Disturbance and Persistence of Sitka Spruce (Picea sitchensis (Bong) Carr.) in Coastal Forests of the Pacific Northwest, North America

Alan H. Taylor

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ALAN H. TAYLOR *Department of Geography, University of Maryland–Baltimore County, Baltimore, Maryland 21228, U.S.A.*

Abstract. Forests dominated by *Picea sitchensis* (Bong) Carr. and *Tsuga heterophylla* (Raf.) Sarg. occupy a narrow coastal strip along the Pacific Northwest coast of North America. *P. sitchensis* is considered seral to *T. heterophylla* but descriptions of groups of *P. sitchensis* saplings and small trees in light gaps created by small canopy disturbances (<0.25 ha) suggest that *P. sitchensis* may persist by gap-phase regeneration after small-scale disturbance. This study combines analyses of the disturbance regime (gap size distribution, gap age distribution, the spatial distribution of gaps, forest turnover time), patterns of tree regeneration and tree growth in gaps to determine if *P. sitchensis* can persist under a small gap disturbance regime. Tree replacement models derived from tree replacement patterns in gaps were used to predict abundances of *P. sitchensis* and *T. heterophylla* in the next generation. Tree replacement models did not predict a decline in *P. sitchensis* abundance in the next generation. Gaps of 800–1000 m^2 appear large enough for *P. sitchensis* to persist in these forests.

Key words. Disturbance, succession, forest dynamics, Pacific Northwest, *Picea sitchensis*.

INTRODUCTION

Natural disturbances are a common feature of forested landscapes that influence the spatial and temporal patterns of species abundance (Veblen & Ashton, 1978; White, 1979; Runkle, 1981; Sousa, 1984). Infrequent catastrophic fire, for example, is considered the most important disturbance affecting the distribution and abundance of some species (e.g. *Pseudotsuga menziesii* (Mirb.) Franco) in the coniferous forests of the Pacific Northwest (Hemstrom & Franklin, 1982). *Pseudotsuga menziesii* requires catastrophic fire to regenerate and persist except as residual trees in old-growth forest (Franklin & Dyrness, 1973). Frequent smaller-scale disturbances undoubtedly influence the composition, structure and community dynamics of coniferous forests in the Pacific Northwest but they have been little studied.

Coniferous forests dominated by *Picea sitchensis* (Bong.) Carr. and *Tsuga heterophylla* (Raf.) Sarg. (referred to below as *Tsuga* and *Picea*, respectively) occupy a narrow coastal strip from near Coos Bay Oregon to Prince William sound in Alaska (Fig. 1) (Ruth & Harris, 1979). The distribution of *Picea*, which defines the range of this forest type, is associated with a mild mesic maritime climate (Fowells, 1965; Franklin & Dyrness, 1973; Ruth & Harris, 1979). *Picea* declines in importance away from the coastal zone and other conifers become major associates of *Tsuga* (Franklin & Dyrness, 1973; Ruth & Harris, 1979).

Throughout most of its range *Picea* is considered seral to *Tsuga*. Catastrophic disturbances such as fire, windthrow, landslides and insect attacks initiate secondary succession. Both species regenerate prolifically after catastrophic disturbance but as stands mature mixed forest is replaced by *Tsuga* (Franklin & Dyrness, 1973; Fonda, 1974; Ruth & Harris, 1979). Some sites deviate from this general pattern. *Picea* population structures in mixed forest on mesic alluvial flats in coastal valleys, and in the salt spray zone indicate that *Picea* will remain codominant with *Tsuga* (Cordes, 1972; Franklin & Dyrness, 1973; Kratz, 1975; Mckee, LaRoi & Franklin, 1982). *Picea* reproduction in mixed forest on typical sites is present, however, suggesting that young *Picea* could replace canopy trees as they die (Hines, 1971; Juday, 1976; Quay, 1982; Greene, 1982; Hemstrom & Logan, 1986). Hines (1971), Juday (1976) and Quay (1982) observed groups of *Picea* saplings and small trees beneath light gaps in the forest canopy in older stands and speculated that *Picea* could persist by gap regeneration in opening produced by death of small group of trees. *Picea* clearly persists at landscape scales by regenerating after catastrophic disturbance but smaller disturbances too may provide an opportunity for *Picea* to regenerate and persist at stand scales.

The objectives of this study were to: (1) identify patterns of regeneration in small (<0.25 ha) canopy opening produced by death of one or a few canopy trees; (2) determine if a disturbance regime characterized by treefall gaps is

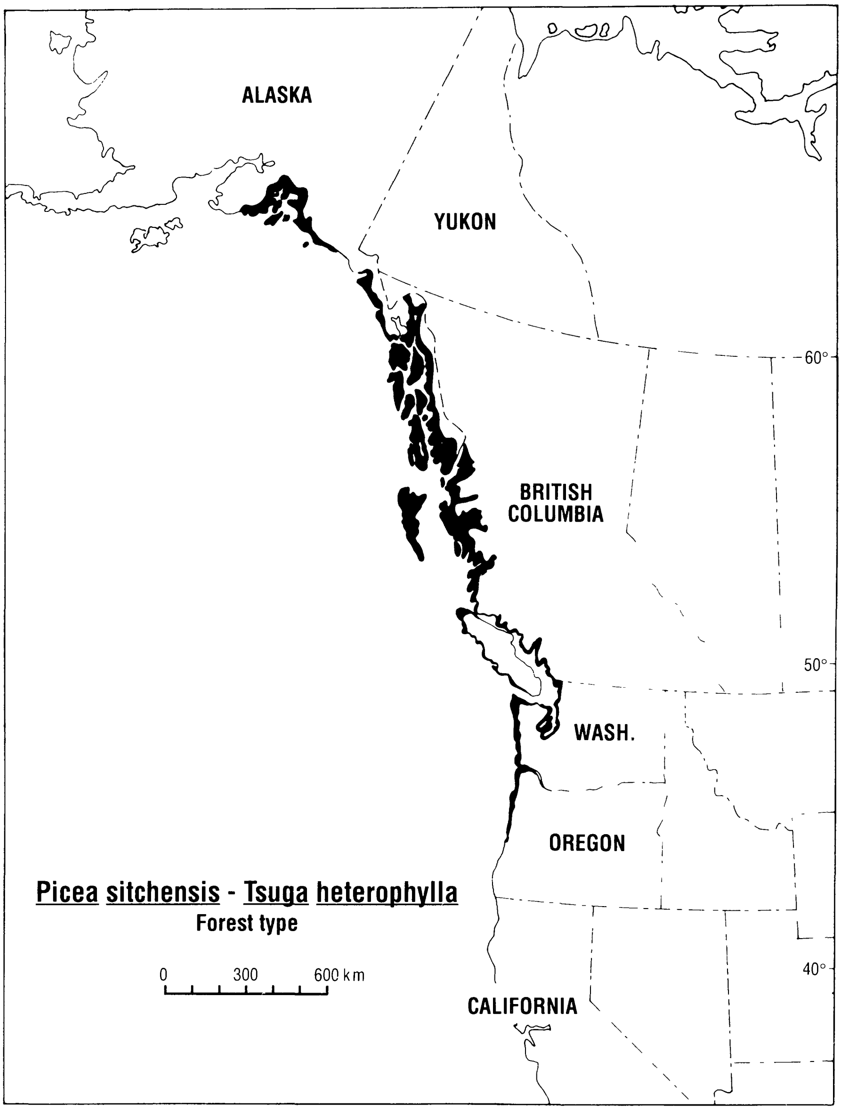

FIG. 1. Distribution of the *Picea sitchensis* (Bong) Carr.–*Tsuga heterophylla* (Raf.) Sarg. forest type in the Pacific Northwest (adapted from Ruth & Harris, 1979).

adequate for *Picea* regeneration; and (3) predict future forest composition from tree replacement patterns in gaps.

