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University of Washington
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The data sets from the Olympic peninsula permanent plots were provided by the Permanent Sample Plot (PSP) program, a partnership among the Forest Science Data Bank (FSDB), the Department of Forest Science at Oregon State University, the U.S. Forest Service Pacific Northwest Research Station, and the National Science Foundation's Long-Term Ecological Research Program (NSF-LTER).

INTRODUCTION

The Pacific Northwest of the United States has a wealth of natural resources among which coniferous forest, particularly old-growth, stand out for their productivity and beauty. The *Picea sitchensis - Tsuga heterophylla* zone, which occupies a narrow strip extending from Coos Bay, Oregon (43°20'N), to Prince William Sound, Alaska (61°00'N), is considered one of the most productive coniferous zones in the world (Fujimori et al. 1976).

These forests, like other natural forests, include a variety of living and dead tree structures as well as vertical and horizontal spatial complexity, structural features that are increasingly recognized as important to the ecological functioning of these ecosystems (Franklin et al. 2002). Furthermore, disturbance patterns are known to have a strong effect on stand structure and development (Deal et al. 1991). Most studies examining the relationship between natural disturbance and forest dynamics have concentrated on species compositional changes over time and space, but biomass change and related patterns of mortality are also important (Sprugel 1985; Harcombe et al. 1990; Greene et al. 1992).

Tree mortality plays a major role in development of the distinctive structure of old-growth forest, as well as providing unique habitat for certain species of biota (Craig et al.

2001). Although tree mortality is an important process in the development of forest ecosystems, foresters and ecologists have amassed limited knowledge of the overall process (Bible 2001). Most of the published information on mortality represents the studies of single-species and single-cohort stands. Consequently, considerably less is known about causal agents of mortality and concomitant effects on ecosystem structure, composition, and function in more complex and older forests (Franklin and DeBell 1988). Results of studies show that mortality rates in old-growth stands can affect stand structure; maximum size and ages of trees; formation rates of snags; logs and canopy gaps; and development of multilayered vegetation (Tyrell and Crow 1994; Tyrell et al. 1998; Bible 2001). Differences in mortality rates among species are also considered to be key life-history attributes that influence long-term changes in forest composition, structure and sustainability (Franklin and DeBell 1988; Craig et al. 2001).

Long-term variation in forest above-ground biomass accumulation is also of interest to ecologists and foresters, as it can potentially reveal much about both ecosystem and population-level controls of ecosystem functions (Harcombe et al. 1990). The amount of standing biomass of tree boles at any given time represents the integration of net primary production of boles (NPPB) and tree mortality from the initiation of the stand until the time in question (Harcombe et al. 1990; Acker et al. 2000; Acker et al. 2002). Temporal patterns of biomass change in forests and their causes are also long-standing, fundamental issues for basic and applied ecology at local and regional scales, both for the aggrading phase leading to maximum biomass and for the phase that follows (Acker et al.

2000). Although there may be no net change in live biomass, old forest may maintain relatively high rates of production; however, this cannot be assessed without knowledge of biomass loss through mortality (Acker et al. 2002).

It is necessary to study representative sample units in both space and time to obtain reliable information to make inferences on biological and ecological processes. Changes in the composition, structure, and functions of forest ecosystems typically occur over longs periods of time (Acker et al. 1998; Franklin et al. 2002). Long-term observations are the only direct means to document and understand the intrinsically slow changes of forests, which are dominated by long-lived trees (Bible 2001; Acker and McKee 2002). One of the best examples of an appropriate system of permanent plots exits in the Pacific Northwest of the United States. This series of permanent forest plots were gradually established across western Oregon and Washington beginning in 1910. The first plots were established to measure forest growth and yield, but subsequently, were established to focus more on ecosystem processes, such as patterns and rates of succession and mortality (Acker et al. 1998; Acker and McKee 2002).

A detailed study of ecosystem, population and structural changes in old-growth Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests is the topic of this thesis. Data are from permanent sample plots at seven forested sites located on the west side of the Olympic Peninsula of Washington; these plots are part of the Pacific Northwest long-term permanent vegetation plot series.

Forests ranged in age from 210 to 256 yr at the time of plot establishment and have long (15 to 22 yr) records of repeated observation. The primary objectives of this study were (1) to evaluate changes in tree population structure, (2) to determine rates and causes of mortality, and (3) to determine trends in biomass accumulation.

