks. The extreme difficulty of cross-dating subcanopy, budworm-defoliated, Douglas-fir has been documented elsewhere (Swetnam 1987) and precluded the use of this technique here.

Ring-width chronologies

Mean ring-width chronologies were developed from ≈ 15 randomly selected cores for each of the common species in each stand. Ring widths were measured to the nearest 0.01 mm using a Henson measuring machine. The resulting series were standardized using horizontal lines and averaged using the INDEX and SUMAC computer programs (Fritts 1976; Graybill 1982). Standardization involves fitting a line to an observed ring-width series and computing a dimensionless index value. Index values are calculated by dividing observed ring widths by the fitted line. Following experimentation with several standardization options (e.g., polynomial, exponential, and cubic spline function), the horizontal-line standardization was selected because it scales the variances both within and among the cores but does not remove all low-frequency variations in the time series. This facilitates the detection of deviations from average growth rates, such as those associated with major canopy disturbances including defoliation or tree death (Veblen *et al.* 1991).

Earlier work by Swetnam *et al.* (1985) indicates that Douglas-fir and ponderosa pine respond similarly to climate. Accordingly, growth reduction due to drought, for example, would be apparent in both species over the same period. Consequently, growth deviation between Douglas-fir and other tree species during periods of host-specific and documented outbreaks can be reasonably attributed to

insect attack instead of interspecific differences in response to climatic variation.

Results

Size structure

Size frequency distributions for Douglas-fir were analyzed using 1-cm size classes (Fig. 3). Assuming that mortality among smaller suppressed trees and saplings is due to budworm defoliation, and that mortality among larger trees is due to bark beetle infestation, these data provide a relative measure of disturbance severity caused by the respective insects on the same host population. In high-density, mixed stands susceptible to natural thinning, higher mortality of the relatively shade tolerant Douglas-fir versus that of the seral pines suggests that in these cases, budworm defoliation is a primary cause of tree mortality rather than mortality due to natural thinning.

Stands EC and PC exhibit high mortality in both the smaller and larger size classes, suggesting both budworm and bark beetle mortality (Fig. 3). Stand LH also shows high host tree mortality, but over the entire range of size classes. Stands with lower host densities (CC, GL, RE, SD) have fewer dead trees that are distributed over a range of size classes. Mortality in stand TJL is concentrated in the smaller size classes, whereas stand TJU shows high mortality among both saplings and larger trees. BV, the youngest stand sampled, and LL, the highest stand sampled, have the fewest dead trees.

Mortality among nonhost species, analyzed in 10-cm size classes, is associated with the natural thinning of dense populations of small, seral lodgepole pine and aspen, and the death of canopy dominant pines due to mountain pine beetle (*Dendroctonus ponderosae* Hopk.; Hadley 1990). The low mortality among suppressed trees of nonhost, seral pines in stand TJL (Table 2) suggests that the death of small Douglas-fir, which is more shade tolerant, is the result of budworm defoliation rather than self-thinning.

Age structure

Age distributions reveal a range of postfire age structures (Figs. 4–6). Six of the stands (BV, EC, PC, LH, TJL, LL) have narrow age distributions. These stands represent successively older, even-aged stands initiated during the middle to late 1800s. Colonization at these sites followed an "initial floristics" (*sensu* Egler 1954) pattern where the climax