Study areas. Forests at two sites, Cascade Head and Cape Lookout, both on the northern Oregon coast, were selected for sampling. These sites were chosen for the following reasons: (1) previous descriptions of their forest structure suggested that *Picea* might persist by gap-phase regeneration; (2) reconnaissance showed gaps to be common at both sites; and (3) stands were undisturbed by recent human activity.

Cascade Head. Sampling was conducted in the Neskowin Crest Research Natural Area (Greene, 1982). Cascade Head is a deeply dissected headland composed primarily of marine tuffaceous sandstone overlying volcanics (Baldwin, 1964; Greene, 1982). Altitudes vary between sea level and 400 m. Soils are strongly acidic, high in nitrogen and organic matter, and vary in texture from silt loam to silty clay loam and are moderately well drained (Grier, 1978). Root systems are shallow and rarely penetrate below 1 m in depth (Harmon, 1986).

The forest canopy is dominated by *Picea* and *Tsuga* and there is a well-developed shrub–forb–moss understorey. Important shrubs include *Rubus spectabilis* Pursh, *Vaccinium parvifolium* Smith, *V. ovalifolium* Smith, *Sambucus racemosa* L. var. *arborescens* (T. & G.) Gray, *Menziesia ferruginea* Smith and *Oplopanax horridum* (J. E. Smith) Miq. The most common forbs are *Oxalis oregana* Nutt. ex T. & G., *Polysticum munitum* (Kaulf.) Presl. and *Montia siberica* (L.) How. (Quay, 1982). Much of the forest established after a human-set conflagration in the mid-nineteenth century (Morris, 1934; Munger, 1944; Greene, 1982; Harcombe, 1986) but there are groups of trees scattered throughout the area that did not burn in this fire.

Cape Lookout. Cape Lookout is a long (4 km) narrow (≈1 km) peninsula that juts into the Pacific Ocean. Parent material consists primarily of basaltic deposits and soils vary in texture from loam to silty clay loam and may exceed 1 m in depth (Quay, 1982). Altitudes vary from sea level to 100 m and overall the topography is less rugged than that at Cascade Head.

Picea–Tsuga forests on Cape Lookout apparently did not originate after the mid-nineteenth century fire that burned forests on Cascade Head. Various stand ages were present of Cape Lookout including young, mature and old-growth suggesting that stand initiating disturbances have been common over the last 200 years. The forest understorey is similar to that at Cascade Head but the shrubs *R. spectabilis* and *Gaultheria shallon* Pursh. and the forbs *Blechnum spicant* (L.) Roth and *Maianthemum dilatatum* (Wood) Nels. & Macbr. are more common (Quay, 1982).

Climate. The climate at both sites is strongly influenced by proximity to the Pacific Ocean. Conditions are mild and moist. Average annual precipitation at a representative station (Otis, Oregon, altitude=60 m) is about 250 cm with little falling between June and August (16 cm). Recorded precipitation in summer at Otis is lower than actual summer precipitation on the headlands. Fog shrouds the headlands most days increasing precipitation by fog drip. Temperatures are mild; the mean annual temperature is 10.3°C and January is the coolest month (mean minimum=2.2°C), the warmest month is July (mean maximum=20.9°C). High velocity winds are common along the Oregon coast and they frequently blow down trees and whole stands (Ruth & Harris, 1979; Quay, 1982, Greene, 1982; Harcombe, 1986).

METHODS

Forest structure, gap vegetation structure, gap size. A total of thirty-seven transects varying in length from 50 to 150 m were established parallel to slope contours to characterize forest composition and sample treefall gaps. Forest composition was estimated by the point centered quarter method (Cottham & Curtis, 1956). Distance (m) and diameter (dbh, cm) of the nearest tree (stems ⩾5.0 cm dbh) were measured in each quarter at 25 m intervals along each transect. Transects were spaced at least 25 m apart to prevent duplicate sampling.

Each treefall gap intersected by a transect was sampled. Gaps were defined as canopy opening above 20–25 m in height; old gaps became indistinguishable from forest when trees reached 20–25 m in height. Gap size was estimated for both expanded gaps and canopy gaps (*sensu* Runkle, 1981) by measuring the length of a long and short axis that divided an opening into four quadrants. Endpoints of axes for expanded gaps extended to the base of adjacent canopy trees. Lengths of axes for canopy gaps were determined by projecting the canopy edges onto the axes used to estimate expanded gaps. Gap area was calculated using axis lengths and assuming an elliptic shape. Dead, downed and snapped trees that made openings were identified to species, measured (dbh), classified by gap type (i.e. dead standing, uprooted, snapped stem), and their direction of fall determined.

All trees in a gap quadrant were measured (dbh) and saplings (⩾1.4 m tall <5.0 cm dbh) and seedlings (0.5–1.4 m tall) were counted. Site of establishment (e.g. logs, mineral soil) of each seedling, sapling or tree were recorded. Additional detail on rooting substrates were obtained by classifying each log by decomposition class (*sensu* Fogel, Ogawas & Trappe, 1972). The tallest tree (>5.0 cm dbh) in a quadrant was designated as the successor tree, or tree most likely to fill the gap quadrant (*sensu* Barden, 1981). No successor tree was designated for a quadrant if no stems were ⩾5.0 cm dbh. Four successor trees could be designated per gap. All trees within a gap were cored 30 cm above the base and their age was estimated by counting annual growth rings.

The relationship between age and dbh of canopy trees was determined using least squares regression for a sample of at least five trees of each species in 10 cm cbh classes beginning at 5.0 cm and ending at 85 cm dbh, at each site.

Gap age, gap expansion, tree growth rates, canopy disturbance. Ages of canopy gaps were estimated in one of two ways: (1) by dating the oldest sudden increase in annual tree ring width (release) found in gap occupants; or (2) by the age of the oldest stem in a gap. The first method assumes that the date of the first release was the time of gap formation while the second method assumes that a stem initially established in a gap. The latter method was used if there were no stems with a growth release.

Average annual radial growth was estimated for each gap occupant by dividing core length by age. Ring widths of subsamples of *Picea* successor trees, and subcanopy *Picea* trees were measured so annual growth rates for these two types of *Picea* could be compared.