METHODS

STUDY SPECIES

The primary species of interest are Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) of the *Picea sitchensis* Zone in the Olympic Peninsula Province (Franklin and Dyrness 1988). Sitka spruce is a large, long-lived, evergreen, species of medium shade tolerance that grows best on sites with deep, moist, well-drained soils (Harris 1966). It can attain heights of greater than 65 m with a diameter at breast height (DBH) of 5 m on productive sites (Harris 1990; Pojar and Mackinnon 1994). This species has a strong affinity for soils high in calcium, magnesium, and phosphorus in the soil orders Entisols, Spodosols, Inceptisols, and Histosols, which are usually acidic with pH typically ranging from 4.0 to 5.7 (Harris 1990). As a species of intermediate tolerance, Sitka spruce is both a pioneer and a climax species. It acts as an early pioneer on the undeveloped soils of landslides, sand dunes, uplifted beaches, and deglaciated terrain; it is a climax species in the coastal forests (Harris 1966). In this latter situation, the "nurse log syndrome" has a key role in regeneration providing this species protection and nutrition sources (Figure 1).

Figure 1. Sitka spruce seedlings growing on a log of the same species. South Fork Hoh River area, Olympic Peninsula.

Western hemlock is a large, long-lived, shade-tolerant species that can also recruit after major disturbances, but it typically establishes in the later stages of forest development (Franklin and Hemstrom 1981; Spies 1997). Its initial growth may be slow; 2-year-old seedlings are commonly less than 20 cm tall. However, once established, seedlings in full light may have an average growth rate of 60 cm or more annually (Worrell and Malcolm 1990). Individual western hemlock can live for centuries and grow to 50-60 m in height and 90-120 cm in diameter (Franklin and Waring 1980; Franklin and Hemstrom 1981). Although western hemlock grows on soils derived from almost all bedrock types, its best growth is on sedimentary, metamorphic, and igneous materials (Packee 1990). In general, the best stands are found in the humid coastal region (Arno and Hammerly 1977; Pfister et al. 1977). In the absence of a major wildfire, western hemlock gradually

increases its importance in the stand (Munger 1940; Arno and Hammerly 1977), until hemlock looper (*Lambdina fisceralla lugubrosa*) outbreaks decimate vast areas of mature western hemlock (Edmonds et al. 2000). It is generally considered a climax species either alone, or in combination with its shade-tolerant associates (red alder, bigleaf maple) but it can be found in all stages of succession (Packee 1990).

Several other conifer species inhabit the *Picea sitchensis* Zone, but Sitka spruce and western hemlock, singly or jointly typically dominate throughout the entire course of forest development. Associated species include the conifers, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western redcedar (*Thuja plicata* Donn.), and the deciduous trees, red alder (*Alnus rubra* Bong.) and bigleaf maple (*Acer macrophyllum* Pursh).

STUDY SITES

Seven forested study sites were selected from the Permanent Sample Plot (PSP) database to provide a comparison of several old-growth Sitka spruce/western hemlock forests on the Olympic Peninsula of Washington. The database for this work is property of the PSP program, which is a partnership among the Forest Science Data Bank (FSDB), the Department of Forest Science at Oregon State University, the U.S. Forest Service Pacific Northwest Research Station, and the National Science Foundation's Long-Term Ecological Research Program (NSL-LTER) (Acker and McKee 2002). These datasets

include information on plant association, tree size (DBH and height), and condition at mortality. Data are collected from tagged trees on permanent plots. Minimum DBH for inclusion in these datasets was 5 cm.

The study areas are located in a maritime climate, characterized by mild temperatures with prolonged cloudy periods, muted extremes, and narrow diurnal extremes (6° to 10° C); wet, wild winters and cool, relatively dry summers, and a long frost-free season; and heavy precipitation (Franklin and Dyrness 1988). Climatic data from a meteorological station located close to the Quinault RNA study area indicates an average annual temperature of 10.6° C, and average minimum and maximum temperatures of 1.2° C and 23.8° C, respectively. The average annual precipitation and snowfall are 3,371 mm and 300 mm, respectively (Franklin and Dyrness 1988).

Soils are derived from sedimentary parent materials in the interior and are primarily classed within the Spodosol and Inceptisol orders. The Spodosols have thin, gray sandy loam B2 horizons, while the Inceptisols have very dark grayish-brown sandy loam subsurface horizons (Franklin and Dyrness 1988).