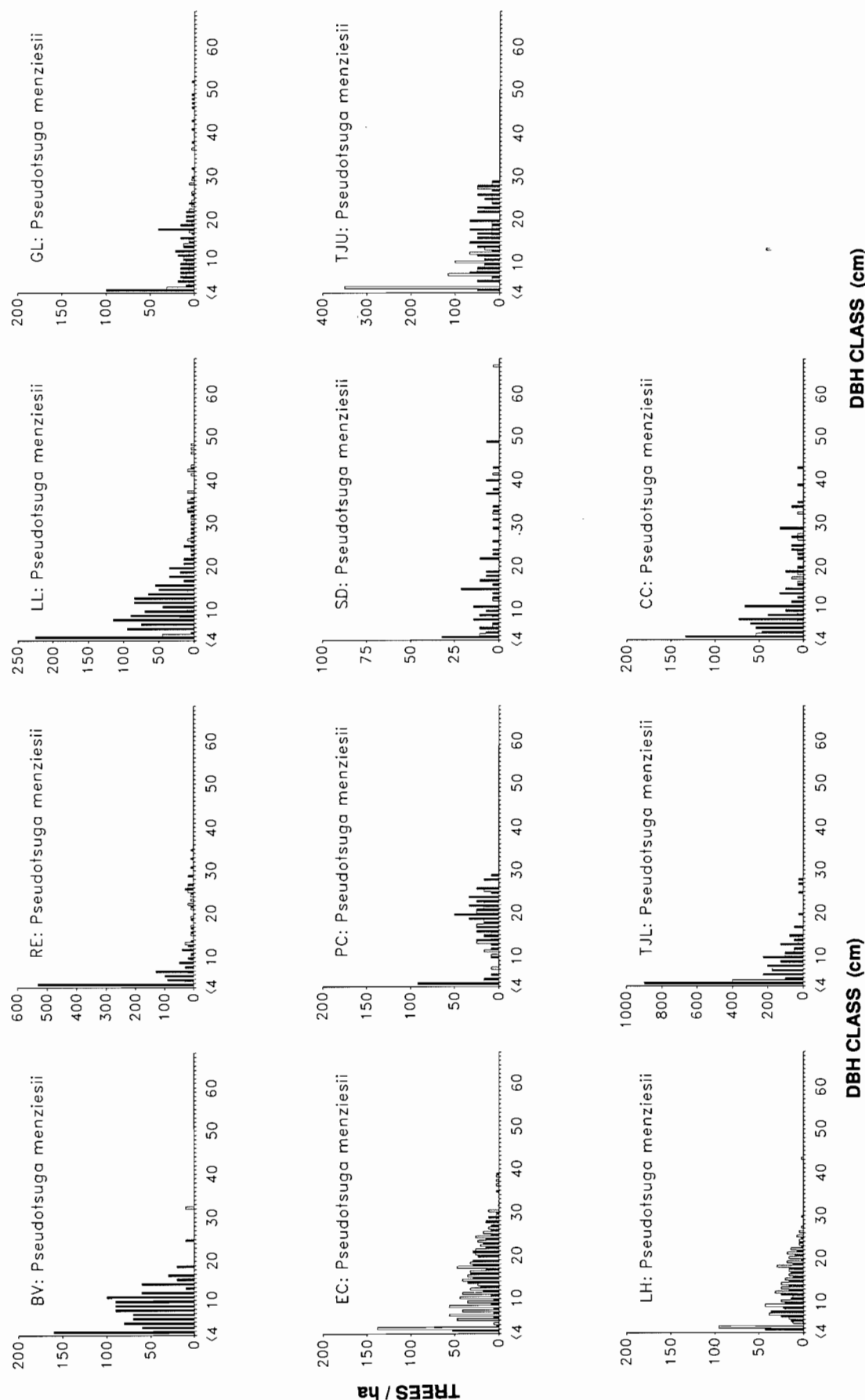


FIG. 3. Frequency distributions of live (solid bars) and dead-standing (empty bars) Douglas-fir trees and saplings in 1-cm DBH classes. The DBH frequency distributions for live trees include both aged and unaged trees. Stand abbreviations are defined in Fig. 1.

TABLE 2. Tree densities and basal areas of live and dead-standing trees for the sampled stands

Stand*	Species†	Density (no./ha)		Basal area (m ² /ha)	
		Live	Dead standing	Live	Dead standing
BV	PM	870	10	7.10	0.76
	PC	30	0	0.24	0.00
	PP	20	0	0.23	0.00
	PF	240	10	2.93	0.03
	PT	70	100	0.38	0.36
	PE	10	0	0.10	0.00
	Total	1240	120	10.98	1.15
CC	PM	573	80	10.42	2.21
	PC	87	20	2.14	0.05
	PP	47	7	1.59	0.23
	PF	13	0	0.18	0.00
	PT	180	60	4.98	0.73
	JS	7	0	0.02	0.00
	Total	907	167	8.91	3.22
EC	PM	403	806	12.01	15.31
	PC	53	24	0.94	0.23
	PP	309	3	10.85	0.21
	PF	0	3	0.00	0.02
	JS	3	0	0.01	0.00
	Total	768	836	23.81	15.77
GL	PM	284	156	4.38	6.41
	PP	91	0	3.72	0.00
	PF	59	6	2.20	0.07
	PT	12	81	0.15	0.37
	Total	446	243	10.45	6.85
LH	PM	293	409	2.54	6.31
	PC	564	45	6.85	0.63
	PP	27	0	0.50	0.00
	PF	5	0	0.11	0.00
	PT	0	166	0.10	0.91
	AL	2	0	0.01	0.00
	Total	891	620	10.11	7.85
LL	PM	1060	145	16.17	9.59
	PC	535	100	12.12	1.89
	PP	15	0	0.27	0.00
	PF	5	0	0.49	0.00
	PE	210	15	3.11	0.15
	AL	40	0	1.52	0.00
	Total	1865	260	33.68	11.63
PC	PM	417	192	11.77	4.58
	PC	250	25	6.75	0.16
	PP	133	8	2.91	0.02
	PT	33	208	0.55	0.69
	PE	42	0	0.73	0.00
	Total	875	433	22.71	5.45
RE	PM	650	210	9.61	4.90
	PC	50	10	0.85	0.23
	PP	60	0	1.71	0.00
	PT	150	230	3.02	1.35
	PE	0	10	0.00	0.18
	Total	910	460	15.19	6.66
SD	PM	189	21	6.99	1.96
	PC	305	121	13.82	4.67
	PP	57	18	2.10	0.63
	PF	104	75	2.03	2.24
	PT	14	0	0.11	0.00
	Total	669	235	25.05	9.50

TABLE 2 (concluded)

Stand*	Species†	Density (no./ha)		Basal area (m ² /ha)	
		Live	Dead standing	Live	Dead standing
TJL	PM	1600	500	13.35	2.50
	PC	1775	150	19.74	0.71
	PP	175	0	3.76	0.00
	Total	3550	650	36.85	3.21
TJU	PM	983	633	21.68	9.65
	PC	117	0	2.31	0.00
	PP	317	0	9.23	0.00
	PF	183	0	1.80	0.00
	Total	1600	633	35.02	9.65

*Abbreviations are defined in Fig. 1.