The importance of gap expansion as a process was estimated by examining all cores of gap occupants for growth releases. More than one date of release was taken as evidence that a tree adjacent to the original gap died, or was damaged, releasing space-related resources such as light, soil moisture, or mineral nutrients that were used by gap occupants. A growth release was defined as a 200% increase in radial growth over a 5-year period compared to growth in the previous 5 years.

If canopy mortality is a relatively continuous small-scale single-tree process, then the frequency of growth releases in a sample of canopy stems should be approximately constant through time. In contrast, large-scale intermittent mortality such as that caused by windthrow would produce synchronous growth releases in many trees. A frequency distribution of growth releases provides a rough estimate of the magnitude and timing of canopy mortality (Lorimer, 1984). Trees were cored over several hectares in three areas at each site. Dates of releases in each core were recorded and a time frequency distribution of growth releases was prepared for each site. Only trees >70 years old were used for the frequency distribution of releases.

The temporal and spatial distribution of larger-scale patch disturbances (windthrow) were estimated at Cascade Head from a sequence of aerial photographs (1961, 1969, 1984, 1986). Only patch sizes ⩾1000 m^2 could be identified; indiscrete patches with partial windthrow were not mapped.

Tree replacement models. Tree-by-tree replacement in a forest may be modelled as a Markov process using transition probabilities for each species (Horn, 1975). Predicted canopy compositions using tree replacement models vary with species lifespan, and the method used to construct the initial probability matrix (Horn, 1975; Runkle, 1981; White, MacKenzie & Busing, 1985a). For this reason three transition matrices were constructed to determine if their predictions would be similar. Probabilities in the first matrix (method 1) were the relative densities of trees in gaps. Those in the second matrix (method 2) were the relative frequencies of trees in gap quadrants and those in the third matrix (method 3) were the relative frequencies of successor trees in gap quadrants (method 3). Composition of the next forest generation was computed with probabilities weighted by current composition (Runkle, 1981).

RESULTS AND INTERPRETATION

Forest structure

Tsuga stems were about three-fold more abundant than *Picea* but basal area of the two species was about equal, or greater for *Picea* (Table 1). This pattern is typical of *Picea–Tsuga* forests in parts of the Pacific Northwest (Cordes, 1972; Fonda, 1974; Mckee *et al.*, 1982; Hemstrom & Logan, 1986) and for other stands at Cascade Head and Cape Lookout (Juday, 1976; Quay, 1982; Greene, 1982; Harcombe, 1986) but structural variation is great and *Tsuga* basal area can be greater than that of *Picea* (Ruth & Harris, 1979; Alaback, 1982).

Diameter (dbh) and age were significantly correlated ($P<0.001$) for both species at each site (Fig. 2). However, similar-aged *Picea* at Cascade Head that established after the mid-nineteenth century fire have a wide diameter range

TABLE 1. Characteristics of *Picea–Tsuga* forests at Cascade Head and Cape Lookout.

	Cascade Head		Cape Lookout	
	Picea	*Tsuga*	*Picea*	*Tsuga*
Basal area (m^2 ha^{-1})	56.0	51.2	67.9	43.0
Stems (>5.0 cm dbh ha^{-1})	41.0	152.0	62.0	177.0

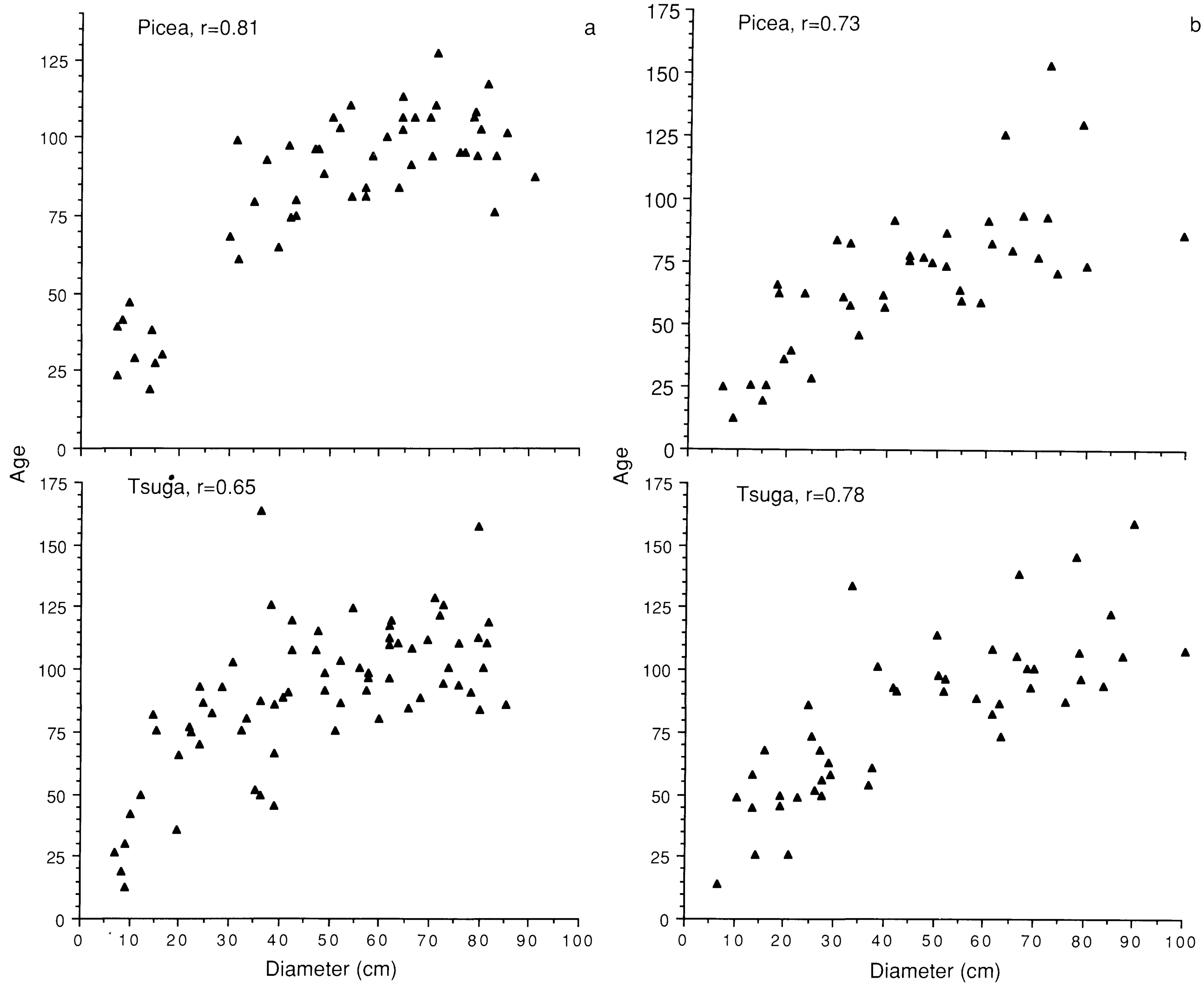

FIG. 2. Plots of age versus diameter for *Picea* and *Tsuga* at Cascade Head (a) and Cape Lookout (b), *r* is the pearson product moment correlation between age and dbh.