The old Sitka spruce/western hemlock forests of these study areas have lush understories with dense growth of shrubs, dicotyledonous herbs, ferns, and cryptogams. Common understory species associated with them are, among others, swordfern (*Polystichum munitum* (Kaulf.) Presl), Oregon oxalis (*Oxalis oregana* Nutt. Ex T. & G.), three-leaved

coolwort (*Tiarella trifoliata* L.), western springbeauty (*Montia sibirica* (L.) How.), evergreen violet (*Viola sempervirens* Greene), red huckleberry (*Vaccinium parvifolium* Smith), and rustyleaf (*Menziesia ferruginea* Smith) (Franklin and Dyrness 1988).

When the plots were established the forests in the study areas ranged in age from 210 to 256 years. The study areas range in elevation from 122 to 250 meters and their north-south distribution is from Twin Creek RNA to Quinault RNA (Figure 2, Table 1).

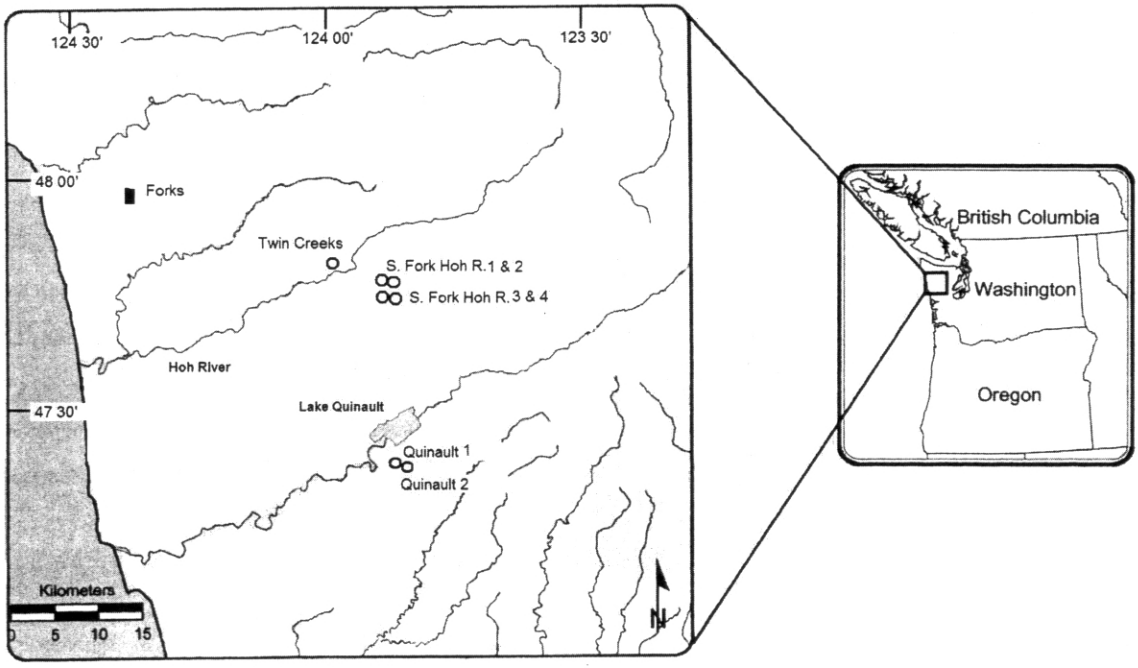

Figure 2. Location of the seven study plots on the Olympic Peninsula of Washington.

Table 1. Forest age, length of data record, total plot area, and geographic position for the seven study areas.

Study area	Forest age (yr) at		Data record (yr)	Plot area (ha)	Geographic position		
	Plot establishment	Last reneasurement			Latitude N (°)	Longitude W (°)	Elevation (m)
S. Fork Hoh R. 1	256	278	22	1.0	47.779	123.908	244
S. Fork Hoh R. 2	256	278	22	1.0	47.779	123.908	244
S. Fork Hoh R. 3	256	278	22	1.0	47.779	123.908	250
S. Fork Hoh R. 4	256	278	22	1.0	47.779	123.908	250
Quinault RNA 1	210	228	18	1.0	47.429	123.873	122
Quinault RNA 2	211	228	17	1.0	47.430	123.873	122
Twin Creeks RNA	212	227	15	1.0	47.834	123.990	152

Source: Adapted from Smithwick et al. 2002

South Fork Hoh River plots

The four South Fork Hoh River plots were established in 1978, two plots in each of two 256-yr-old stands that developed about 1720. The plots lie on flat topography in a valley bottom. The plant association for these plots is *Tsuga heterophylla - Picea sitchensis/Oplopanax horridum/Athyrium filix-femina* (Hines 1971).