†PM, *Pseudotsuga menziesii*; PC, *Pinus contorta*; PP, *Pinus ponderosa*; PF, *Pinus flexilis*; PT, *Populus tremuloides*; PE, *Picea engelmannii*; AL, *Abies lasiocarpa*; JS, *Juniperus scopulorum*.

species, Douglas-fir and Engelmann spruce (LL), established synchronously with the seral pines and aspen. Douglas-fir in stand RE exhibit a bimodal age distribution, with the older trees occupying a toe-slope position near the upper portion of a small fluvial terrace. The aspen at this site are similar in age to the older cohort of Douglas-fir. TJL and LL include rare remnant trees that survived the most recent catastrophic fire (Table 3).

The remaining four stands (GL, SD, TJU, CC) have varying age structures due to unfavorable environmental conditions or to a longer interval since stand initiation. Stands GL and SD occupy unfavorable, xeric sites having coarse, permeable soils and correspondingly low tree densities. GL was initiated during the late 1800s but shows continuous regeneration since then. Stand SD occupies a similar site and has not experienced a stand-initiating fire during the past 250 years. Currently, lodgepole pine that initially colonized the site are being slowly replaced by Douglas-fir and limber pine.

Stand TJU shows a continuous but decreasing rate of Douglas-fir recruitment since stand initiation during the early 1700s. Stand CC is a young postfire stand that occupies a mesic site and includes Douglas-fir remnants in several older age-classes as well as numerous younger trees that are replacing the older aspen. A small population of young lodgepole pine is also present in the stand.

Stand characteristics

Here we characterize our stands using estimates of defoliation and tree, sapling, and seedling mortality. These data provide measures of disturbance severity following the most recent budworm and Douglas-fir bark beetle outbreaks.

Defoliation indices

Douglas-fir in each of the 11 sampled stands show foliar evidence of budworm defoliation during the 1976–1985 outbreak. Percentages of defoliated Douglas-fir trees range from 16 to 98% (Table 4). For the most severely defoliated stands (EC, LH, LL, PC, TJL), >50% of the host trees are almost completely defoliated. In contrast, in stands with <50% of the trees recovering from defoliation, the majority of trees show little or no evidence of defoliation (BV, CC, RE). Engelmann spruce, where present, show little or sporadic evidence of budworm defoliation.

TABLE 3. Age and DBH characteristics of the stands sampled, including remnant trees

Stand*	Species†	Age			DBH			% trees aged
		<i>n</i>	Mean (years)	Range (years)	<i>n</i>	Mean (cm)	Range (cm)	
BV	PM	86	46	29–60	87	9	4–24	99
	PF	24	55	38–86	24	11	4–29	100
CC	PM	85	60	25–200	86	12	4–42	99
	PC	13	49	20–171	13	16	5–35	100
	PT	15	115	82–152	27	18	14–23	56
EC	PM	137	92	46–162	140	19	4–39	98
	PC	15	105	87–119	18	15	8–23	83
	PP	99	98	53–372	104	20	4–63	95
GL	PM	87	74	22–162	87	13	4–31	100
	PP	29	90	29–189	29	21	4–47	100
	PF	19	116	31–241	19	19	5–43	100
LH	PM	126	82	34–108	129	12	5–23	98
	PC	243	104	46–120	248	19	5–38	98
	PP	10	84	44–107	12	14	6–31	83
LL	PM	189	116	81–321	212	12	4–42	90
	PC	82	116	54–181	109	15	5–32	75
	PE	35	120	78–140	46	12	4–38	76
PC	PM	49	89	54–103	50	18	4–28	94
	PC	30	95	41–115	30	17	5–29	100
	PP	16	90	68–111	16	15	5–31	100
RE	PM	65	56	29–105	65	11	4–34	100
	PT	13	95	79–107	15	16	8–21	87
SD	PM	52	127	51–259	53	18	4–48	98
	PC	70	193	50–282	88	22	4–41	80
	PP	15	214	171–248	15	19	7–38	100
	PF	29	171	88–259	29	13	4–39	100
TJL	PM	63	107	76–245	64	9	4–27	98
	PC	67	111	68–249	71	11	4–23	94
TJU	PM	53	208	89–254	56	16	5–28	95
	PP	19	210	175–251	19	18	8–35	100

NOTE: Data for tree species with an *n* < 10 are excluded.

*Abbreviations are defined in Fig. 1.

†Abbreviations are defined in Table 2.

TABLE 4. Defoliation indices for Douglas-fir for the sampled stands

Stand*	Defoliation index†				% of host trees defoliated
	0	1	2	3	
BV	45	22	25	8	55
CC	84	9	5	2	16
EC	2	4	31	63	98
GL	19	26	29	26	80
LH	2	5	19	74	98
LL	6	11	25	58	94
PC	2	12	19	67	98
RE	53	15	26	6	46
SD	8	26	34	32	92
TJL	9	22	17	52	91
TJU	21	26	21	32	79

*Abbreviations are defined in Fig. 1.