so size is not a good predictor of age except for stems <40 cm dbh. Diameter seems a reasonable estimator of age for *Tsuga*, and for *Picea* at Cape Lookout. *Tsuga* were present in all size-classes up to the 140–155 cm dbh class and small stems were abundant indicating that *Tsuga* is continuously regenerating at both sites (Fig. 3a, b). *Picea* at both sites were present in most diameter-classes <200 cm dbh and 5–20 cm dbh trees were abundant indicating that *Picea* has recently established at both sites. However, there were few intermediate sized *Picea* (35–65 cm) suggesting that recruitment of young trees into the subcanopy is infrequent. Overall, *Tsuga* regeneration was abundant and *Tsuga* seems capable of replacing *Picea*. Replacement of *Picea* by *Tsuga* is the typical replacement pattern suggested for this forest type (e.g. Franklin & Dyrness, 1973; Ruth & Harris, 1979; Alaback, 1982). It is unclear from tree diameter distributions whether *Picea* recruitment in these mature/old growth stands is adequate to replace old *Picea* that die.

Gap size distribution

Most gaps intersected by transects were small <400 m^2 (Table 2; Fig. 4). Patch sizes identified on aerial photographs were mostly small too (1000–2000 m^2; Fig. 5). About half of the gaps (46%) were made by single trees,

TABLE 2. Number of seedlings (0.5–1.5 m tall) and saplings (>1.5 m tall and <5.0 cm dbh) in gaps on logs by log decomposition class (Fogel *et al.*, 1973) at Cascade Head and Cape Lookout.

Log decomposition class	Cascade Head		Cape Lookout	
	Picea	*Tsuga*	*Picea*	*Tsuga*
I	22 (12)	9 (0)	–	2 (1)
II	116 (15)	190 (9	15 (9)	54 (11)
III	361 (111)	172 (163)	43 (45)	132 (42)
IV	42 (55)	10 (22)	–	(4)
V	17 (80)	6 (1)	–	–
Not on log	143 (244)	35 (44)	1 (2)	3 (1)

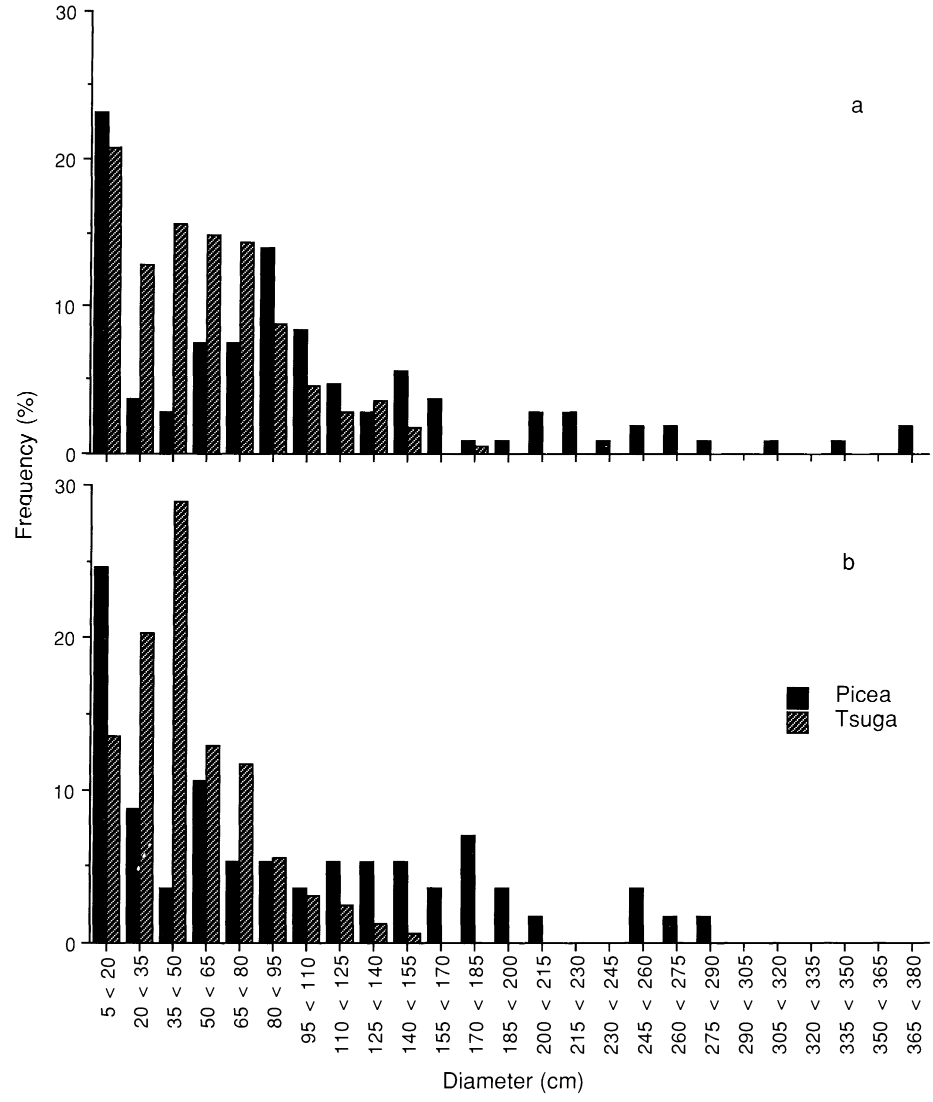

FIG. 3. Size-class distributions of *Picea–Tsuga* forests at Cascade Head (a) and Cape Lookout (b). Size is depicted in 15 cm classes beginning at 5 cm. Sample sizes are 339 and 163 for *Tsuga* and 108 and 57 for *Picea* at Cascade Head and Cape Lookout, respectively.

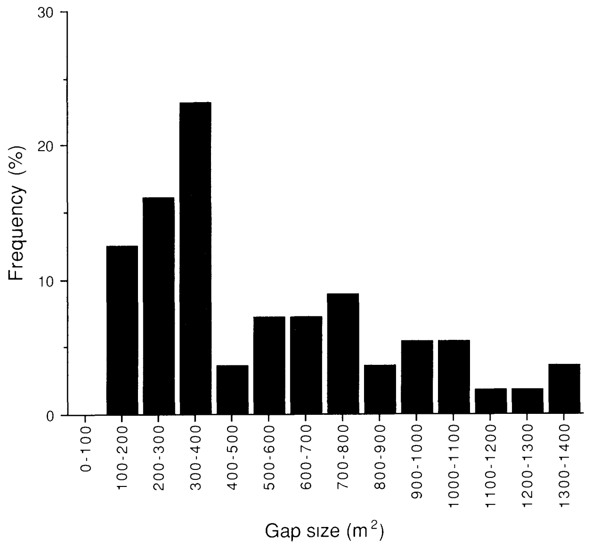

FIG. 4. Size-class distributions of gaps (expanded gaps) intercepted by transects at Cascade Head and Cape Lookout; size is depicted in 100 m² size-classes; n=56.

