POPULATION ECOLOGY

Roberta Parish · Joseph A. Antos

Structure and dynamics of an ancient montane forest in coastal British Columbia

Abstract Old-growth forests are common in the snowy, montane environments of coastal western North America. To examine dynamics of a stand containing four canopy tree species (*Abies amabilis*, *Chamaecyparis nootkatensis*, *Tsuga mertensiana* and *T. heterophylla*), we used four stem-mapped, 50 m ×50 m plots. From measurements of annual rings, we obtained ages from basal discs of 1,336 live trees, developed master chronologies for each species, reconstructed early growth rates, and delineated periods of release. The stand was ancient; individuals of all four species exceeded 900 years in age, and the oldest tree exceeded 1,400 years. The four plots differed in the timing of events, and we found no evidence of major, stand-level disturbance. Instead the stand was structured by small-scale patch dynamics, resulting from events that affected one to several trees and initiated episodes of release and relatively rapid early growth. The species differed in age structure and dynamics. *A. amabilis* and *T. heterophylla* had a classical reverse-J age structure indicative of stable populations, whereas *C. nootkatensis* and *T. mertensiana* appeared to rely on local episodes of increased recruitment, which were often separated by centuries, and were probably related to multiple-tree gaps that occurred infrequently. However, such gaps could be considered normal in the long-term history of the stand, and thus these species with their long life spans can persist. Most individuals of all four species grew extremely slowly, with trees typically spending centuries in the understory before reaching the canopy, where they were able to persist for additional centuries. Thus, the key features of this forest are the very slow dynamics dominated by small-scale events, and the slow growth of stress-tolerant trees.

Keywords *Abies amabilis* · Age structure · *Chamaecyparis nootkatensis* · Patch dynamics · *Tsuga mertensiana*

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Introduction

The dynamics of ancient forests are often complex. Stand composition and structure are molded by environmental conditions such as climate, geology, and physiography, by interactions of tree species, and by disturbances of various types, sizes, and intensities. In many landscapes, major disturbances are pivotal in controlling the structure of stands within the context set by environmental factors and the pool of available species (White 1979; Pickett et al. 1989; Johnson 1992; Wimberly and Spies 2001). As stands age, the effects of initiating disturbances fade, and patch dynamics become of paramount importance. Some forests show little or no evidence of an initiating disturbance (e.g., Despain 1983; Runkle 1990; Lusk and Smith 1998; Antos and Parish 2002a), and where intense, large-scale disturbances are infrequent or absent, patch dynamics are key for canopy tree replacement (e.g., Denslow 1987; Oliver and Larson 1990; Runkle 1990; Lertzman and Krebs 1991; Lertzman 1992; Brett and Klinka 1998).

The concept of patch dynamics has a long history in ecology, being first brought to prominence by Watt (1947). In tropical rainforests, re-growth in canopy gaps produced by small-scale processes results in a mosaic of patches of different ages (Richards 1952). Similarly, patch dynamics predominate in old, temperate deciduous forests that have escaped major disturbance for long periods relative to tree life span (Runkle 1990). However, patch dynamics are not restricted to forests that have escaped large-scale disturbances for extended periods. Weaver (1943) and Cooper (1960, 1961) both recognized that *Pinus ponder-*

osa forests, which are maintained by frequent but low-intensity fires, were also composed of a mosaic of variously aged, small patches. Even in northern coniferous forests, which typically have rather frequent stand-initiating disturbances, some regions have low enough disturbance frequencies that stands structured by gap processes are common (e.g., Bartemucci et al. 2002). Thus patch dynamics can predominate in many kinds of forests.

Disturbance encompasses a variety of phenomena, all of which can destroy or damage plants, releasing resources and altering microenvironments, and can vary greatly in spatial scale, frequency, and intensity. Studies of the response of tree populations to disturbance at various spatial scales have resulted in a greatly increased understanding of natural forests in many parts of the world (e.g., Runkle 1982; Veblen et al. 1992). Meticulous reconstruction of stand history using age structure, growth patterns, and the spatial distribution of trees have yielded numerous insights into processes controlling stand development and the role of disturbances of various kinds (Henry and Swan 1974; Deal et al. 1991; Johnson et al. 1994; Antos and Parish 2002b). Detailed age and size structure of trees, in conjunction with data on spatial pattern, have uncovered past disturbances and identified the consequences of both small and large, intense disturbances (e.g., Stewart 1986; Johnson and Fryer 1989; Lusk and Ogden 1992).

Forests on the northwest coast of North America receive high amounts of precipitation, and stand-initiating disturbances can be infrequent (Agee 1993). Along the coast of British Columbia, gap processes often predominate in forests at both low (Lertzman et al. 1996; Gavin et al. 2003a, b) and high elevations (Brooke et al. 1970; Lertzman and Krebs 1991; Lertzman 1992; Brett and Klinka 1998). The mountain hemlock biogeoclimatic zone is the highest-elevation forest zone along the coast of British Columbia and is very wet, with deep snowpacks and short, cool summers (Brooke et al. 1970). Fires and major windthrow events are infrequent (see Hallett et al. 2003 for an exception), as are defoliating insect outbreaks (Otvos et al. 2001). *Tsuga mertensiana* (mountain hemlock), *Chamaecyparis nootkatensis* (yellow cedar), and *Abies amabilis* (amabilis fir) dominate forests of this zone. *Tsuga heterophylla* (western hemlock) is also common in the lower parts of the zone. Both *A. amabilis* and *T. heterophylla* are very shade tolerant and establish in abundance in the forest understory; *C. nootkatensis* and *T. mertensiana* are also shade tolerant, but somewhat less so (Minore 1979; Burns and Honkala 1990; Zobel and Antos 1991). *C. nootkatensis* is a very long-lived stress tolerator found in a wide variety of habitats, which appears to need some opening of the stand to reach the canopy in most forests (Antos and Zobel 1986). *T. mertensiana* is also very long-lived, but its establishment may be related to moisture conditions as well as disturbance (Agee and Smith 1984; Peterson and Peterson 2001).

In this study, we describe the structure and reconstruct the development of an ancient montane stand (>1,000 years old) on northern Vancouver Island using mapped plots and dendrochronological analysis of ca.

2,000 trees. Because the great age of the stand would preclude catastrophic disturbance within historical times, we expected that patch dynamics would predominate. We also predicted that gaps of moderate size would support the recruitment of *T. mertensiana* and *C. nootkatensis* and that the mix of small and moderate gaps would facilitate the long-term coexistence of the tree species present. Specific objectives were to: (1) evaluate the size and age structure of the constituent species, (2) determine size-age relationships of each species, (3) delineate periods of release and of rapid early growth, and (4) assess spatial patterns of inferred disturbance.

Materials and methods

Study site

The study site at Mt. Cain (50°14′N, 126°20′W) was located on northern Vancouver Island, British Columbia, in the lower part of the mountain hemlock biogeoclimatic zone. The site was on a gentle (10–15°) southwest slope at ca. 1,000 m elevation in an extensive area of old-growth forest (until recent logging). The soil parent material was glacial till. Substrates were wet, occasionally water-logged in depressions. The surface was hummocky, with abundant rotten wood in the substrate, and a ca. 40 cm mor humus layer over much of the surface. The upper portion of the site had a 2 cm eluviated horizon over a ca. 30 cm aluminium and iron illuviated loam layer. The lower portion of the site had areas of organic soil.

There are two climate stations within 115 km of Mt. Cain, and both are at low elevation. Thus, we used a method (PRISM, Daly et al. 1994, 1997) that interpolates climate data from spatially distributed point data and a digital elevation model. Mean annual temperature was estimated to be 4.9°C. Maximum monthly temperature (18.7°C) occurred in August and minimum monthly temperature (−4.6°C) in December and January. Annual precipitation was estimated to be 3,825 mm. Mean April 1 snow depth at nearby Newcastle Ridge (50°24′N, 126°03′ W, 1,170 m elevation) averaged 340 cm for the period 1961–1990 with a maximum accumulation of 488 cm (BC Ministry of Water, Land Air Protection, historical dataset).

Four tree species occurred in the canopy: *A. amabilis*, *C. nootkatensis*, *T. mertensiana* and *T. heterophylla*. The understory contained a prominent shrub layer ca. 1.5 m tall formed by the deciduous huckleberries, *Vaccinium alaskaense* and *V. ovalifolium*, but had low cover of herbaceous plants. In the plots 19 species were recorded; *Listera cordata*, *Rubus pedatus*, and *Veratrum viride* were among the most abundant. The moss layer was nearly continuous, with *Rhytidiopsis robusta* the most abundant species. Numerous small individuals (<1.3 m tall) of tree species, mostly *A. amabilis*, occurred in the seedling bank and formed a conspicuous component of the understory. Densities of *A. amabilis*, less than 1.3 m tall, were > 100,000/ha (J. A. Antos et al., unpublished data).