†Index classes range from 0 (no defoliation) to 3 (almost complete defoliation). The data represent the percentages of trees in each class.

Tree, seedling, and sapling mortality

The average relative density of dead Douglas-fir (the percentage of trees that are dead) for all stands was 29%. Relative densities of dead Douglas-fir are greatest in the young, multi-storied stands EC and LH (66 and 58%). BV, the youngest and single-storied stand, exhibits the lowest relative density of dead Douglas-fir (1%).

The highest relative density of dead Douglas-fir seedlings also occurs in the multistoried stand EC (56%). Similarly, the young and single-storied stand BV has no dead seedlings. The relative density of dead host seedlings is considerably lower than that for dead trees when averaged among all stands (16%).

The highest relative density of dead Douglas-fir saplings occurs in the oldest and multistoried stand TJU (86%). The lowest relative density of dead Douglas-fir saplings (6%) occurs in the young stands: BV and RE. The average relative density of dead Douglas-fir saplings for all stands is higher (35%) than that for either trees or seedlings.

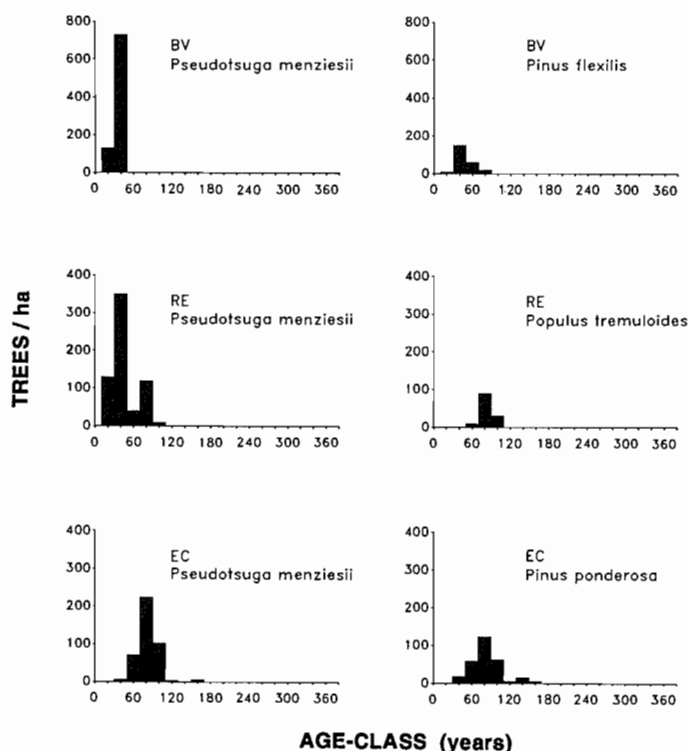


FIG. 4. Age distributions of trees in stands BV, RE, and EC using 20-year age-classes. The percentage of trees successfully aged for each species by stand is given in Table 3. Stand abbreviations are defined in Fig. 1.

Tree growth responses

Suppression and release frequencies

Ring-width suppressions and releases are used to show the timing and growth response of trees to canopy changes corresponding to the periods of documented insect outbreaks. These data show three general patterns (Fig. 7). First, suppression patterns generally correspond to one or more documented periods of budworm outbreak during the late 1930s, 1950s, and 1970s following a lag period of one to several years. Second, release frequencies for codominant nonhost trees coincide with Douglas-fir suppression responses, with the most notable nonhost responses occurring during the 1976–present budworm and bark beetle outbreaks. Third, suppression frequency patterns among stands show considerable variability regarding the timing, duration, and severity of outbreaks.

The clearest correspondence between suppression frequencies and the documented record of budworm outbreak are found among younger stands with high host densities (BV, EC, LH, PC, RE, TJL). The pattern at BV shows that this stand was too young to have been affected by earlier outbreaks. Remaining stands are predictably less susceptible to defoliation and growth reduction because of the greater sizes of their host trees (TJU, SD), their lower host densities (SD, GL, TJL), or their occupation of more mesic (CC) or higher elevation sites (LL, SD). Stand TJU, the only stand with a record before 1880, shows additional periods of high suppression frequencies during the 1800s.

Ring-width indices

These data show the average growth trends for trees in each of the sampled stands since stand initiation and deviations

from these trends during periods of documented insect outbreaks. In all stands except CC, LH, and SD, Douglas-fir exhibit rapid growth rates during the first 10–20 years following postfire stand initiation. Following initial site colonization, growth rates declined rapidly as a result of competition during canopy closure (Fig. 7). In stand CC, mesic conditions and canopy competition with aspen contribute to relatively constant growth rates. In stand LH, the even growth rates of Douglas-fir before the 1976–1985 budworm outbreak reflect its understory status in a stand dominated by lodgepole pine. Douglas-fir in stand SD also colonized after lodgepole pine (Fig. 6).

Past budworm outbreaks are evident in the Douglas-fir chronologies but with considerable variation in the timing, duration, and degree of growth reduction. The 1938–1945 and 1958–1965 outbreaks are generally more apparent among older (CC, SD, TJU) and less vigorous stands (GL, LH, RE). Engelmann spruce, a secondary budworm host and common species in stand LL, showed a declining growth curve but with no notable episodes of growth reduction during periods of budworm outbreak.