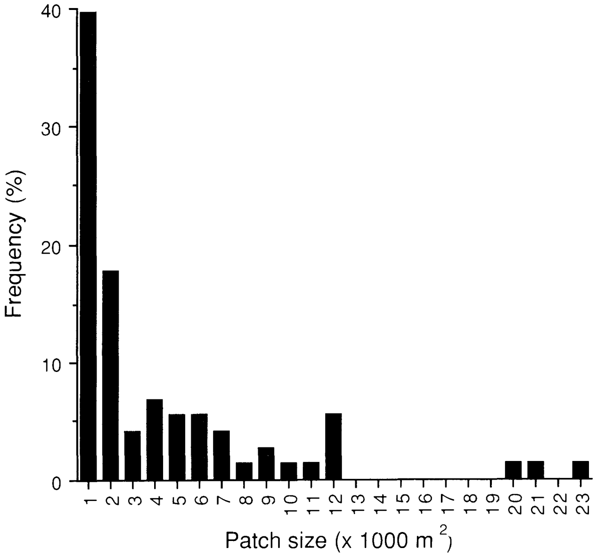

FIG. 5. Size-class distribution of disturbance patches identified from aerial photographs at Cascade Head. Size is depicted in 1000 m² classes beginning with the first class of 0–1000 m²; n=73.

others were multiple tree gaps (54%). Stem snap (84%) was the most common type of gap followed by windthrow (12%) and dead standing (4%). Wind was probably the agent responsible for upturning and snapping trees. *Tsuga* made most gaps (68%). Azimuths of treefalls at Cascade Head were concentrated in the northern quadrant (315–45°, $P<0.001$) and reflect the prevailing southwesterly winter winds. Direction of treefalls at Cape Lookout were random ($P>0.05$).

Percentage of forest in gaps

Fractions of forest land in treefall gaps were similar at both sites. Values were: Cascade Head (24.2.% and 14.2%) and Cape Lookout (29.0% and 18.4%) for expanded gaps and canopy gaps, respectively. Ranges in percentages of forest area in gaps in *Picea–Tsuga* forest were similar to reported values for deciduous forests in the United States (Runkle, 1982) and Japan (Nakashizuka, 1984), and Appalachian conifer forests (White, MacKenzie & Busing, 1985b; Foster & Reiners, 1986).

Gap-age distribution and gap expansion

Gap ages ranged from 11 to 105 years (mean=41) when the date of the oldest release was taken as gap age (Fig. 6). However, 75% of the gaps showed multiple releases, and within that group, the average time between first and last release was 36.1 years (SD=21.9). The high frequency of multiple releases, suggesting gap expansion, indicates that the process is important, as it is in forests elsewhere in the temperate zone (Runkle, 1985; Foster & Reiners, 1986). Gap expansion processes produce complex growth patterns in gap occupants, making it difficult to assign ages to gaps and assess time-specific patterns of forest development in gaps. Nevertheless, the abrupt decline in gaps >60 years of age suggest that it takes about 60 years for most gaps to fill.

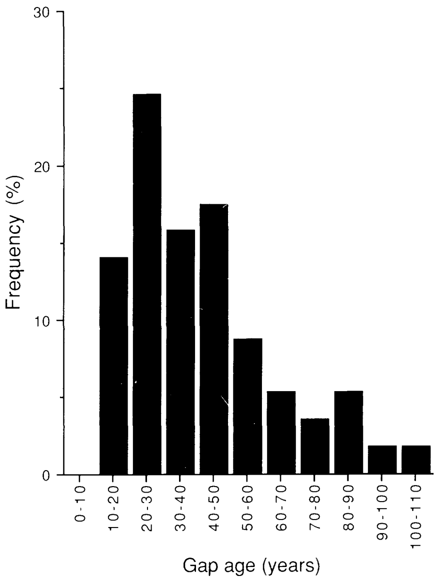

FIG. 6. Age-class distribution of gaps in 10-year classes; n=56.

Regeneration patterns of seedlings and saplings

Seedling and sapling populations of both species were large: *Picea* was more abundant than *Tsuga* at Cascade Head while the opposite pattern occurred in Cape Lookout gaps (Fig. 7; Table 3). Seedling–sapling abundance data from other *Picea–Tsuga* forests generally show *Tsuga* to be more abundant than *Picea* (i.e. Hines, 1971; Quay, 1982; Hemstrom & Logan, 1986; Juday, 1976; Alaback, 1982). Most seedlings (87%) and saplings (68%) had established on logs in various stages of decomposition (Table 3) that cover about 6–14% of the forest floor (Mckee *et al.*, 1982; Harmon *et al.*, 1986). Similar percentages of seedlings and saplings on logs are characteristic of other *Picea–Tsuga*