At the time of plot establishment, there were 167 trees per hectare (TPH) composed of 46.7% Sitka spruce and 52.1% western hemlock in Plot 1, 133 TPH composed of 48.1% Sitka spruce and 50.4% western hemlock in Plot 2, 70 TPH composed of 61.4% Sitka spruce and 34.3% western hemlock in Plot 3, and 76 TPH composed of 36.8% Sitka spruce and 61.8% western hemlock in Plot 4 (Table 2). Plots were remeasured in 1984, 1989, 1995 and 2000.

Quinault RNA plots

The two Quinault RNA plots were installed in 1982 (Plot 1) and 1983 (Plot 2) in two 210-yr-old stands that regenerated after a disturbance at the end of the 1780s. The plots lie on undulating topography at the interface of mountains slopes and the Coastal plain. According to Hines (1971), the plant association for these plots is *Tsuga heterophylla-Picea sitchensis/Gaultheria shallon-Blechnum spicant.*

At the time of plot establishment (forest age 210 yr for Plot 1, and 211 for Plot 2), there were 225 TPH composed of 0.4% Sitka spruce and 99.6% western hemlock in Plot 1, and 370 TPH constituted of 8.1% Sitka spruce and 91.9% western hemlock in Plot 2 (Table 2). Plots were remeasured in 1989, 1995 and 2000.

Twin Creeks RNA plot

The Twin Creeks plot was installed in 1984 in a 212-yr-old stand that regenerated after a disturbance at the end of the 1780s. The plot lies in a valley bottom on undulating topography. According to Hines (1971), the plant association for this plot is *Tsuga heterophylla-Picea sitchensis/Gaultheria shallon-Blechnum spicant.*

At the time of plot establishment (forest age 212 yr), there were 221 TPH composed of 45.7% Sitka spruce and 53.4% western hemlock (Table 2). This plot was remeasured in 1989, 1995 and 1999.

Table 2. Basic statistics at plot installation for the South Fork Hoh River, Quinault RNA, and Twin Creeks RNA study sites. TPH = trees per hectare (≥5 cm DBH), BA = basal area (m^2 ha^{-1}), Volume = wood and bark volume (m^3 ha^{-1}), Biomass = above-ground stem wood and bark only (Mg ha^{-1}).

S. Fork Hoh R. 1	TPH	BA	Volume	Biomass
256 yr (1978)				
Sitka spruce	78	52.9	1,051.1	456.2
Western hemlock	87	19.5	272.1	101.7
Western redcedar	1	0.7	7.4	2.4
Douglas-fir	1	1.4	18.5	8.3
Total	167	74.5	1,349.1	568.6
S. Fork Hoh R. 2				
256 yr (1978)				
Sitka spruce	64	92.4	1,897.4	893.5
Western hemlock	67	11.1	144.0	53.9
Western redcedar	1	0.2	2.2	0.7
Douglas-fir	1	1.7	23.7	10.7
Total	133	105.4	2,067.3	958.8
S. Fork Hoh R. 3				
256 yr (1978)				
Sitka spruce	43	46.5	1,021.4	443.3
Western hemlock	24	6.5	100.0	37.4
Western redcedar	1	2.4	30.8	9.8
Red alder	2	0.6	7.0	2.6
Total	70	56.0	1,159.2	493.1
S. Fork Hoh R. 4				
256 yr (1978)				
Sitka spruce	28	53.8	1,162.5	504.5
Western hemlock	47	22.1	361.1	135.1
Red alder	1	0.4	5.3	2.2
Total	76	76.3	1,528.9	641.6

Quinault RNA 1	TPH	BA	Volume	Biomass
210 yr (1982)				
Sitka spruce	1	6.9	181.7	78.9
Western hemlock	224	58.1	813.9	304.4
Total	225	65.0	995.6	383.3
Quinault RNA 2				
211 yr (1983)				
Sitka spruce	30	35.3	651.8	282.9
Western hemlock	340	33.8	463.9	173.5
Total	370	69.1	1,115.7	456.4
Twin Creeks RNA				
212 years (1984)				
Sitka spruce	101	39.6	731.4	317.4
Western hemlock	118	28.4	439.1	164.2
Douglas-fir	2	7.0	104.1	46.8
Total	221	75.0	1,274.6	528.4

In the Results chapter data were pooled for S. Fork Hoh River plots 1 and 2 and for S. Fork Hoh River plots 3 and 4 because they are located adjacent to each other in the same stands. For reference the study sites were named South Fork A (S. Fork Hoh River plots 1 and 2), South Fork B (S. Fork Hoh River plots 3 and 4), Quinault A (Quinault RNA plot 1), Quinault B (Quinault RNA plot 2), and Twin Creeks. Separate results for each of the study plots are presented in Appendices 1, 2, and 3.