Nonhost trees also exhibit rapid radial growth during the first 10 to 20 years following stand initiation (Fig. 7). Growth after this period generally decreased exponentially until the late 1970s or very early 1980s. During the subsequent budworm (1976–1985) and overlapping (1984–present) bark beetle outbreaks, most nonhost trees experienced moderate to high growth rates in response to insect-induced canopy reduction. Aspen in stand CC was an exception to this trend, showing relatively sustained increase in growth since the 1930s (Fig. 5).

Discussion

Effects of insect outbreaks on stand structure

The effects of western spruce budworm and Douglas-fir bark beetle outbreaks on forest structure appear to be primarily related to the developmental stage of stands following postfire initiation and secondarily to environmental factors including climate, which affect tree vigor. Outbreak severities for both insects have been greatest among younger stands with high host densities, large basal areas, and a wide range of stem sizes (Table 2; Fig. 3). Budworm outbreaks are likely responsible for the high mortality of suppressed seedlings, saplings, and small-diameter trees (Fig. 3). In contrast, Douglas-fir bark beetles appear responsible for the mortality of larger trees, especially those previously weakened by budworm defoliation.

Young, postfire stands lacking a multistoried structure have been least affected by the combined agents. These stands, exemplified by stand BV, lack the vertical dispersal vector for budworm from canopy to subcanopy individuals (Carlson *et al.* 1983; Fellin *et al.* 1983), are growing vigorously, and lack large-diameter trees susceptible to bark beetle infestation.

Somewhat older, dense stands such as TJL predictably show high budworm mortality among host individuals that may result in minor changes in dominance (Table 2). In this case, budworm mortality hastens the on-going thinning process but disproportionately affects the more shade tolerant Douglas-fir to the advantage of its competitor, lodgepole pine.

Older, multistoried stands and low-density, open stands exhibit mortality in a range of tree size classes. In both types of stands, mortality is related to the spatial distribution of host trees and their role as dispersal vectors. As noted in earlier

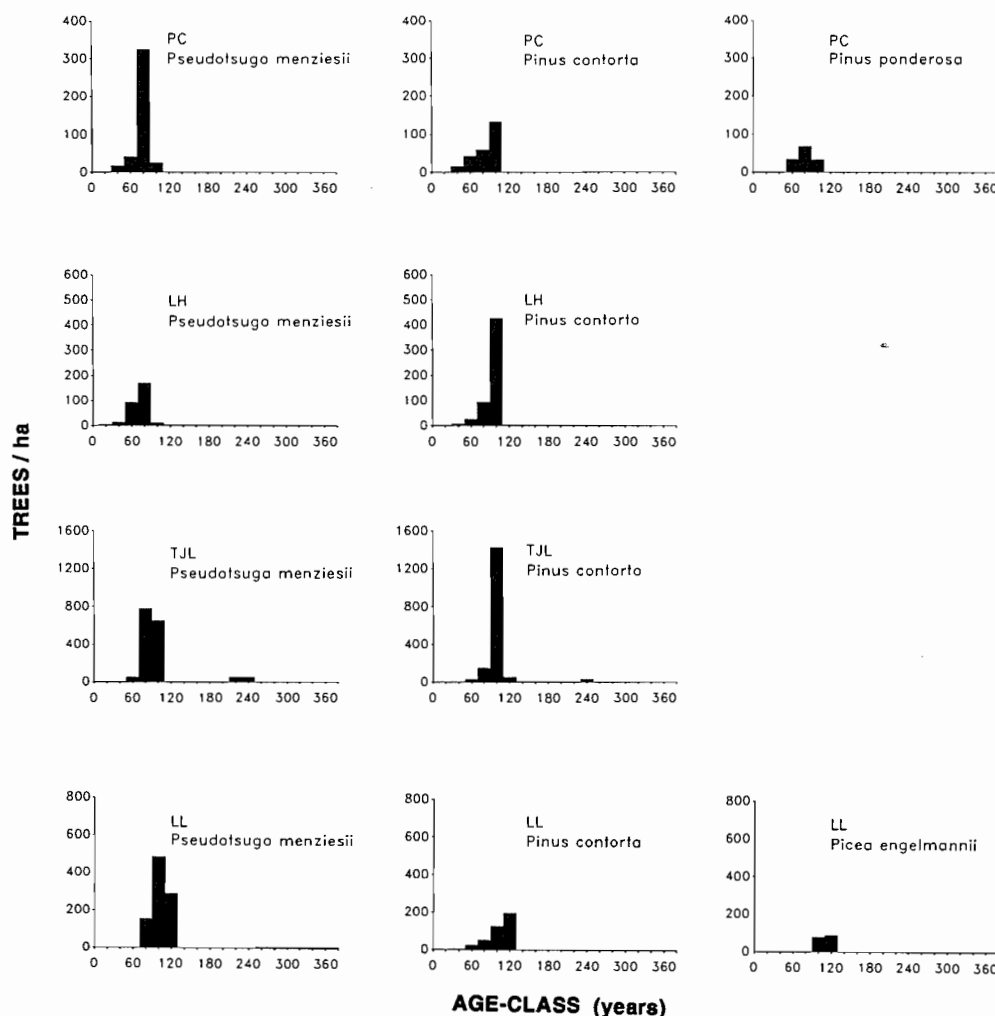


FIG. 5. Age distributions of trees in stands PC, LH, TJL, and LL using 20-year age-classes. The percentage of trees successfully aged for each species by stand is given in Table 3. Stand abbreviations are defined in Fig. 1.