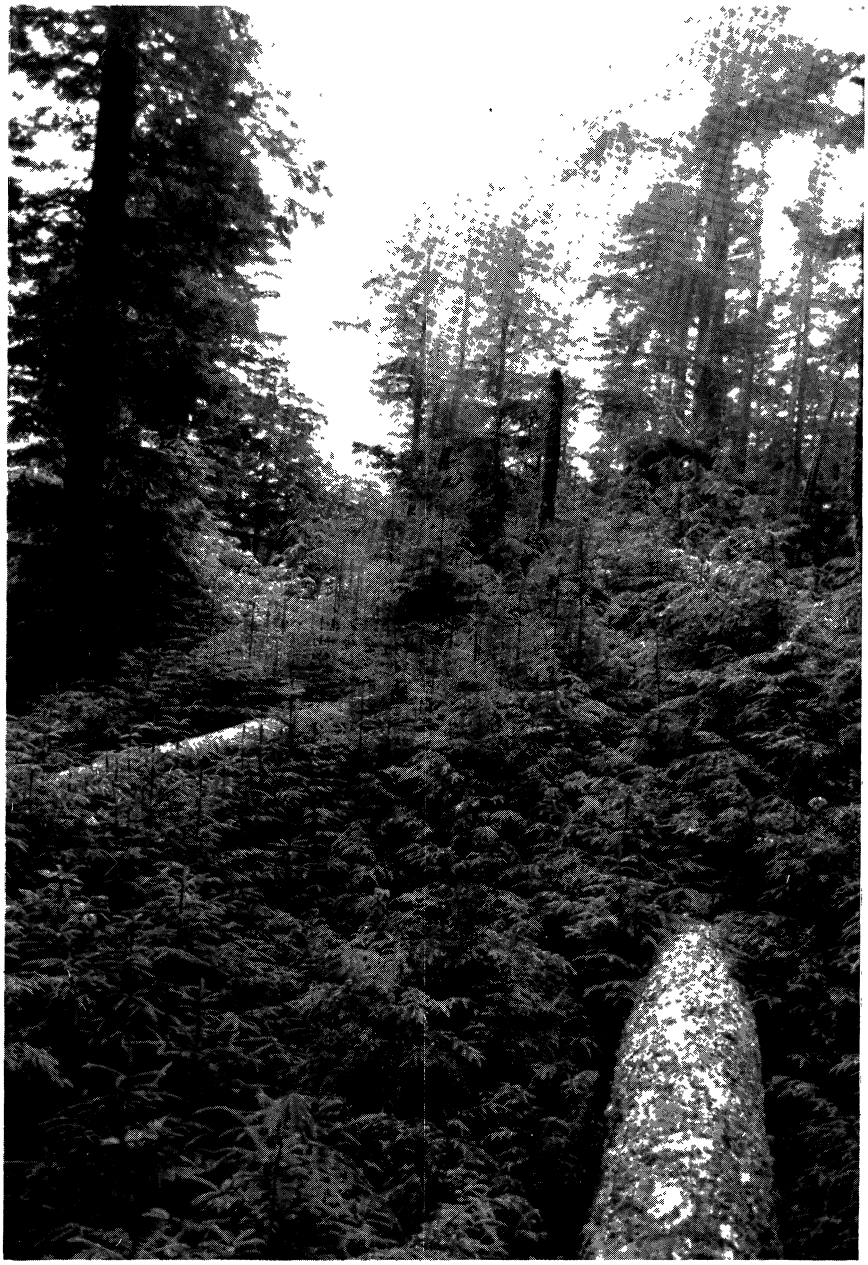

FIG. 7. Patch of *Picea* and *Tsuga* regeneration in a treefall gap of ≈1000 m² at Cascade Head.

TABLE 3. Characteristics of gaps and gap occupants.

	Cascade Head (*n*=35)		Cape Lookout (*n*=21)	
	Median	Range	Median	Range
Expanded gap size (m²)	532	111–1360	346	166–1283
Canopy gap size (m²)	233	12–851	181	16–695
Picea stems (>1.5 m tall gap⁻¹)	7	0–284	2	0–61
Tsuga stems (>1.5 m tall gap⁻¹)	7	0–66	7	2–28
Picea Basal area (cm² gap⁻¹)	21	0–2695	124	0–23325
Tsuga basal area (gap⁻¹)	1046	0–5389	1555	26–11024
Picea age (stems >5.0 cm dbh)	17	6–92	34	9–89
Tsuga age (stems >5.0 cm dbh)	36	8–155	51	7–134

forests (Sharpe, 1956; Juday, 1976; Quay, 1982; Mckee *et al.*, 1982; Harmon, 1986). Except for *Picea* saplings at Cascade Head, seedlings and saplings were found most frequently on decay-class 3 logs ($P<0.001$) which probably represents the most abundant decomposition class on the forest floor (Harmon *et al.*, 1986). The virtual restriction of regeneration to logs appears to be the result of competition between tree seedlings and mosses and forbs on the forest floor, and on older logs, that prevents tree seedling establishment (Harmon, 1986).

Age structure of gap occupants

81% of the gap occupants (trees only) were successfully aged ($n=434$). The age frequency distributions of populations of *Picea* and *Tsuga* in gaps were significantly different at both sites ($P<0.001$) (Fig. 8a, b; Table 2). *Tsuga* were more abundant than *Picea* and they were older. Many *Tsuga* established under a closed canopy remaining suppressed for long periods until gaps opened above them. *Picea* recruitment, in contrast, seems to occur from seedlings that establish in gaps after they form or from a short-lived seedling–sapling pool that turns over frequently due to low light conditions. The presence of *Picea* seedlings, saplings and young trees in gaps and the relatively fewer intermediate-aged *Picea* trees in gaps or in the forest suggested that mortality of young *Picea* is high. Conditions necessary for *Picea* recruitment into the canopy seem to occur intermittently.

An alternative explanation for the *Picea* age structure would be that *Picea* was confined to a few younger larger gaps. *Picea* successor trees were significantly associated ($P<0.01$) with large gaps (>400 m^2), *Tsuga* successor trees were equally abundant in gaps of all sizes. This pattern suggests that large gaps were disproportionately important for *Picea* regeneration, though *Picea* regeneration was not restricted to large gaps. The relationship between gap age and tree age structures was unclear due to the confounding effect of gap expansion on population recruitment into gaps.

Growth rates and gap size

Average annual radial growth of *Picea* and *Tsuga* in gaps was quite variable but *Picea* (mean=2.31 mm year^{-1}) grew significantly ($P<0.01$) faster than *Tsuga* (mean=1.91 mm year^{-1}). Average maximum growth rates in gaps (*Picea*=3.12 mm year^{-1}; *Tsuga*=2.6 mm year^{-1}) followed the same pattern ($P<0.01$). Faster growth by *Picea* than *Tsuga* in gaps is consistent with growth rates measured in clearcuts (Minore, 1979), and in partially open canopy conditions (Harmon, 1987).

Gap size (canopy gap) and growth rates of successor trees of both species were significantly correlated (*Picea* $r_s=0.48$; *Tsuga* $r_s=0.34$, $P<0.01$). Successor trees seem to respond to more open conditions by increasing radial growth. *Picea* successor trees (mean=3.01 mm year^{-1}) grew significantly faster ($P<0.01$) than *Tsuga* successor trees (mean=2.11 mm year^{-1}) and this pattern suggests that *Picea* could exert dominance over *Tsuga* in gaps if both established simultaneously. However, advanced regeneration of *Tsuga* is usually present at the time of gap formation so *Tsuga* fills most gaps. Patterns of growth suppression and release support this interpretation of forest development in gaps.