Field sampling

In 1999, we located four 0.25 ha square plots (50 m ×50 m) at the Mt. Cain study site. To facilitate stem mapping, the plots were located on level ground such that plots 1 and 2 were closely adjacent on a fairly flat area at the top of a rise and plots 3 and 4 about 0.5 km distant, near the bottom of the slope and away from noticeably wet depressions. The distance and bearing from the centre of each plot to all live and dead trees ≥4.0 cm diameter at breast height (DBH) were recorded. Trees were tagged, species recorded, DBH measured to the nearest centimetre, height measured to the nearest metre, and height to the lowest live branch recorded for all live trees. A fallen log was considered to be in a plot if the base originated within that plot. The length and diameter at base and top of pieces >5 cm diameter at the base were recorded. The location of logs was mapped and the decay class recorded. Saplings (≥1.3 m tall but <4 cm DBH) were tallied within each plot in a randomly located, 15 m ×15 m subplot.

Before logging commenced in autumn 1999, we obtained basal discs from saplings in the subplots and from trees too small to be of commercial value (<15 cm DBH). In spring 2000 we collected discs from the base of stumps of commercially sized trees. No effort was made to excavate stumps to determine the point of germination, but discs were cut as low as possible without incurring damage to the saw. Many trees had established on logs so that the point of germination was above ground level and, in some instances, considerably so. Basal discs were obtained from both live and standing dead trees. Few fallen logs yielded usable discs.

Discs provide a major advantage over increment cores for determining age and growth patterns of trees. In high-elevation forests, tree radial growth is often very asymmetric and preliminary examination of annual rings indicated that this was the case for *C. nootkatensis*. In addition, scars, which can be important in determining stand history and disturbance, are easy to observe on discs but unlikely to be seen on increment cores. By using discs we were able to determine the detailed growth history of individual trees.

Dendrochronological analyses

Discs were prepared following standard methodology (Stokes and Smiley 1968). We sanded basal discs with progressively finer grades of sandpaper until the ring structure was clearly visible. Annual ring widths were measured to the nearest 0.01 mm using a Measu–chron digital positiometer along one radius for small discs (<15 cm) and along two to three radii on large discs. We used pointer years and the computer program COFECHA (Holmes 1983) to detect measurement and cross-dating errors. We used the program ARSTAN (Cook and Holmes 1984) to standardise ring-widths and to develop a master chronology for each of the four canopy species. COFECHA was used to cross-date radii from standing dead trees against the master chronologies to determine the year of death.

Release, an abrupt increase in growth, indicates a sudden increase in resource availability to a tree, generally as the result of mortality of canopy trees. We used an abrupt doubling of ring width sustained for a period of at least 10 years as the operational definition of release (Parish et al. 1999; Antos and Parish 2002a, b). After determining the date, or dates, of release for each tree we aggregated the number of releases into 50-year periods. Because the sample sizes of live trees varied greatly among decades, we calculated release as the percentage of trees showing growth increases among those that were alive in the last decade of the 50-year period. We used both live and dead trees to reconstruct the timing of releases.

Reconstructing the conditions of establishment for trees currently in the canopy is critical to understanding stand dynamics and the role of disturbance. Trees that established under unusually favourable conditions, such as a canopy opening, may grow quite rapidly, a strong indication that disturbance was responsible for their initiation. We used rapid early growth as a proxy measure for establishment under favourable conditions. We calculated the average ring-width increment within 10, 20, 30, 40, and 50 years of the pith for each live tree and for those dead trees that we could reliably cross-date (*n*=1,357). Growth rates over the different time periods were similar so that we chose the mid period, 30 years. Because we did not locate germination points, it is possible that some of the trees showing rapid early growth had actually released prior to the date determined as the minimum age; thus we grouped individuals into 50-year establishment periods.

Nearby trees that showed rapid early growth or release at a similar date would indicate a probable canopy gap, likely formed by the death of more than one tree. To discern spatial patterns of disturbance, we plotted trees showing rapid early growth and trees showing release on stem maps of the plots. We visually examined the maps and delineated clumps of trees with dates of early rapid growth within a 15-year period or release within a 5-year period. If rotten or hollow trees, from which we were unable to get ring data, separated two or more such clumps of trees with dates within ≤5 years we assumed that the entire group represented a single disturbance.

Age structure and size relationship

To examine the relationship between tree size (height and DBH) and age, we used regression for each species separately in each plot, the two plot groups (1+2 and 3+4), and all plots combined. We used the difference in the residual sum of squares from regressions among the different plot groupings to test for significant differences in growth rates. Initial examination of the relationships of height, DBH, and age, suggested that these were non-linear. We used PROC NLIN (SAS 1995) to explore a suite of non-linear models and chose a model by

comparing residual variance and examining plots of residual versus predicted values (Ratkowsky 1990).

We estimated stem volume using taper equations developed for coastal species in British Columbia (Kozak 1988). To examine age structure, which provides important insight into the population dynamics of a species, we produced histograms of age by decade for each species for each plot and plotted ages on the stem maps. We also produced histograms for tree height and diameter for each species in each plot.

Results

Size and age structure

In each plot *A. amabilis* was most abundant, but all four tree species were present (Table 1). There were 1,542 live trees (≥4.0 cm DBH) per hectare, of which 938 were *A. amabilis*, 268 *T. heterophylla*, 169 *T. mertensiana*, and 167 *C. nootkatensis*. The last two species were less abundant in plots 1 and 2 than in plots 3 and 4. When saplings from subplots were included, the overall densities of trees (≥1.3 m tall) per hectare were: 2,471 *A. amabilis*, 512 *T. heterophylla*, 381 *T. mertensiana*, and 223 *C. nootkatensis*. The numbers of individuals decreased rapidly with increasing diameter, especially for *A. amabilis* and *T. heterophylla*, for which about half of the stems ≥4.0 cm DBH were <10 cm DBH. Small individuals of *C. nootkatensis* and *T. mertensiana* were also common but only in plots 3+4. In contrast to diameter, height showed a bimodal distribution, which distinguished canopy and subcanopy strata. The canopy comprised trees 20–30 m tall whereas most trees in the subcanopy were <6 m tall. Trees ca. 14–19 m tall were under represented in the distribution, a pattern similar for all species. The tallest tree measured was 35.2 m; all four species reached a maximum height of ca. 30 m.

Gross stem volume to a 10 cm top diameter outside the bark was estimated at 1,038 m^3/ha. A number of trees were hollow at the base but sound above. The merchantable volume estimate, 964 m^3, which excluded the stump to 30 cm may provide a reasonable compromise estimate of actual volume. The distribution of volume among species in the plots did not reflect the number of stems (Table 1). The numerous *A. amabilis* in the understory had a negligible contribution to stem volume whereas large *C. nootkatensis* or *Tsuga* might contain 5–10 m^3 of wood.

We were able to determine minimum ages at the base of 1,336 live trees. Interior rot was the main barrier to determining age, especially for *C. nootkatensis*. The distributions of minimum tree ages resembled a classical reverse-J curve for both plot groups, though there were differences in the shape of the distributions. In plots 1 and 2 (Fig. 1a), there was a rather steady decline in numbers with age, although more trees dated from the 1500s than 1600s. In plots 3 and 4 (Fig. 1b), the number of trees declined rapidly to ca. 1720, before which time the number of trees, although quite variable among decades, showed little decrease until before 1300 (Fig. 1b). The decreased numbers of trees from the 1800s and almost complete lack of trees from the 1900s (Fig. 1) relate to the very long periods that were required for trees to reach 4 cm DBH. Saplings (>1.3 m tall but <4.0 cm DBH) from the subplots were generally between 100 and 200 years old; none were less than 80 years and the oldest was 274 years.