studies (Carlson *et al.* 1983; Fellin *et al.* 1983), the tiered structure of multistoried stands has promoted the vertical dispersal of budworm larvae from canopy to suppressed sub-canopy trees, saplings, and seedlings. Open stands benefit from lower probabilities of successful dispersal due to lower host densities.

Each of the sampled stands exhibits evidence of recovery since the most recent budworm outbreak (Table 4). Stands exhibiting the least evidence of defoliation include BV, the youngest stand sampled, and CC and RE, which occupy the most mesic sites sampled.

The high host mortality during the most recent overlapping budworm and bark beetle outbreaks suggests that stand susceptibility to budworm epidemics may be an important precursor to Douglas-fir bark beetle outbreaks in these forests. Additional circumstantial evidence supports this interpretation. First, the only other locally observed bark beetle outbreak (1950–1951) developed among stands defoliated during the 1938–1945 budworm outbreak (Anonymous 1952). Second, the high beetle-caused mortality of many large, fire-remnant Douglas-fir during the most recent outbreak suggests that bark beetle outbreaks are comparatively rare in these forests.

Tree growth response to insect disturbance

Suppression and release frequencies and radial growth measurements (Fig. 7) suggest that the 1976–1985 budworm outbreak was the most severe since stand initiation for the majority of the sampled stands. Earlier, less severe, outbreaks also appear to be less synchronous among the sampled stands. Both of these results are consistent with those previously reported for the northern (Carlson *et al.* 1983; McCune 1983; Anderson *et al.* 1987) and southern Rockies (Swetnam and Lynch 1989).

Most stands also exhibit host growth reduction during earlier budworm outbreaks (Fig. 7). Older, less vigorous stands (CC, SD), xeric stands (GL, SD), and stands with primarily suppressed Douglas-fir (LH) were most susceptible to budworm defoliation during these outbreaks.

In general, host growth rates returned to predisturbance or higher levels following all but the 1976–1985 outbreak. Nonhost species, with the exception of aspen in stand CC, exhibit little or no growth variation during or following earlier, less severe outbreaks (Fig. 7). These results suggest that for earlier, less severe outbreaks, surviving host individuals gained short-term growth advantages, but that the