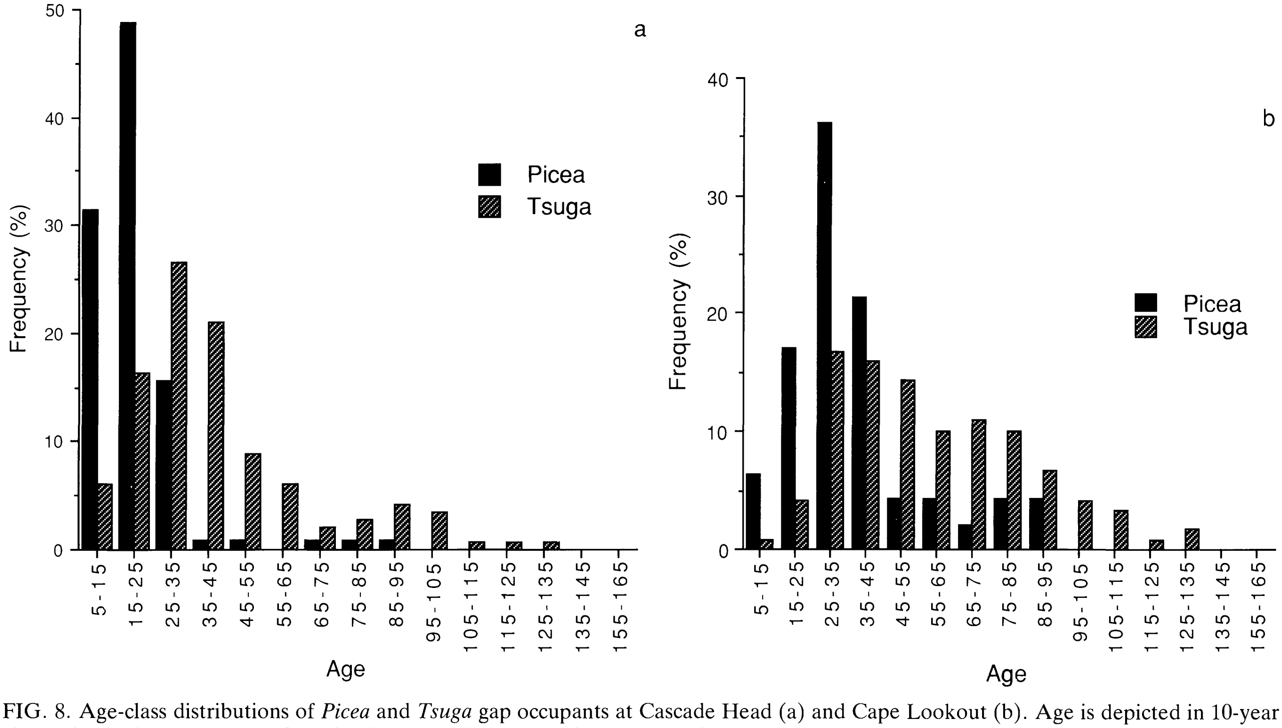

FIG. 8. Age-class distributions of *Picea* and *Tsuga* gap occupants at Cascade Head (a) and Cape Lookout (b). Age is depicted in 10-year classes beginning at 5 years. Sample sizes are 147 and 119 for *Tsuga* and 121 and 47 for *Picea* at Cascade Head and Cape Lookout, respectively.

Tsuga usually had multiple releases (>55%) but few *Picea* (16.5%) did. *Picea* is less successful than *Tsuga* in using multiple episodes of gap formation or expansion to enter the canopy.

A comparison of growth rates of *Picea* successor trees in large (1000–2000 m^2) and small (200–300 m^2) gaps (Fig. 9a, b) with subcanopy *Picea* suggests that *Picea* requires larger gaps to regenerate and enter the canopy. Young individuals in large gaps were growing at a rate characteristic of subcanopy *Picea* early in their lives. Subcanopy *Picea* probably established and grew into the subcanopy in large gaps.

Patterns of canopy disturbance and forest turnover

Since 1950, seven high velocity windstorms have occurred along the Oregon coast (1951, 1962, 1963, 1971, 1981, 1983) (Ruth & Harris, 1979; Harcombe, 1986; S. Greene, personal communication). Peaks in the time frequency distribution of releases generally occur soon after these storms (Fig. 10) and suggest that gap formation is greater during years with severe windstorms. Growth releases were also frequent in other years since 1925 suggesting that less severe windstorms increase the rate of gap formation too.

Forest turnover was estimated at both sites by assuming that gaps take 60 years to fill. Turnover for expanded gaps (248 and 206 years) and canopy gaps (422 and 327 years) were somewhat longer at Cascade Head than at Cape Lookout, respectively. Harcombe (1986) estimated a 384-year turnover time for *Picea–Tsuga* forest at more protected inland sites at Cascade Head using long-term mortality data. Forest turnover estimated from canopy gaps was similar to the value derived from long-term observations on marked populations.

Forest turnover estimated from patch disturbances iden-

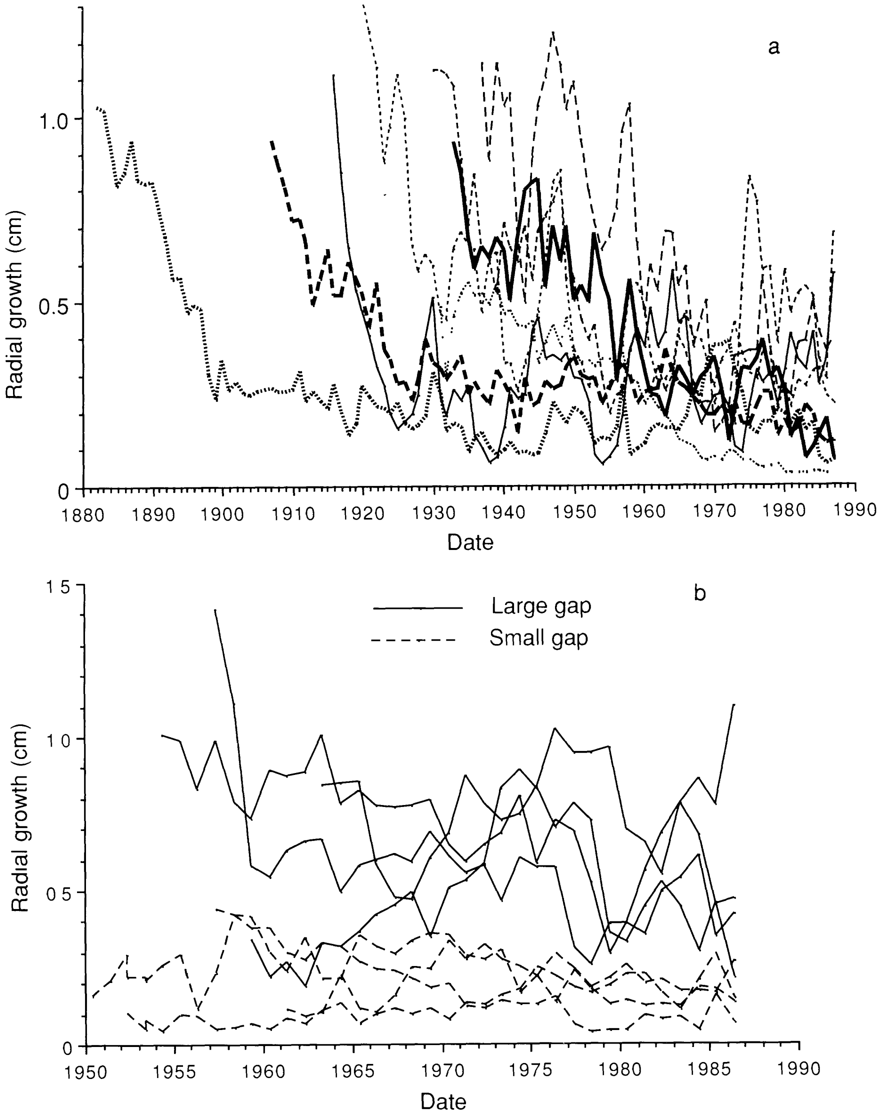

FIG. 9. Annual radial growth of eight subcanopy–canopy *Picea* (a) and eight *Picea* treefall gaps (b). Large gaps were 1000–1200 m^2, and small gaps were 200–300 m^2.