POPULATION STRUCTURE

Trees (stem ha^{-1}) were placed in 10-cm DBH classes (5.0-15, 15.1-25, 25.1-35 cm, etc.) but are reported as DBH class midpoints (10, 20, 30 cm, etc.). Classes were considered small enough to provide a detailed frequency distribution diagram for living (survival trees and ingrowth) trees.

MORTALITY RATES

Average mortality rates were calculated using Hamilton and Edwards' (1976) negative compound formula.

$$M = [1 - \{(N_t / N_o)^{1/t}\}] * 100 \qquad (1)$$

Where M is the annual mortality rate (%), N_t is the number of surviving trees at the end of remeasurement interval of *t* years, N_o is the number of tagged trees at the beginning of a remeasurement interval of *t* years, and *t* is the period of survival (yr).

MORTALITY DISTRIBUTIONS

Similar to the population structure, dead trees (stem ha^{-1}) were placed in 10-cm DBH classes as above and reported as DBH class midpoints. DBH of all missing trees were estimated as the DBH at the previous measurement.

CAUSES OF TREE MORTALITY

PSP datasets include information on the probable causes of tree mortality as well as more objective descriptors of the physical condition of dead trees. A total of 19 cause/condition codes range from very clear physical causes of death such as "crushed by fallen tree", to more subjective ratings based on less easily determined caused of death such as "unknown pathogen". To ensure a less subjective categorization of mortality each case was reassigned to one of nine broader groups emphasizing conditions of mortality: suppression, windthrow, windbreak, crushing, snow loading, butt or root rots, insects, unknown and other. I describe these conditions/causes of mortality in the paragraphs that follow.

Suppression

Suppression mortality, also referred to as competitive or density-dependent mortality, is usually related to low levels of light and soil moisture (Franklin et al. 1987; Oliver and Larson 1996; Spies 1997). For this study, death by suppression was assigned to standing dead trees in subordinate canopy positions with small, and flat-topped crowns.

Windthrow

Windthrow mortality was assigned to dead trees that were blown over by the wind as well as trees that died due to collateral effects of windthrow, such as trees knocked over by other windthrow trees (co-opted windthrow).

Windbreak

Windbreak consisted of standing dead trees whose boles had been broken by wind (windsnap) (Figure 3).

Figure 3. Tree death caused by windbreak. Quinault RNA, Olympic Peninsula.

Crushing

Crushing mortality was assigned to small dead trees that were crushed by fallen green or dead trees (snags), or limbs.

Snow loading

Mortality due to snow was assigned to leaning small trees that were still rooted, had broken stems and no outward signs of insects, pathogens, or mechanical damage. Heavy snow loads cause the branches to bend and separate from the center of the plant. If the snow load is heavy enough it can produce torque, which in turn results in branch or stem breakage (Sathers et al. 1994; Päätalo et al. 1999).

Butt or root rots

Butt or root rot is a decay due to fungi that occurs near the tree base or in the roots (Edmonds et al. 2000). There are a variety of fungi that attack old-growth Sitka spruce and western hemlock, but the most important in terms of presence and damage are velvet-top fungus (*Phaelous schweinitizzi*), a butt rot, and laminated root rot (*Phellinus wierii*) (Edmonds et al. 2000; Jerry Franklin, *personal communication*). Trees infected with velvet-top butt rot can exhibit thinning crowns, poor shoot growth and branch dieback (British Columbia Ministry of Forests 2003). Additionally, decay is limited to heartwood and normally is confined to roots and the butt of the host, which can lead to breakage or windthrow (USDA Forest Service 1983) (Figure 4).

Figure 4. Sitka spruce blown over by wind as a consequence of a *Phaelous schweinitizzi* infestation. South Fork Hoh River, Olympic Peninsula.

Trees infected with laminated root rot showed a clear reduction in height growth, foliage yellowing, a distress cone crop, and slow crown decline (USDA Forest Service 1983; Edmonds et al. 2000; British Columbia Ministry of Forests 2003).