The age distributions of trees ≥4 cm DBH spanned the range from before 550 to 1900 AD. The oldest trees were *C. nootkatensis* (age estimated >1,450 years) but several *T. mertensiana*, two *T. heterophylla* and one *A. amabilis* were >900 years old. The shape of the distribution varied greatly among species (Fig. 2). *A. amabilis* showed a decreasing number of individuals with age (Fig. 2a,b)—the expected pattern for a population near equilibrium. The number of individuals of *T. heterophylla* also declined rapidly with age back to ca. 1650 in plots 1 and 2 and to ca. 1750 in plots 3 and 4; before that time the distribution had no overall temporal trend (Fig. 2c,d). Both *T. mertensiana* and *C. nootkatensis*, however, showed no clear pattern of decline in number of individuals with age (Fig. 2e–h). *T. mertensiana* appeared to have a pulse of successful establishment in the mid-1500s in plot 1 and in the early 1300s and early to late 1800s in plots 3 and 4. *C. nootkatensis* showed a pulse of successful establishment in the late 1200s in plot 2 and in the 1300s and late 1800s in plots 3 and 4. There was a 130-year period centred on the 1600s with only one individual represented, whereas in

Table 1 Number and gross stem volume (m^3) of live and dead stems ≥4 cm DBH in four 0.25 ha plots in the ancient coastal montane forest at Mt. Cain, Vancouver Island. Volume was calculated to 10 cm top diameter outside bark using equations in Kozak (1988)

	Plot 1				Plot 2				Plot 3				Plot 4			
	Live		Dead		Live		Dead		Live		Dead		Live		Dead	
	No.	Volume	No.	Volume	No.	Volume	No.	Volume	No.	Volume	No.	Volume	No.	Volume	No.	Volume
Total stems ≥4 cm DBH	266	262.8	50	25.8	460	244.9	56	20.0	401	283.6	25	17.2	415	247.4	26	24.9
A. amabilis	170	129.6	35	15.2	317	89.4	36	6.3	237	36.5	15	4.5	214	37.8	12	3.3
C. nootkatensis	3	8.2	1	0.5	34	81.8	12	8.0	62	128.6	6	2.3	68	106.2	11	7.8
T. mertensiana	34	78.8[a]	14[b]	10.0[a]	22	43.6[a]	8[b]	5.7[a]	54	71.5[a]	4[b]	10.4[a]	59	58.7[a]	3[b]	13.8[a]
T. heterophylla	59	45.2			87	30.1			48	47.0			74	44.7		

[a] Volume for *T. mertensiana* calculated using coefficients for *T. heterophylla*
[b] Dead *Tsuga* could not be reliably identified to species

Fig. 1a,b Age structure (percentage of trees by decade of origin) for live trees ≥4.0 cm DBH present in four 0.25 ha plots at Mt. Cain, Vancouver Island: plots 1 and 2 (**a**), plots 3 and 4 (**b**). Sample sizes are 639 for plots 1 and 2, and 697 for plots 3 and 4. Three trees that predate 1000 AD are not included
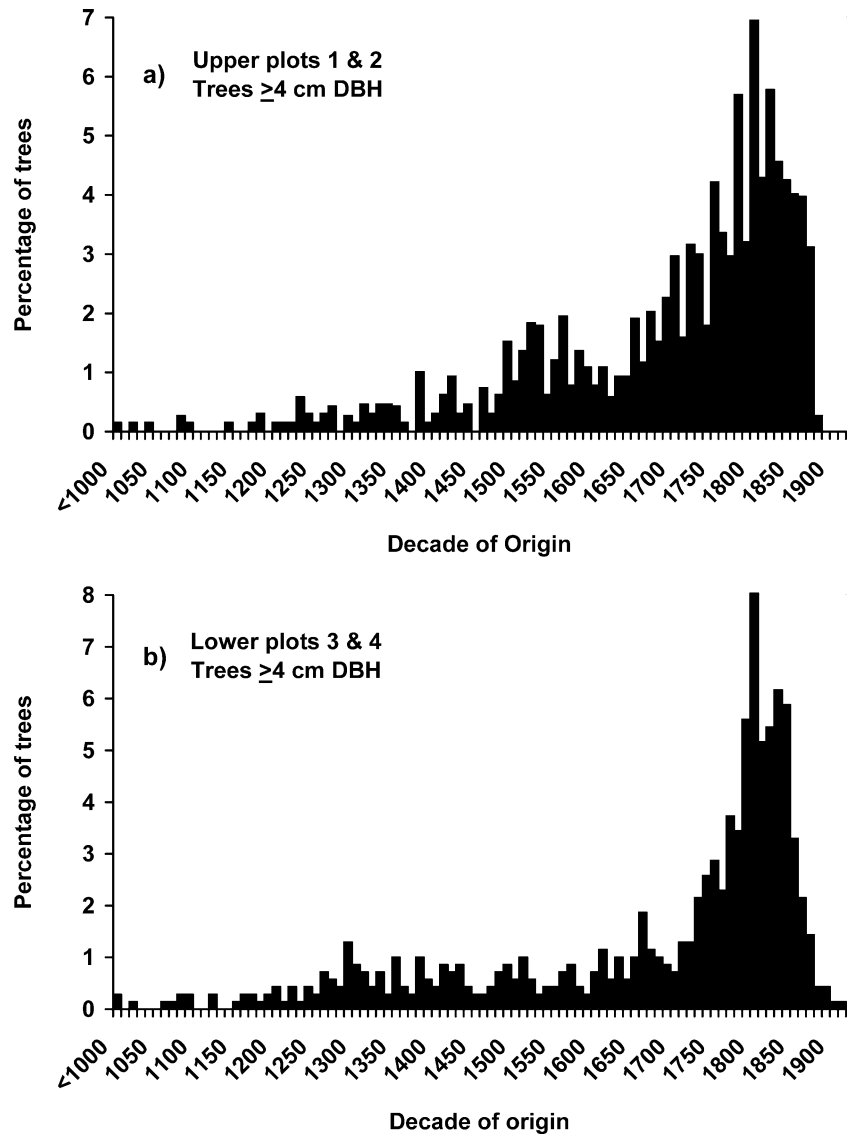
almost all decades after 1720 at least one individual successfully survived to the present. However, the number of *C. nootkatensis* in any given decade was low and many individuals could not be aged because of internal basal rot; thus the distribution needs to be interpreted cautiously.

Size-age relationships

Much of the variation in age could be related to size (diameter) for all four species. The power function gave the best fit for *Chamaecyparis* age-diameter data whereas various three-parameter, saturating functions fit *Abies* and the *Tsuga* species (Fig. 3). The *Tsuga* species fit two closely related functions: the logistic (*T. mertensiana*) and the Chapman–Richard's (*T. heterophylla*). The Gompertz function, which is similar to the logistic function but not symmetrical about the point of inflection, provided the best fit for *Abies* age-diameter data. Growth of *A. amabilis* and *T. mertensiana* in the upper and lower plot groups

differed significantly, whereas *C. nootkatensis* and *T. heterophylla* growth was not significantly different among plots. *Abies amabilis* and *T. mertensiana* had on average a larger diameter at a given age in plots 1+2 than in plots 3 +4 (Fig. 3). Diameter growth *of A. amabilis* and *T. mertensiana* in plots 1+2 began to asymptote at ca. 570 and 840 years of age respectively, whereas this did not happen in plots 3+4 until ca. 680 and 1,010 years respectively. Diameter growth in *T. heterophylla* reached an asymptote at ca. 630 years of age whereas in *C. nootkatensis* diameter continued to increase with increasing age.

Although age and diameter were always significantly related, considerable range in diameter occurred at a given age for all four species and thus the size-age relationship for an individual tree could deviate from the predicted relationship. For example, *T. heterophylla* could exceed 60 cm DBH at 300 years, but could also be less than 30 cm DBH at 700 years (Fig. 3f). Because the shade tolerance of *A. amabilis* and *T. heterophylla* is greater than that of *T.*

mertensiana and *C. nootkatensis*, the range of age at a given diameter tended to be larger (Fig. 3). The spread of possible ages for *C. nootkatensis*, however, might be as much as 600 years at the same diameter. Height–age relationships had more scatter (r^2 ranging from 0.54 to 0.87) than diameter–age relationships. The power function provided the best fit for *A. amabilis* and *T. mertensiana* and the logistic function for *C. nootkatensis* and *T. heterophylla*. Contrary to the diameter relationship, height–age relationships for *A. amabilis* showed no significant differences among plots whereas the differences were upheld for *T. mertensiana* (data not shown).

Growth rates of all species were extremely slow. Regressions indicated that for all species-plot group combinations, trees averaged <30 cm DBH at 400 years of age. *T. mertensiana* in plots 1+2 had the fastest average growth, but *T. heterophylla*, which reached 30 cm DBH in 150 years, demonstrated the fastest potential growth (Fig. 3).

Time to reach canopy height (≥20 m) could be as little as 160 years but ranged to >700 years. Many trees had spent 3 or 4 centuries in the canopy at time of cutting. The tree with the longest canopy residence time was a live *C. nootkatensis*, which established ca. 1030 and probably attained the canopy ca. 1330 (based on time at which basal diameter was ≥30 cm). It was still vigorous at time of cutting, 670 years later.

Early growth

The distribution of growth rates 30 years from the pith indicated that very slow early growth is typical for all four species in this forest. The mean radial growth rate was very similar for all species, 0.182–0.187 mm per year for the first 30 years, except for *C. nootkatensis*, which averaged 0.213 mm/year. Trees in the canopy averaged somewhat faster early radial growth (0.253 mm/year for 30 years; $n=375$) than the population of all trees ≥4 cm DBH (0.186 mm/year; $n=1,357$). Radial growth rates over the 30-year period from the pith differed little from the 50-year period, negating the assumption that growth of surviving trees would increase with time even if early growth was slow.