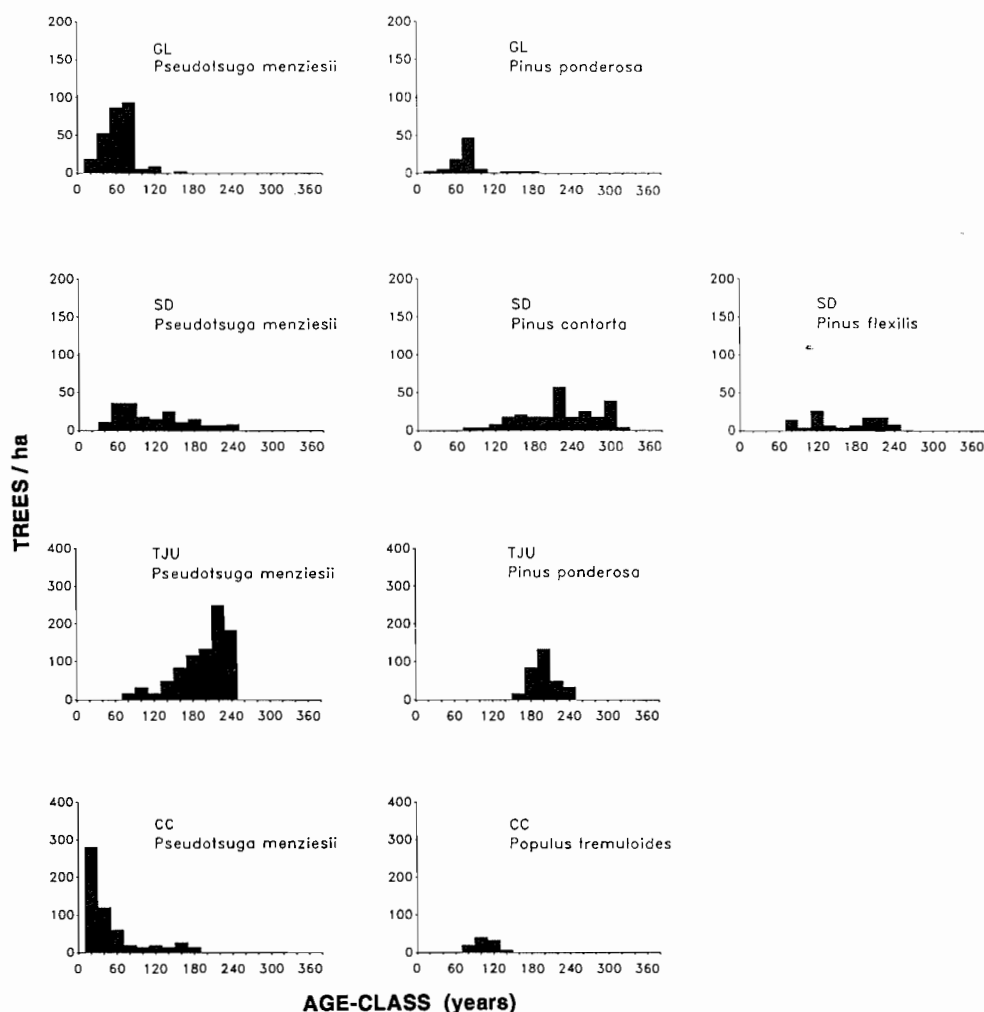


FIG. 6. Age distributions of trees in stands GL, SD, TJU, and CC using 20-year age-classes. The percentage of trees successfully aged for each species by stand is given in Table 3. Stand abbreviations are defined in Fig. 1.

amount of canopy removal was insufficient to elicit strong positive growth responses from nonhost trees.

Nonhost growth responses to the 1976–present insect outbreaks appear stronger relative to earlier outbreaks (Fig. 7). However, nonhost responses to these disturbances vary considerably by species. Within-stand comparisons suggest that ponderosa pine is the most responsive to increases in resources following canopy reduction and host mortality, followed by lodgepole pine and aspen.

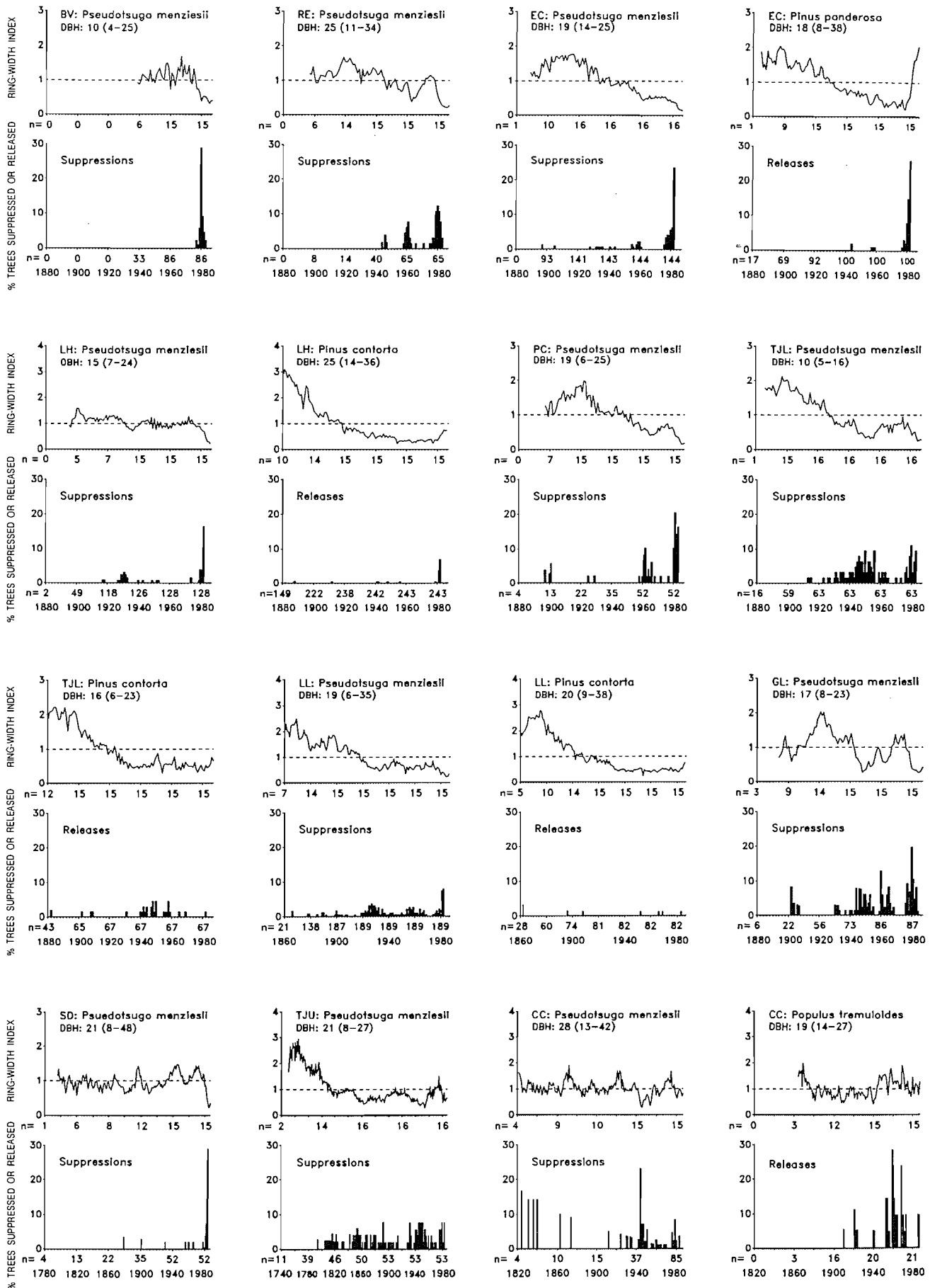
Fire suppression and budworm outbreak severity