Insects

Insects that can cause death of trees in this type of forest are mainly bark beetles and defoliators. Bark beetles belong to the family Scolytidae, a family that contains extremely destructive forest insects. Their broods feed on subcortical tissues or phloem making vertical galleries from the cortical tissues or xylem (Edmonds et al. 2000). The primary bark beetles found in these forests are Spruce beetle (*Dendroctonus rufipennis*) and engraver beetles (*Scolytus* spp.) Defoliation is caused by larvae of the orders Lepidoptera, Hymenoptera, and Coleoptera. Insect defoliation of the forest can be recognized by the thinning or absence of foliage and the raining of frass (Edmonds et al. 2000). The western hemlock looper (*Lambdina fisceralla lugubrosa*) is the most important defoliator in terms of coverage and aggressiveness in this type of forest (Sheperd 1976). During severe infestations or outbreaks, which occur more or less each 200 years, stands of western hemlock are completely defoliated and killed (Edmonds et al. 2000; Robert Gara, *personal communication*).

Unknown

"Unknown" was assigned as the cause of death when none of the prior defined mortality causes could be assigned. Dead trees classified as "broken top" were also reassigned to

this category due to the lack of specificity of this classification. Dead trees with presence of hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G. N. Jones) were also assigned to this category because mistletoe generally does not cause tree death in these stands. Severe infestations can occasionally cause mortality (Smith 1969; USDA Forest Service 1983; Hildebrand 1995), but it was not the case in these study plots. Hemlock dwarf mistletoe is a vascular parasite that taps into branches of western hemlock via a modified root system and robs the tree of moisture and carbohydrates (USDA Forest Service 1983; Mathiasen 1996). Missing trees were also classified as unknown.

Other

Other was a miscellaneous category of mortality causes composed primarily of animal kill (bears and deer), loss of soil by erosion, and lightning.

BIOMASS

Biomass (Mg ha^{-1}) of above-ground stem wood and bark was calculated for each study plot for each measurement year. These components of biomass account for 65-75% of the total stand biomass in the Pacific Northwestern coniferous forests (Keyes and Grier 1981). Branch and foliage components were not estimated because equations were either

unavailable or considered unreliable. My primary goal was to illustrate trends in biomass accumulation rather than to rigorously quantify biomass.

Wood and bark volumes (m3 ha^{-1}) were calculated using Browne's (1962) logarithmic equations for British Columbia species, which were considered appropriate for the study stands (Table 3). The volume equations are of the form:

$$\log V = B_0 + B_1 \log D + B_2 \log H \qquad (2)$$

Where V is wood and bark volume (ft^3), D is diameter at breast height (in), H is total height (ft), and B_0, B_1, and B_2 are regression coefficients. Volumes in cubic feet were converted to volumes in cubic meters by multiplying volumes in cubic feet by the factor 0.0283. Total heights were estimated using the non-linear Curtis-Arney height-diameter function fitted by Donnelly (1997) for Olympic Peninsula species (Table 4).

$$H = 4.5 + P_0 * e^{(-P_1 * D^{P_2})} \qquad (3)$$

Where H is total eight (ft), D is diameter at breast height (in), e is exponential constant, and P_0, P_1 and P_2 are regression coefficients. Estimates of wood and bark biomass were then obtained by multiplying volume estimates by wood densities for each species (Table 3).

Table 3. Volume coefficients and density multipliers for species. Volume equations are of the form $\log V = B_0 + B_1 \log D + B_2 \log H$.

Species	B_0	B_1	B_2	Density ($Mg\ m^{-3}$)
Sitka spruce	-2.700574	1.754171	1.164531	0.434
Western hemlock	-2.663834	1.790230	1.124873	0.374
Western redcedar	-2.379642	1.682300	1.039712	0.318
Douglas-fir	-2.712153	1.659012	1.195715	0.450
Red alder	-2.672775	1.920617	1.074024	0.370

Sources: Browne (1962) for volume; Harmon and Sexton (1996) for wood density.

Table 4. Height coefficients for species. Height equations are of the form $H = 4.5 + P_0 * e^{(-P_1 * D^{P_2})}$

Species	P_0	P_1	P_2
Sitka spruce	3844.3880110	7.06797723	-0.21215743
Western hemlock	609.4235299	5.59188376	-0.38409559
Western redcedar	665.0944184	5.50023202	-0.32464617
Douglas-fir	1091.8525990	5.29359685	-0.26482488
Red alder	139.4551455	4.69894302	-0.76818138

Source: Donnelly (1997).

Red alder equations were used to estimate biomass of cascara (*Rhamnus purshiana* DC.), a minor species in terms of size and frequency.

As a way to elucidate the stand biomass dynamic were also computed biomass loss from mortality and net primary production of boles (NPPB). Biomass of a tree at death was estimated by using the diameter at the previous measurement. Net primary production of boles was calculated as follows:

$$NPPB = \Delta B + M \quad (4)$$

Where ΔB is the difference in standing live biomass between one measurement period and the next, and M is the biomass of the trees that died during the interval. This method is equivalent to calculating the sum of biomass increments for all stems that survived a remeasurement interval (Harcombe et al. 1990).