We selected the growth rate of the 90th percentile over the first 30 years, which was ≥0.3 mm/year, as our criterion for rapid early growth. Early growth in the stand was much slower than in *Picea Abies* forest, where we had used an average ring-width increment of 0.8 mm/year (Antos and Parish 2002b)—a criterion that would have been inappropriate here because only four trees would have been classified as showing rapid early growth. The percentage of trees with rapid early growth was similar among species (9.8–14.7%), but was much higher in plots 1 and 2 (16.6%) than in plots 3 and 4 (4.9%). In all plots, trees with early rapid growth, on average, maintained their advantage and their growth rate (measured as years taken to achieve the 1999 DBH) was significantly higher ($F=166.6$, $P<0.0001$) than for the general population. In plots 1 and 2, trees with rapid early growth formed ca. 50% of the current canopy whereas in plots 3 and 4, it was ca. 10%.

The timing of rapid early growth among 50-year periods provided evidence for small-scale disturbance in the stand (Fig. 4). Although trees with rapid early growth occurred in almost all 50-year periods in plots 1+2, there was a pronounced peak in the distribution centred on the first half of the 1500s (Fig. 4a). At the decade scale, the pith of these trees dated from 1490 to 1560, but showed no pattern within this period. Thus these trees could have established following a single disturbance in the late 1400s, the date of which has been obscured by the method of disc cutting, or from a series of local disturbances spread over 70 years. Evidence from growth releases presented in the next section suggests more than one event. The distribution of rapid early growth in plots 3+4 (Fig. 4b) suggests a small event in the first half of the 1800s, but tree establishment was not concentrated in any decade. Small, local disturbances, therefore, appeared to be responsible for episodes of rapid early growth, but these did not extend to the entire stand.

Timing of release

Growth release was common in all four plots in the stand. We identified release in 549 (38.5%) of the 1,425 trees with sufficient ring information to examine. Fewer releases occurred in plots 1+2 (32.1% of trees) than in plots 3+4 (44.1%). Most released trees showed only one growth release but, 17.1% of trees with release had two events, and 6.0% had three or more releases.

Although growth releases occurred throughout the history of the stand, some periods had a high percentage of releases (Fig. 5). These periods differed between the two plot groups. In plots 1+2 there was a peak in release in the first half of the 1500s (Fig. 5a). This peak was centred in the 1520s with about half of these releases in that decade, primarily in plot 1. Other periods of heightened release occurred in the late 1400s, late 1700s and early 1900s. In plots 3 and 4, there were minor peaks in the first half of the 1500s and in the last half of the 1600s. A large peak (Fig. 5b) was centred at ca. 1930.

Scars were infrequent; 166 basal discs had a total of 209 scars. Only 18 scars were found before the mid-1700s, which suggests that damaged trees might not survive as well as undamaged trees. Incidental corroboration of this was the presence of internal rot associated with some scars. About 7% of scars were near the pith and almost invariably small; these probably resulted from small mammal damage. A small number of scars, however, was associated with nearby release episodes or trees showing early rapid growth.

Plots 1+2
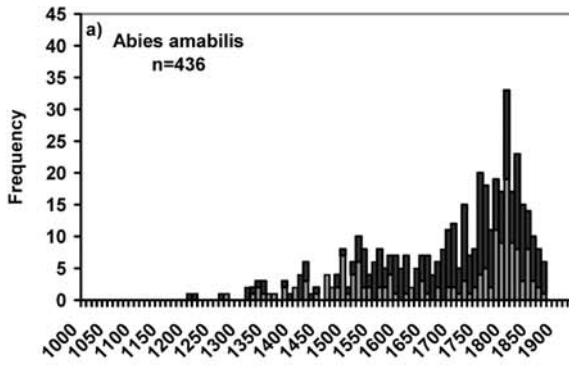
Plots 3+4
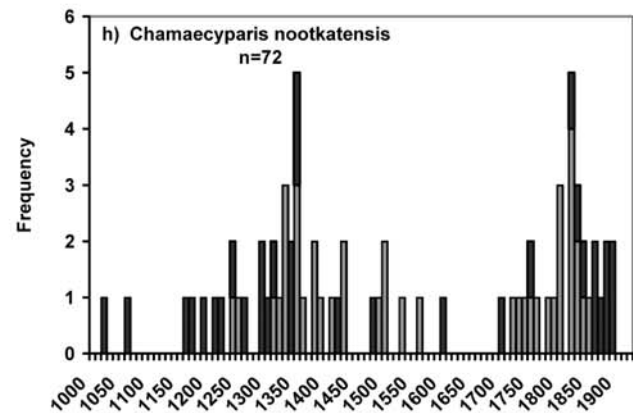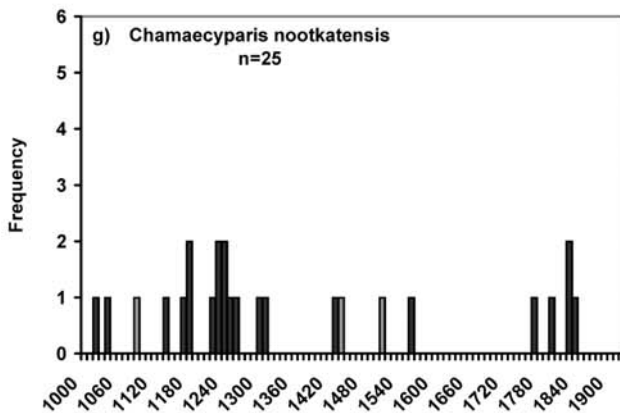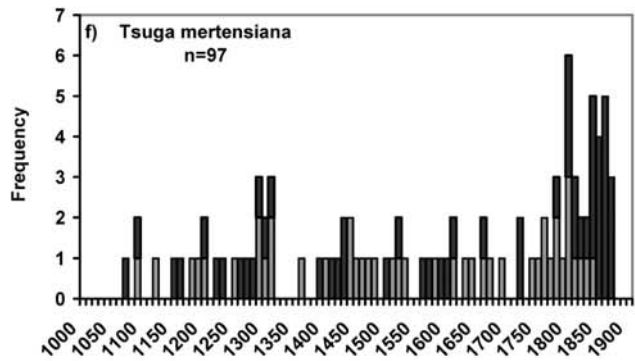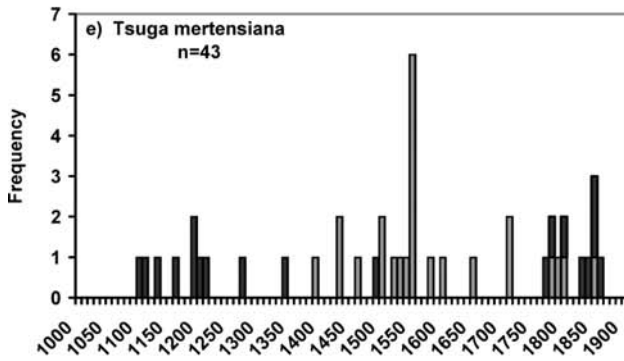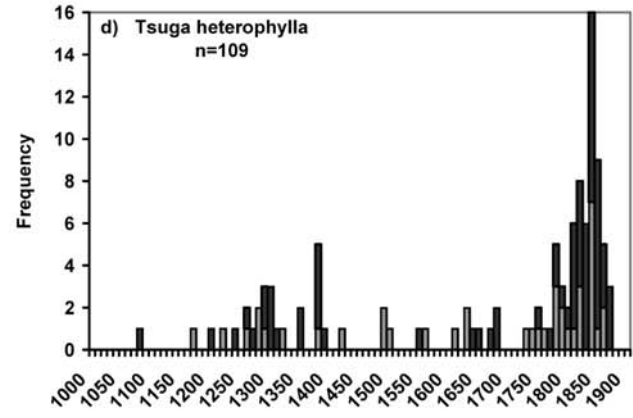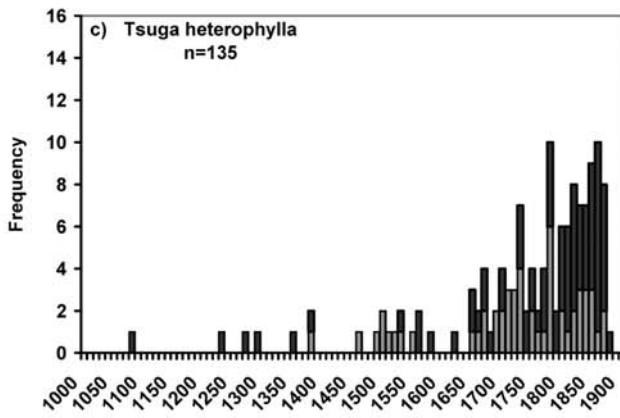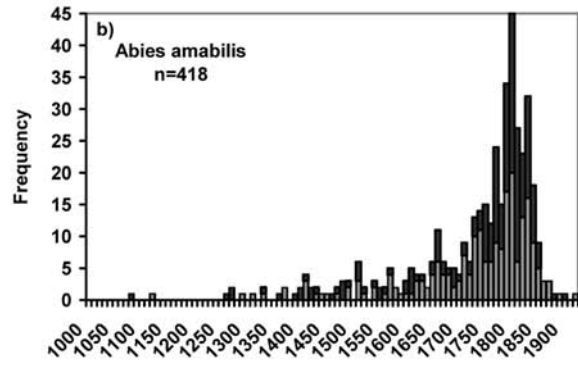
Decade of origin