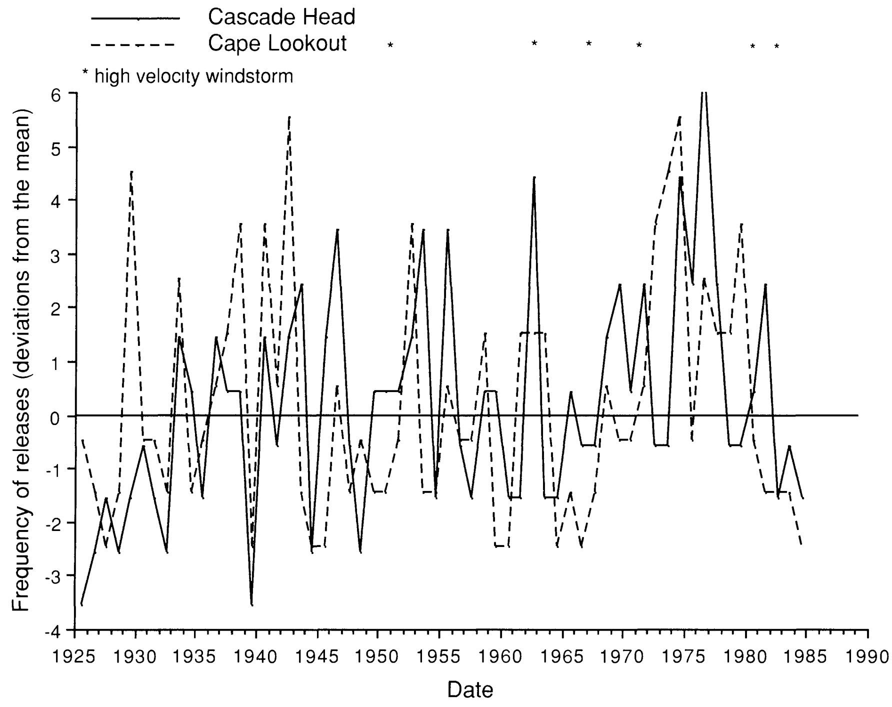

FIG. 10. Dates of growth releases during the last 60 years from canopy trees at Cascade Head (n=225) and Cape Lookout (n=157).

tified on aerial photographs was 279 years (9.3% of the forest in 26 years). This rate is faster than turnover by patch disturbance at inland sites estimated by Harcombe (1986). The percentage of forest at Cascade Head in patches ranged from 1.6% to 4.2% for years with photo coverage. Patches were concentrated on the flanks of ridges and on ridgetops where winds are higher in velocity and more turbulent (Ruth & Harris, 1979). The concentration of patch disturbances on ridgetops and upper slopes and the lower frequency of patches at more inland positions suggest that forest turnover times vary by topographic settings and along a coastal–inland gradient. Patch expansion by blow down of exposed trees on patch edges occurred in some patches (n=10). Average annual rate of patch expansion for these patches was 7.1% (range 2.2–20.5%).

Future composition

Predicted canopy compositions varied somewhat by the methods used to estimate transition probabilities. *Picea* importance in the next generation was highest using density of gap occupants and lowest using predicted successor trees (Table 4). Predicted composition using successor trees was most similar to current composition. Increased *Picea* predicted from probabilities derived from density data probably reflects *Picea*'s ability to establish in gaps. Less tolerant gap-phase regenerators tend to be over represented in gap samples compared to their abundance in the canopy (White *et al.*, 1985b). None of the tree-by-tree replacement models methods predicted disappearance of *Picea* in the next generation.

DISCUSSION

Picea regeneration in canopy gaps was abundant but it was not uniformly distributed and most *Picea* had established in large gaps. *Tsuga*, in contrast, was abundant in small and large gaps. This pattern may be partially explained by relative differences in species life history. *Picea* seedling survival and growth is greater than *Tsuga*'s in partially open conditions. The opposite pattern is typical under closed canopy conditions (Harmon, 1986). *Picea* in clearcuts

TABLE 4. Transition probabilities and predicted equilibrium compositions (% in parentheses) of coastal *Picea–Tsuga* forests.

Gapmaker	Gap occupants								
	Method 1			Method 2			Method 3		
	Picea	*Tsuga*		*Picea*	*Tsuga*		*Picea*	*Tsuga*	
Cascade Head									
Picea (21)	0.42	0.58	(34)	0.29	0.71	(27)	0.27	0.73	(21)
Tsuga (79)	0.32	0.68	(66)	0.27	0.73	(73)	0.19	0.81	(79)
Cape Lookout									
Picea (26)	0.40	0.60	(44)	0.33	0.67	(30)	0.31	0.69	(28)
Tsuga (74)	0.46	0.54	(56)	0.29	0.71	(70)	0.27	0.72	(72)

grows faster than *Tsuga* (Minore, 1979) and *Picea* grew faster than *Tsuga* in gaps at Cascade Head and Cape Lookout. *Picea* is also longer lived than *Tsuga* (Franklin & Dyrness, 1973). If growth rates of individuals in gaps reflect gap sizes needed by *Picea* to enter the subcanopy, then *Picea* probably requires gaps of 800–1000 m^2 to persist at stand scales in these forests. Gaps of this size in *Picea–Tsuga* forests were common. 19% of the gaps <60 years old was ⩾800 m^2 and patch sizes of 0.1–0.25 ha created by windthrow were abundant too. Long-lived *Picea* would only require a few large gaps every several decades to persist at stand scales. The observed patterns of *Picea* regeneration and growth in gaps are consistent with expected patterns for a relatively light demanding species.

Persistence of less tolerant species in many temperate forests may be partially explained by sufficiently frequent large gaps in a forest (Marks, 1974; Williamson, 1975; Barden, 1981; Runkle, 1982). The regeneration and growth of *Picea* in gaps is consistent with trends identified in other temperate forest types (White, 1979; Nakamura, 1985; Ellenberg, 1988).

Clearly, *Tsuga* was several-fold more abundant than *Picea* in gaps and *Tsuga* filled most gaps, including large ones. *Tsuga* advanced regeneration was abundant in some large patches of windthrow and it appeared that residual *Tsuga* would replace mixed forest. However, regeneration in patches of windthrow had even-aged populations of both (or either) species too. Some patches had two or more age-classes of both species.

Regeneration patterns in smaller canopy gaps were usually less complex and residual *Tsuga* usually dominated canopy opening and replaced trees that died. *Tsuga* did not fill all gaps, however, and *Picea* appears to persist at stand scales by gap-phase regeneration in moderate sized gaps.

Environmental and disturbance gradients change markedly from the coast to more inland sites. *Picea* is most abundant along the mild mesic coastal strip and it decreases in abundance as sites become drier and more thermally extreme inland (Cordes, 1972; Franklin & Dyrness, 1973; Kratz, 1975; Ruth & Harris, 1979). Important components of the disturbance regime including the type, frequency, size, severity and spatial distribution of disturbance change along the same gradient. For example, fire is an important catastrophic disturbance in adjacent inland *Tsuga–Pseudotsuga menziesii* forests while wind is a more important disturbance agent in coastal *Picea–Tsuga* forests. Both disturbance and environmental conditions influence the abundance of *Picea* and *Tsuga* regeneration and hence forest replacement patterns. Position of *Picea–Tsuga* stands along disturbance and environmental gradients determine the spatial scale at which *Picea* persists, and the type of disturbance that initiates tree replacement.

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