RESULTS

Results are presented for the total stand as well as for each of the primary species, Sitka spruce and western hemlock, which dominate at the study sites. A few Douglas-fir, western redcedar, red alder, and cascara are present in the plots, but they represent less than 1.5 % of trees (Table 2).

TREE POPULATION STRUCTURE

Density and composition of trees at plot establishment differed among study sites. Total density ranged from 75 stems/ha at South Fork B to 370 stems/ha at Quinault B (Table 5). Sitka spruce generally comprised less than 50% of the stems and was most common in the 10-cm diameter class in most of the study sites, resulting in a relatively negative exponential (reverse J-shaped) diameter distribution (Figures 5A and B). At the South Fork B and Quinault B study sites, Sitka spruce comprised more than 70% of the population in the diameter classes larger than 70 cm, whereas at Quinault A there was only one Sitka spruce of large diameter (300 cm-diameter class).

Western hemlock contributed from 50 to 99.6% of stems at the study sites (Table 5), but its diameter range was smaller than that for Sitka spruce (10-150 cm vs.10-300 cm) (Figures 5A and B, 6A and B). Hemlock had an approximately normal distribution with means in the 40- and 50-cm diameter classes at South Fork A and Quinault A but a

negative exponential distribution at Quinault B (Figures 6A and B). Stems in the remaining study sites did not show a consistent diameter distribution (South Fork B) or were more or less evenly distributed across diameter classes (Twin Creeks) (Figures 6A and B).

At the last remeasurement, total density for the stands had increased dramatically at both of the South Fork study sites and decreased slightly at the Quinault A, Quinault B and Twin Creeks study sites (Table 5). At the South Fork sites these trends were largely attributable to changes in density of Sitka spruce, with marked ingrowth in the smaller diameter classes (Table 5, Figure 5A). At Quinault B, Sitka spruce slightly declined in density, but stems advanced in diameter class. At Twin Creeks, density of Sitka spruce declined by 25%, from 101 to 75 stems/ha, but its diameter distribution remained essentially constant since the decrease was concentrated in the smallest diameter class (Figure 5B). On the other hand, western hemlock density declined at South Fork A, Quinault A, Quinault B, and Twin Creeks and slightly increased at South Fork B (Table 5). Diameter distributions for hemlock also differed among study sites and changed over time (Figures 6A and B). At this time, there is not a clear normal distribution of stems at any study area because most of the stems that were originally located in medium-sized diameter classes have moved to larger ones in a more or less similar way. Additionally, at some study sites there appeared a significant number of stems in the 10-cm (smallest) diameter classes as a consequence of ingrowth (South Fork A, South Fork B, and Quinault A).

Table 5. Population statistics for the total stand, Sitka spruce, and western hemlock by remeasurement year and study site.

	Density (trees/ha)					Ingrowth (trees/ha)				Dead (trees/ha)			
South Fork A	**1978**	**1984**	**1989**	**1995**	**2000**	**1984**	**1989**	**1995**	**2000**	**1984**	**1989**	**1995**	**2000**
Total stand	150	180	213	234	245	40	40	53	41	11	7	33	31
Sitka spruce	71	104	138	166	179	39	39	52	37	7	5	25	24
Western hemlock	77	74	73	66	64	1	1	1	4	4	2	8	6
South Fork B	**1978**	**1984**	**1989**	**1995**	**2000**	**1984**	**1989**	**1995**	**2000**	**1984**	**1989**	**1995**	**2000**
Total stand	75	136	206	289	328	62	73	94	63	0	3	10	21
Sitka spruce	36	96	163	242	276	60	69	89	51	0	2	10	16
Western hemlock	36	37	38	42	47	2	2	5	10	0	1	0	5
Quinault A		**1982**	**1989**	**1995**	**2000**		**1989**	**1995**	**2000**		**1989**	**1995**	**2000**
Total stand		225	213	212	199		15	15	8		27	17	21
Sitka spruce		1	1	1	1		0	0	0		0	0	0
Western hemlock		224	212	211	198		15	15	8		27	17	21
Quinault B		**1983**	**1989**	**1995**	**2000**		**1989**	**1995**	**2000**		**1989**	**1995**	**2000**
Total stand		370	357	359	337		41	29	15		54	27	37
Sitka spruce		30	31	29	27		1	0	0		0	2	2
Western hemlock		340	326	329	309		40	28	15		54	25	35
Twin Creeks		**1984**	**1989**	**1995**	**1999**		**1989**	**1995**	**1999**		**1989**	**1995**	**1999**
Total		221	212	203	164		9	11	4		18	20	43
Sitka spruce		101	96	90	75		8	9	3		13	15	18
Western hemlock		118	114	109	89		1	0	1		5	5	21

Note: The first year corresponds to plot establishment; ingrowth corresponds to the number of trees that have grown past 5 cm in diameter during a measurement interval; missing trees are considered dead.