Decade of origin

Fig. 2a–h Age structure (number of trees by decade of origin) by species for live trees ≥4.0 cm DBH present in four 0.25 ha plots at Mt. Cain, Vancouver Island: *Abies amabilis* in **a** plots 1+2, **b** plots 3 +4; *T. heterophylla* in **c** plots 1+2, **d** plots 3+4; *T. mertensiana* in **e** plots 1+2, **f** plots 3+4; and *C. nootkatensis* in **g** plots 1+2, and **h** plots 3+4. Three trees that predate 1000 AD were not included: two *C. nootkatensis* (1,371 and 1,452 years old) and one *T. mertensiana* (1,053 years old). *Grey* indicates plot 1 or 3 and *black* plot 2 or 4. Note the difference in scales on the *y*-axis

Timing of disturbance

Examination of the stand maps (Fig. 6) indicated that aggregations of trees showing release and rapid early growth occurred frequently in the same time period and often throughout a plot. Although many trees released in isolation from their neighbours (data not shown) all but four trees with rapid early growth were associated with
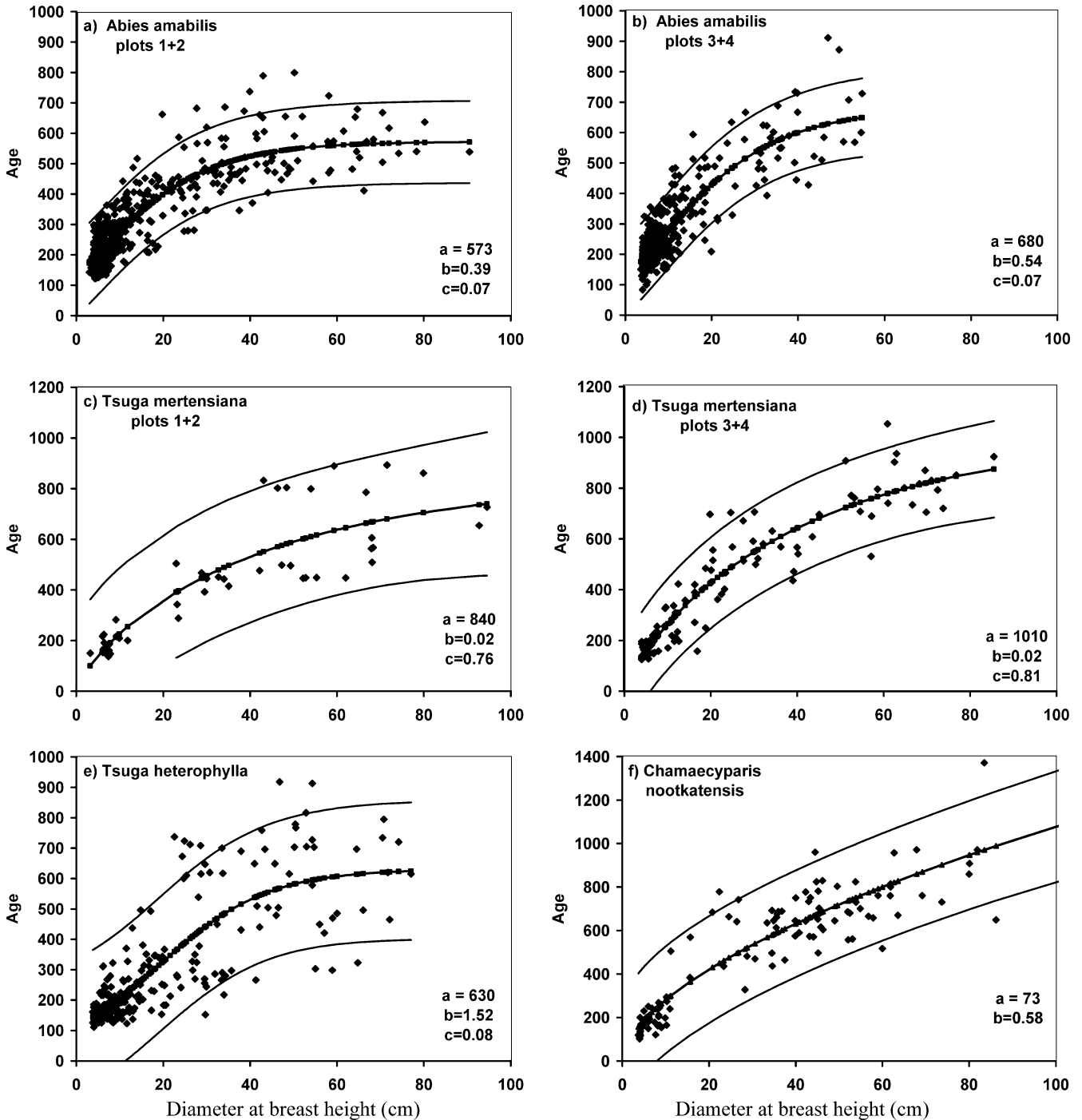

Fig. 3a–f Diameter versus age for live trees ≥4.0 cm DBH by species and plot group at Mt. Cain, Vancouver Island: *A. amabilis* in **a** plots 1+2, and **b** plots 3+4, *T. mertensiana* in **c** plots 1+2, and **d** plots 3+4, *T. heterophylla* in **e** all plots and *C. nootkatensis* in **f** all plots. Parameters for appropriate equations are included on the graph but see text for discussion. *Heavy lines* represent predicted values and *light lines* bound the 95% confidence interval. Note the difference in scales on the *y*-axis
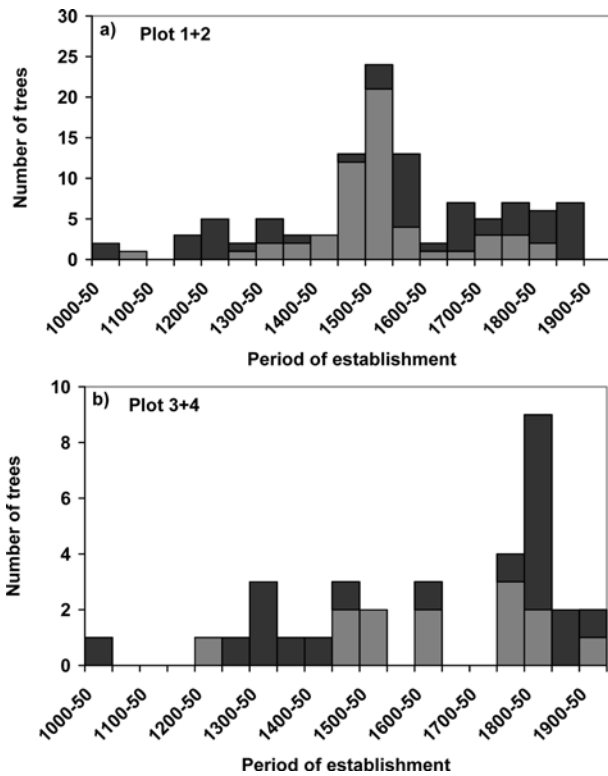
Fig. 4a,b Timing of establishment by 50-year period for trees with rapid early growth (average radial increment >0.3 mm/year over 30 years from the pith) in plots 1 and 2 (**a**), and plots 3 and 4 at Mt. Cain (**b**), Vancouver Island. Values are for 109 trees in plots 1 and 2, and 34 trees in plots 3 and 4. *Grey* indicates plot 1 or 3 and *black* plot 2 or 4
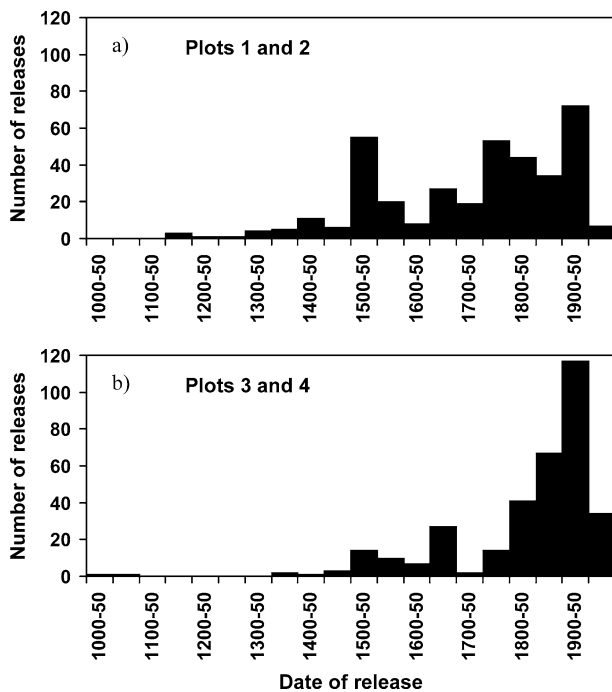