Fire suppression has increased host density in most stands since initiation of fire suppression policy by the National Park Service in 1929 (Ise 1961). However, fire suppression alone does not appear to explain the increased severity of budworm outbreaks in the Colorado Front Range. Although budworm-caused mortality is primarily determined by host density and size structure, these factors are primarily dependent on time

since stand initiation. A more important factor contributing to the increased severity and synchronicity of budworm outbreaks in the Front Range appears to be the large area of montane forest that more or less synchronously reached a stage of stand development susceptible to budworm outbreaks. This is a consequence of stand development following the burning of these forests during the European settlement era from ca. 1860 to the early 1900s (Skinner and Laven 1983; Veblen and Lorenz 1986, 1991; K.S. Hadley, unpublished data).

Fire suppression was probably only a minor contributory factor to the earliest documented (1938–1945) budworm outbreak, as most of the sampled stands would have had ages of 20 to 80 years (Table 3). This minimal effect is suggested by the observation that 55-year-old stand BV was the least severely disturbed stand during the most recent outbreak. This conclusion is consistent with early Park Service records (Barrows 1936) that note the lack of regional insect infestations

FIG. 7. Percentages of suppressed and released trees and mean ring-width indices for randomly selected trees in each stand. Sample depths are shown by the n values below the x axes. Median (with range in parentheses) of DBH (cm) values for trees used in the ring-width chronologies is given. The horizontal broken line shows the theoretical position of the mean index value. See text for definition of suppression and release. Stand abbreviations are defined in Fig. 1.



before a 1926 epidemic of mountain pine beetle. Additional records (Anonymous 1934–1986) verify the 1938 budworm outbreak as the first recorded in the park. These observations are consistent with the regional dendroecological record developed by Swetnam and Lynch (1989), who note a hiatus in budworm activity during and following the period of European settlement.

Radial growth patterns for Douglas-fir further support this interpretation. The majority of sampled stands indicate that host radial growth during earlier outbreaks was generally vigorous and similar to that of nonhost species (Fig. 7). During later outbreaks, most stands experienced canopy closure and increased resource competition, as shown by marked decreases in radial growth and thus, increasing stand susceptibility to budworm outbreaks. As a result, the most recent and most severe outbreak occurred at a time of much greater susceptibility to insect damage.

Successional trends following budworm and bark beetle outbreaks

Despite high host mortality resulting from the recent overlapping budworm and bark beetle outbreaks, Douglas-fir remains the dominant tree species in all but two of the sampled stands (Table 2). Thus, insect outbreaks appear to result in short-term adjustments in stand structure and the competitive status of host and nonhost trees rather than in major, long-term shifts in relative dominance. Although insect outbreaks may retard the replacement of seral pine species and aspen by the relatively shade tolerant Douglas-fir, they do not reverse it.

Among stands with high host densities, the combined insect outbreaks delay the replacement of shade-intolerant species through several mechanisms. Budworm greatly reduces the size of the host seed bank through cone and seed mortality. It also enhances the development of both an arboreal and a nonarboreal understory through canopy reduction. Furthermore, seedling, sapling, and small-tree mortality in these stands is sufficient to significantly delay the replacement of canopy dominants killed during ensuing bark beetle outbreaks. Bark beetle induced tree mortality also contributes to the small number of seedlings in these stands by eliminating many of the cone-bearing trees. Bark beetle induced mortality of canopy trees also provides a competitive advantage for suppressed, shade-intolerant, seral tree species. In sum, the combined effects of these delay mechanisms suggest that the 20th century insect outbreaks may play a role analogous to that of 19th century fires in slowing the rate of replacement of seral pines by Douglas-fir.

High relative disturbance frequencies by fire (Romme and Knight 1981), mass movement and volcanic eruptions (Veblen *et al.* 1981), and blowdown (Lorimer 1977) have been shown to prevent compositional equilibrium in many forest types. Hypothetically, higher frequencies of insect outbreaks in the montane forests of the Front Range could likewise prevent compositional equilibrium. Both continued anthropogenic disturbance and fire suppression increase the likelihood of higher insect outbreak frequencies by promoting landscape homogeneity, decreasing mean stand ages, and increasing the synchronicity of stands reaching a stage of development susceptible to budworm outbreaks.

The youthful character of the montane forest in general is a consequence of extensive burning during the European set-

tlement period. The occurrence of large-diameter, charred Douglas-fir logs, stumps, and spars throughout the montane forests of the Front Range (Clements 1910; Veblen and Lorenz 1986; Hadley 1990) suggests a more heterogeneous (i.e., both old-growth and young, postfire stands) structure for these forests in the past than exists today. As a consequence of late 19th century anthropogenic fires, and to a lesser extent fire suppression, the severity and synchronicity of budworm and subsequent Douglas-fir bark beetle outbreaks have increased as more predominantly young, postfire stands enter an outbreak susceptible stage.

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