Fig. 5a,b Timing of releases by 50-year period for trees in **a** plots 1 and 2, and **b** plots 3 and 4 at Mt. Cain, Vancouver Island. Values are for 370 releases in plots 1 and 2, and 341 releases in plots 3 and 4

other such trees, or with trees showing release. In plot 1 (Fig. 6a), there appeared to be one or two periods leading to release and rapid early growth in patches ca. 100–1,000 m^2 about 500 years ago, in both the late 1490s and 1520s. Episodes of release and rapid early growth were rare in the 1600s but occurred sporadically in 50–100 m^2 patches over the last three centuries. In contrast, plot 2 (Fig. 6b) had very little disturbance in the 1500s except for a 50 m^2 patch, on the western edge and directly east of plot 1. Much of the release and rapid early growth occurred in 25–30 m^2 patches distributed over four centuries. In the two lower plots, there was little evidence of a disturbance in the 1500s. In plot 3 (Fig. 6c) there was one patch ca. 50 m^2 from the 1520s and three patches from the mid-1500s. Only one patch was attributed to an event in the 1700s but several small patches of released trees dated from the 1800s and 1900s. Disturbance in plot 4 was dominated by events in the 1900s (Fig. 6d). Near the plot centre, two downed trees (ca. 1930) produced an extensive area in which subcanopy trees released. This area of the plot had overlapping events in the 1600s, 1700s and 1800s. Other patches of released trees occurred throughout the plot over the last four centuries but few were closely associated with fallen logs.

Dead trees and logs

Dead standing trees comprised a small proportion of stand volume (Table 1) and 9.2% of stems ≥4.0 cm DBH in the stand (Fig. 6). The percentage of dead stems was higher in plots 1 and 2 (15.8 and 10.9%) than in plots 3 and 4 (both 5.9%) although volume was similar (45.8 m^3 in plots 1+2 and 42.1 m^3 in plots 3+4). Many of the standing dead trees were snags with broken tops. Assuming that snags >23 cm DBH had been canopy trees, about 35% of standing dead trees in plots 1 and 2 and 58% in plots 3 and 4 had achieved the canopy prior to death. In subplots, 4.2% of small stems (≥1.3 m tall but <4.0 cm DBH) were dead, which may reflect more rapid decay and falling of small stems. Absence of bark on 22% of the snags made field identification to genus impossible. Among the dead stems identified, 60% were *A. amabilis*, 22% were *Tsuga* spp., and 18% were *C. nootkatensis*. Among those trees that we were able to cross-date to time of death, the maximum time standing was 157 years for *C. nootkatensis*, 49 years for *A. amabilis*, and 27 years for *T. mertensiana*. Numerous compounds enhance resistance to decay in *C. nootkatensis*, which suggests that these snags could remain standing for decades or centuries.

Very few dead canopy trees had complete pith to bark profiles. Among those that did, canopy residence times were estimated as the time spent with basal diameters ≥30 cm, which ranged from 150 to 420 years.

Logs were abundant in the stand but 77% lacked bark and could not be identified in the field. Logs exhibited no clear spatial pattern and were distributed throughout the plots (Fig. 6). There was no consistent directional orientation, which would be expected if a major wind-

Fig. 6a–d Stem maps of four plots each 50 m ×50 m at Mt. Cain, Vancouver Island, **a** plot 1, **b** plot 2, **c** plot 3, and **d** plot 4. Live stems are identified by species: *A. amabilis*, *ABAM*; *T. mertensiana*, *TSME*; *T. hetero-phylla*, *TSHE*; *C. nootkatensis*, *CHNO*. Snags are indicated by *hollow circles* and logs by *tapered lines*. Stems are plotted two-times larger than scale: logs are shown in position to scale. Lines enclose groups of trees with similar timing of release or rapid early growth. The timing of these events is indicated by alphanumeric labels such that E, M and L indicate the early, mid and late part of the century and 14–19 indicate 1400s, 1500s, etc. to 1900s
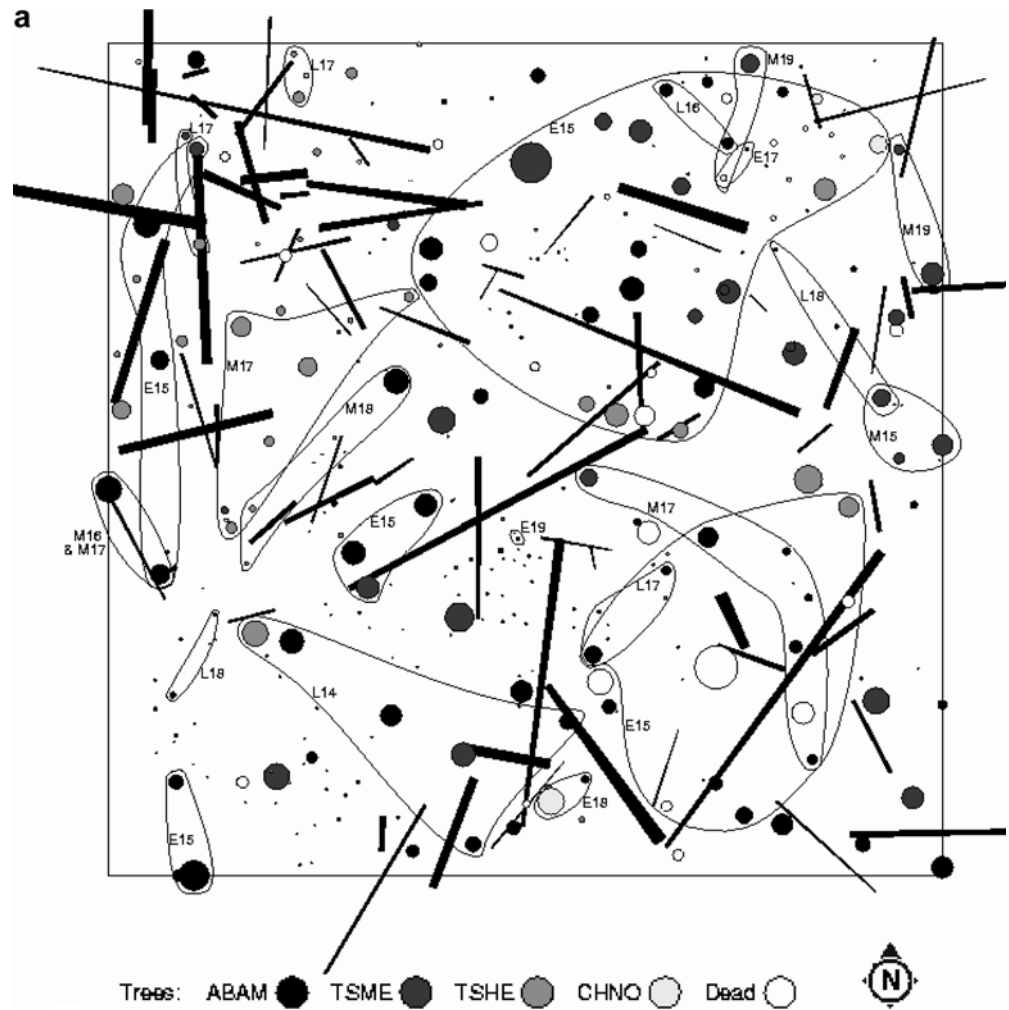
storm was an important factor. A total of 321 logs was measured, and these spanned the full range of sizes represented by standing trees. Approximately 40% (plots 1 +2) to 50% (plots 3+4) of logs had a sufficient base diameter (>30 cm) to have been canopy trees prior to death. Volume was similar in the two plot groups (227 m³/ha in plots 1+2, and 229 m³/ha in plots 3+4). The volume was fairly equitably distributed among decay class (data not shown), except for class 1 (recent logs) which had less volume than the other classes.

Discussion

Life in the slow lane—very old trees and slow growth

Although very old trees occur in a variety of forest types, the forest at Mt. Cain was exceptional in that all four species attained great age, in excess of 900 years, and that many very old trees were still small. All the tree species have much greater potential growth rates than typically exhibited in the stand; tree size was not exceptional and was not indicative of their extreme age. These small, old trees, some >400 years old in the understory, had growth rates more reminiscent of those in harsh, open habitats where trees are often contorted in shape, than of a closed-canopy forest with mainly symmetrical trees. Thus the structure of the forest alone did not indicate the great age of many of the trees.

A primary factor contributing to very old trees was that growth was slow for the majority of trees in the stand when they were small. An average tree in the stand had a basal diameter ca. 1 cm after 30 years growth. Moreover, growth of trees at the Mt. Cain stand often tended to be chronically slow or erratic over much of their lives; thus trees typically spent unusually long periods, often centuries, in the understory and subcanopy prior to attaining the canopy.

Once reaching the canopy, individuals often remained in that position for centuries. We did not have data to calculate canopy turnover rates directly but the residence time for live trees suggests that it is several centuries. Such very slow canopy turnover is consistent with gap studies in other forests of coastal British Columbia (Lertzman and Krebs 1991; Lertzman 1992; Lertzman et al. 1996) and Alaska (Ott and Juday 2002). In most forest types canopy turnover is more rapid (Denslow 1987; Tanaka and Nakashizuka 1997; Runkle 2000; Lorimer et al. 2001).

Fig. 6a–d (continued)

Tree species: ABAM ● TSME ● TSHE ● CHNO ○ Dead ○   (N)
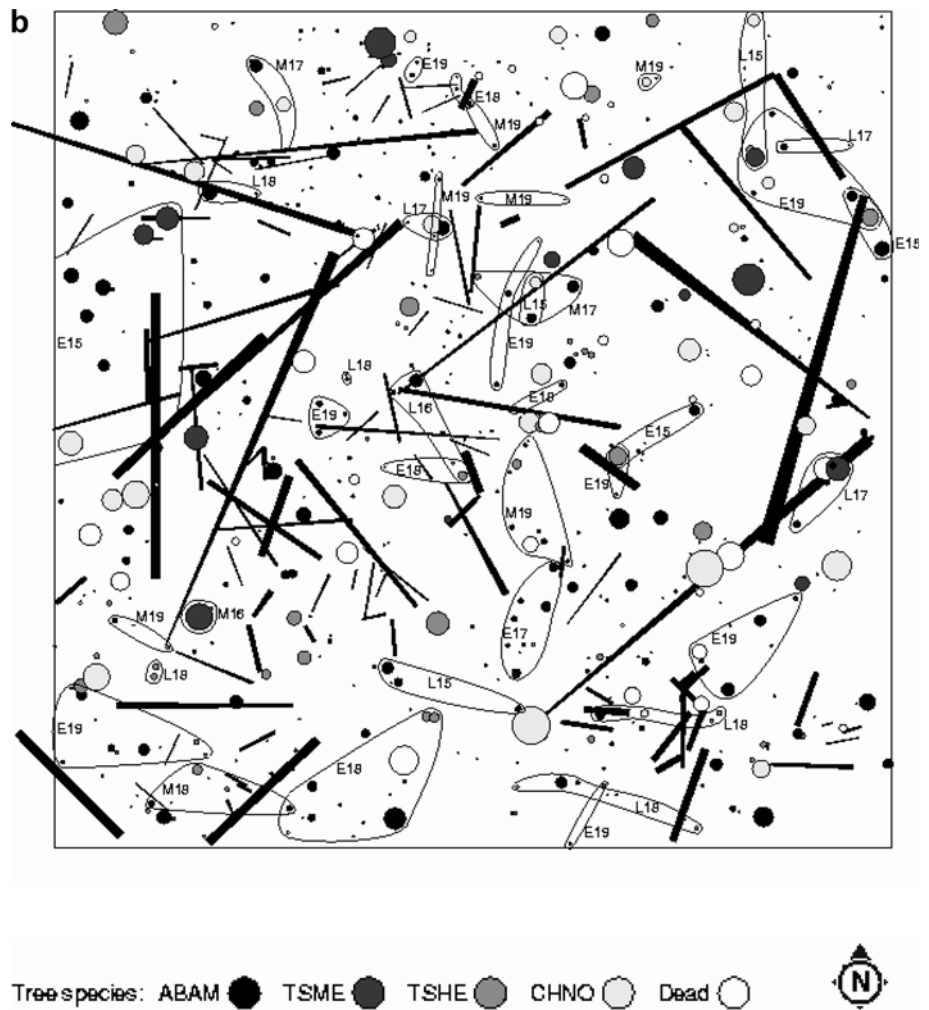
The major factors contributing to the long residence time in the canopy are the great potential age of all the species, and the near absence of major disturbance. Fire intervals are very long and may span thousands of years on wet, low elevation sites in coastal British Columbia (Gavin et al. 2003a, b); the same pattern likely holds for wet, montane sites near the coast. In contrast to many coniferous forests where insects cause major, episodic mortality of mature trees, strongly reducing canopy residence time (Bergeron et al. 1995; Baker and Veblen 1990; Veblen et al. 1991; Parish et al. 1999; Parish and Antos 2002), insect outbreaks appear to be inconsequential in the Mt. Cain area (Otvos et al. 2001). Climate, especially extreme events, may have an important role in small-scale mortality of canopy and subcanopy trees (Vygodskaya et al. 2002). Heavy snow, common at these elevations, may be responsible for considerable local damage through stem breakage.

In closed forests, canopy trees that do not owe their origin to major disturbance would generally be considered competitors in Grime's (1979) classification; however, the trees at Mt. Cain might be better considered stress tolerators. The key features of their life history are persistence in a harsh environment and very slow growth.

They have an impressive ability to tolerate major stresses —low light in the understory, short snow-free periods, and cool, wet summers. Their ability to grow slowly and to persist in the face of adversity is similar to that of obvious stress tolerators, such as desert or arctic shrubs, rather than to most forest trees.

Patch dynamics

Reconstruction of the history of the stand at Mt. Cain provided no evidence of stand-level disturbance. Given the age range of the trees, major disturbance would have left a signal adequate for detection during at least the last 700 years. It seems likely that fire has been absent for 1,500 years or more. Moreover, stand-scale partial disturbances have been infrequent or rare. However, events at scales of single to several trees have contributed to release and establishment (e.g., the early 1500s in plot 1). We conclude that disturbances in the stand have been highly localised. Forests that apparently escape large-scale, intense disturbance for long periods (exceeding the life-span of individual trees) occur in various habitats, including cold coniferous forests (Antos and Parish 2002a;

Fig. 6a–d (continued)

Tree species: ABAM ● TSME ● TSHE ● CHNO ○ Dead ○
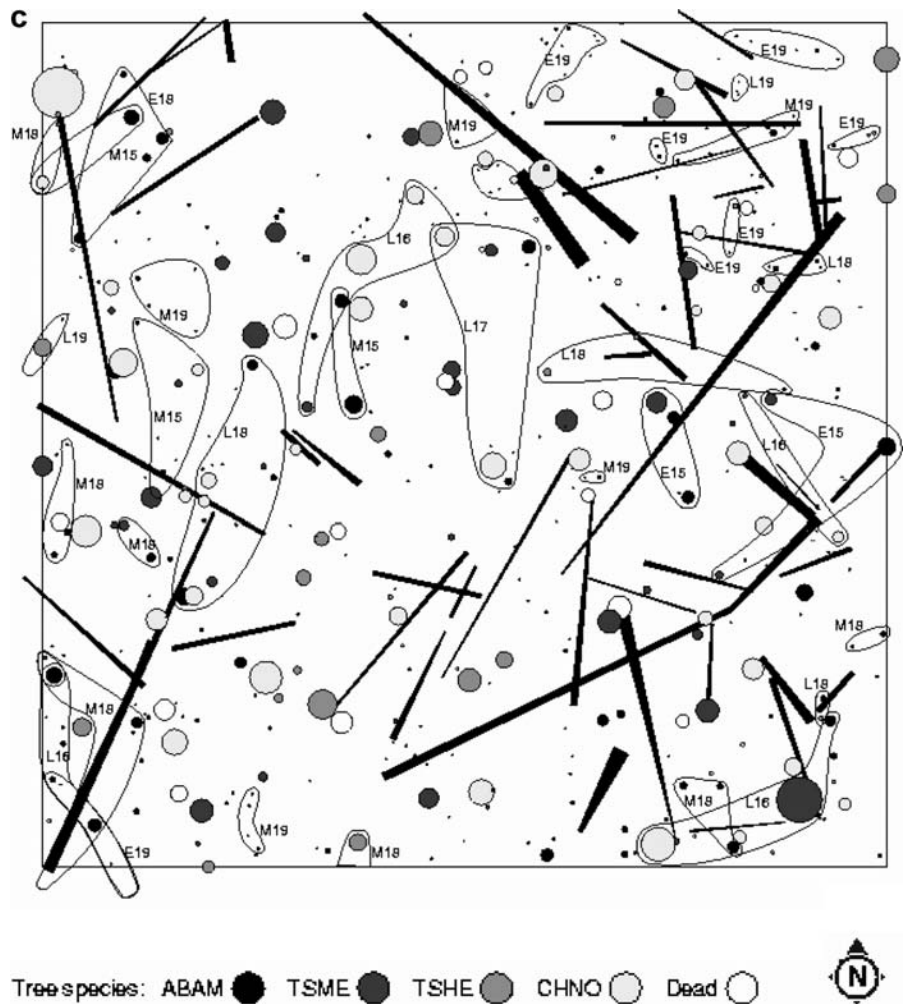
Vygodskaya et al. 2002), temperate deciduous forests (Bormann and Likens 1979; Runkle 1990), and tropical rain forests (Richards 1952; Whitmore 1984).

Small-scale gap processes dominated dynamics in the Mt. Cain stand. Mortality of individual trees and small groups of trees controlled the dynamics. Synchronisation of tree mortality was limited, both spatially and temporally. Thus the stand, to a considerable extent, can be considered a shifting mosaic with a small grain size, primarily the size of individual trees or a few adjacent trees. Patch dynamics has been shown to be the predominant form of dynamics in some forests (see references in the Introduction). However, along the continuum of disturbance sizes, from forests where major disturbance is pivotal to those structured by small-scale patch dynamics, the forest at Mt. Cain clearly approaches one end point.

Stability of species composition

The lack of even low-intensity, large-scale disturbances indicates that the species composition could be near equilibrium in the stand, but the temporal scale of stability varies among species. The age structure of the tree species indicated two very different strategies of persistence. *A. amabilis* and *T. heterophylla* represented a strategy of continuous replacement, exemplified by the classic J-shaped curve with abundant trees in young (<200 years) age classes. *C. nootkatensis* and *T. mertensiana*, on the other hand, had an age structure demonstrating episodic establishment at 500–600 year intervals and great longevity. The oldest trees as well as some of the largest, from which we could not get ages because of interior rot, were *C. nootkatensis* and *T. mertensiana*. Because these species are less shade tolerant than the other two species in the stand (Minore 1979; Burns and Honkala 1990), we expect a gradual decline in their abundance unless a disturbance opens the canopy. Seedling establishment does not appear to be the most critical stage because both species have large numbers of seedlings in the stand (J. A. Antos et al., unpublished data). Thus gap formation does not appear necessary for seedling establishment, but large (multiple tree) gaps appear critical to support growth into the canopy for both *C. nootkatensis* (Antos and Zobel 1986) and *T. mertensiana* (Seidel and Cooley 1974; Seidel 1985). Layering is also common in *C. nootkatensis* in the understory (Antos and Zobel 1986), which could further

Fig. 6a–d (continued)

Tree species: ABAM ● TSME ● TSHE ● CHNO ○ Dead ○
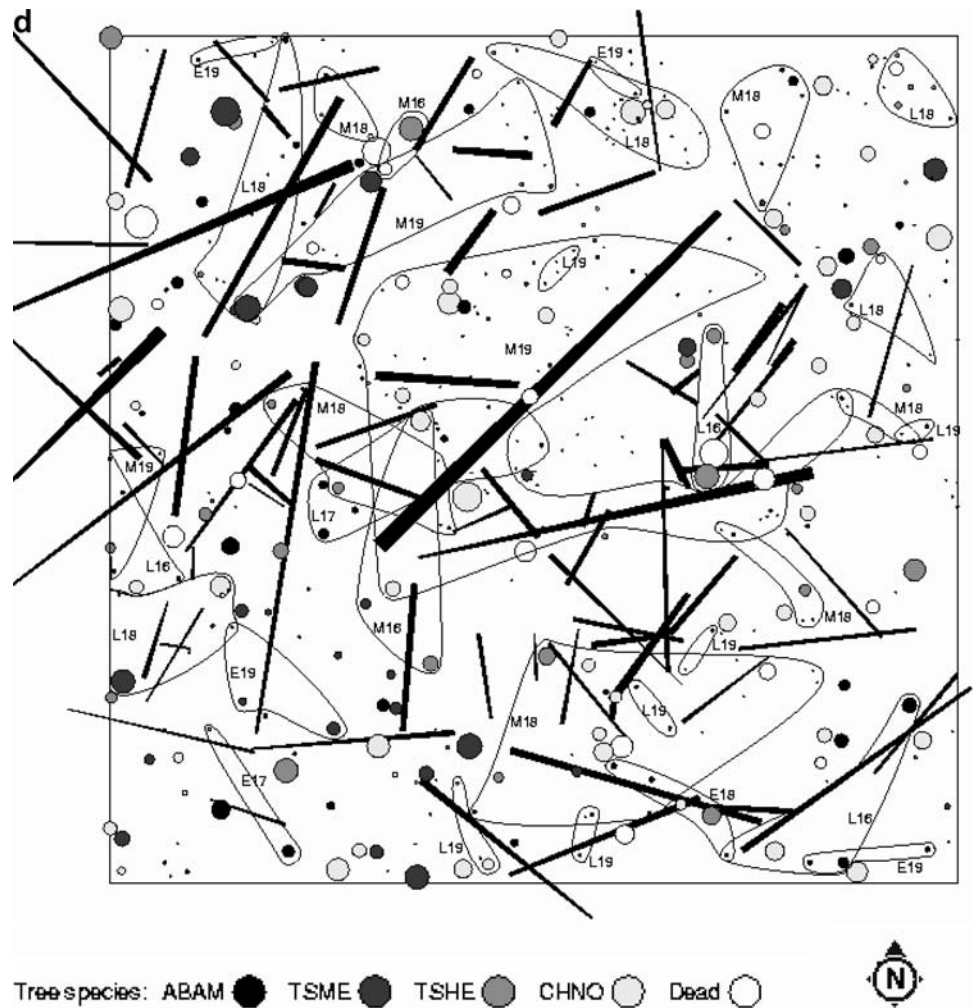
contribute to the presence of understory individuals. In this stand both *T. mertensiana* and *C. nootkatensis* appear to be gap phase species that need multiple-tree gaps to reach the canopy, whereas *A. amabilis* and *T. heterophylla* can attain a canopy position in small (single-tree) gaps. Notwithstanding the above, *C. nootkatensis* had low abundance in plot 1 despite the moderate sized gap (ca. 1,000 m^2) in the early 1500s which supported the early rapid growth and release of all four species. Edaphic or climatic factors in some instances may override the influence of gap size on species abundance.

Gradual changes in composition may be common in forests even after long periods with no major disturbance (e.g., Woods 2000a, b). If all species can establish under closed canopy or small gap conditions, change in relative abundance is likely to be gradual and exclusion of any given species could take a very long time. Given the very slow rates of tree growth and rate of change in the forest that we studied, it is likely that events that altered species composition over 1,000 years ago could still be leaving a signal in the species composition and driving gradual changes. However, disturbance patches large enough to foster effective regeneration of *C. nootkatensis* and *T. mertensiana*, although infrequent, are very likely to occur

within the life-span of these extremely long-lived trees. Thus the stand may be considered to be quite stable, but with long-term oscillations in the species composition.

Dynamics of an ancient snow forest

Slow growth and persistence of individuals are key characteristics of the forest at Mt. Cain. The species thus have characteristics consistent with stress tolerators, and the cool, wet climate with a deep, persistent snowpack appears to be the primary external stress factor that limits growth. Snow can be considered the defining habitat feature of this forest. By analogy with rain forests, such forests could usefully be termed snow forests.

Discrete canopy gaps play an important role in the dynamics of this forest. Trees that established, or released when very small, in gaps maintained a better growth rate than those that grew under a closed canopy. In the upper plots, trees that established in gaps formed a considerable portion of the current canopy. Thus a gap model of dynamics is appropriate for the stand. In contrast, Brett and Klinka (1998) found that a tree-island model, where trees occur in patches because of unfavourable establish-

ment conditions in open areas, was more appropriate at high elevations in the *T. mertensiana* zone, where deep snow strongly limits tree growth.

Discrete canopy gaps, however, do not provide a complete picture of the dynamics. Within a gap growing conditions may vary. At northern latitudes, the north (south-facing) edge receives more solar energy than the south edge. At ca. 50°N latitude, 0.1 ha gaps receive >50% of above canopy light levels only at the north edge, which receives not only more photosynthetically active radiation but also has higher air temperatures which in turn speeds up snow melt compared to the south edge (Spittlehouse et al. 2004). In general, shading effects extend up to one tree height (approximately 30 m) from the south edge; however, openings may ameliorate growing conditions within the forest (Chen et al. 1993). Many trees had a history of generally slow, but variable growth. Minor alterations in the canopy (broken branches, gaps a few trees away, snow sloughing on gap edges) may have been as important in their growth history as opening of the canopy directly above them. Variation in conditions under the canopy may be of major importance to tree growth and differential responses of species, as has been shown in tropical rain forests (Montgomery and Chazdon 2003). A simple dichotomy between gap and non-gap conditions is too simplistic; variations in conditions within gaps and beneath the canopy are also important.

We can summarise the dynamics of this ancient forest as follows. It is structured by a combination of small gap dynamics and processes that occur beneath the canopy. Large disturbances or widespread local disturbances appear to have had little or no influence; however, the mix of small and moderate gaps appears to be responsible for maintaining the abundance of moderately shade-tolerant species. Thus the effects of long-past small disturbance events may still be seen in the forest composition. Major natural disturbance is always possible, but apparently very unlikely in this cool, wet, snowy montane environment. Thus this stand formed a stable ecosystem.

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