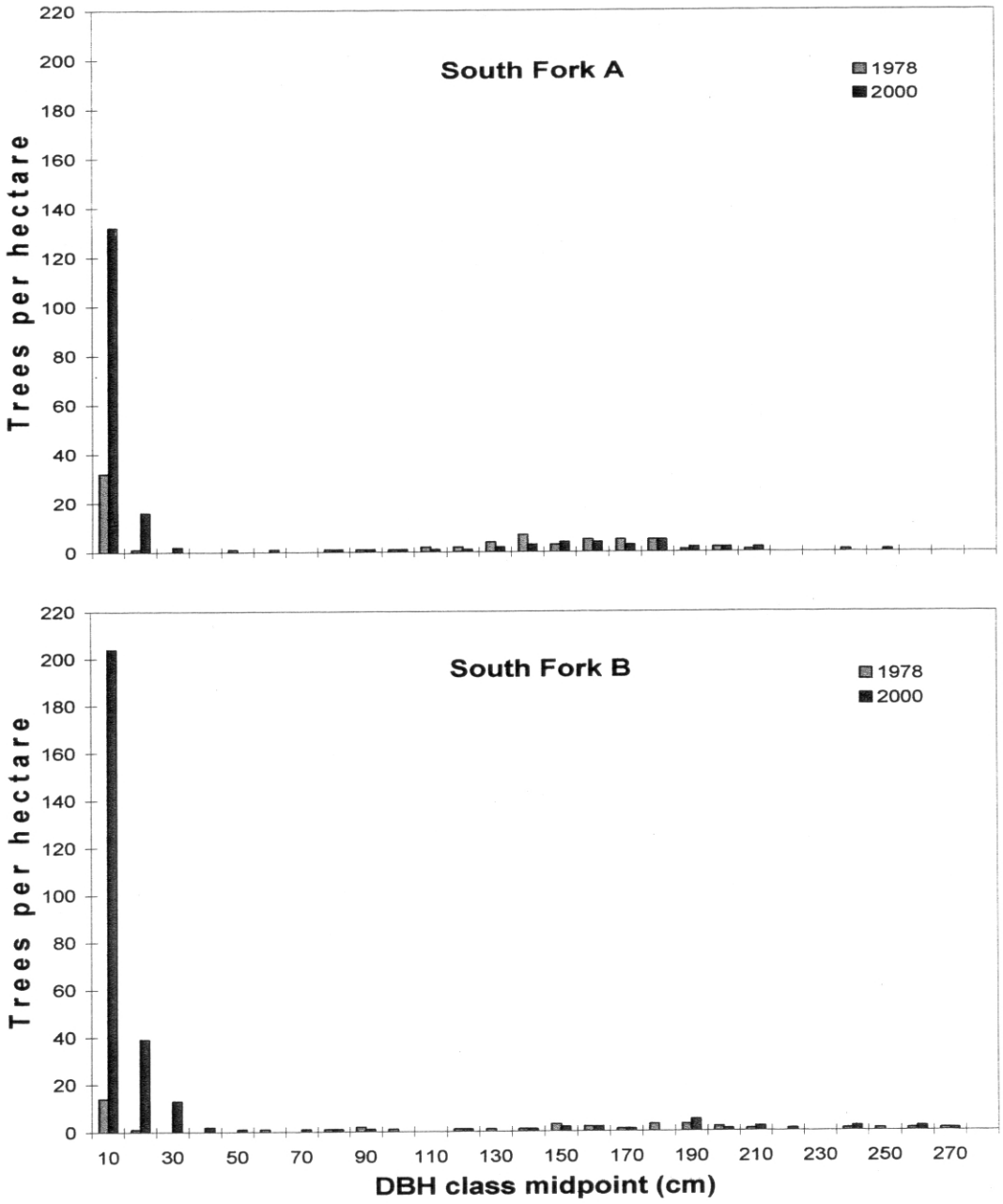

Figure 5A. Diameter distribution of Sitka spruce at the South Fork A and South Fork B study sites at the beginning and end of each study.

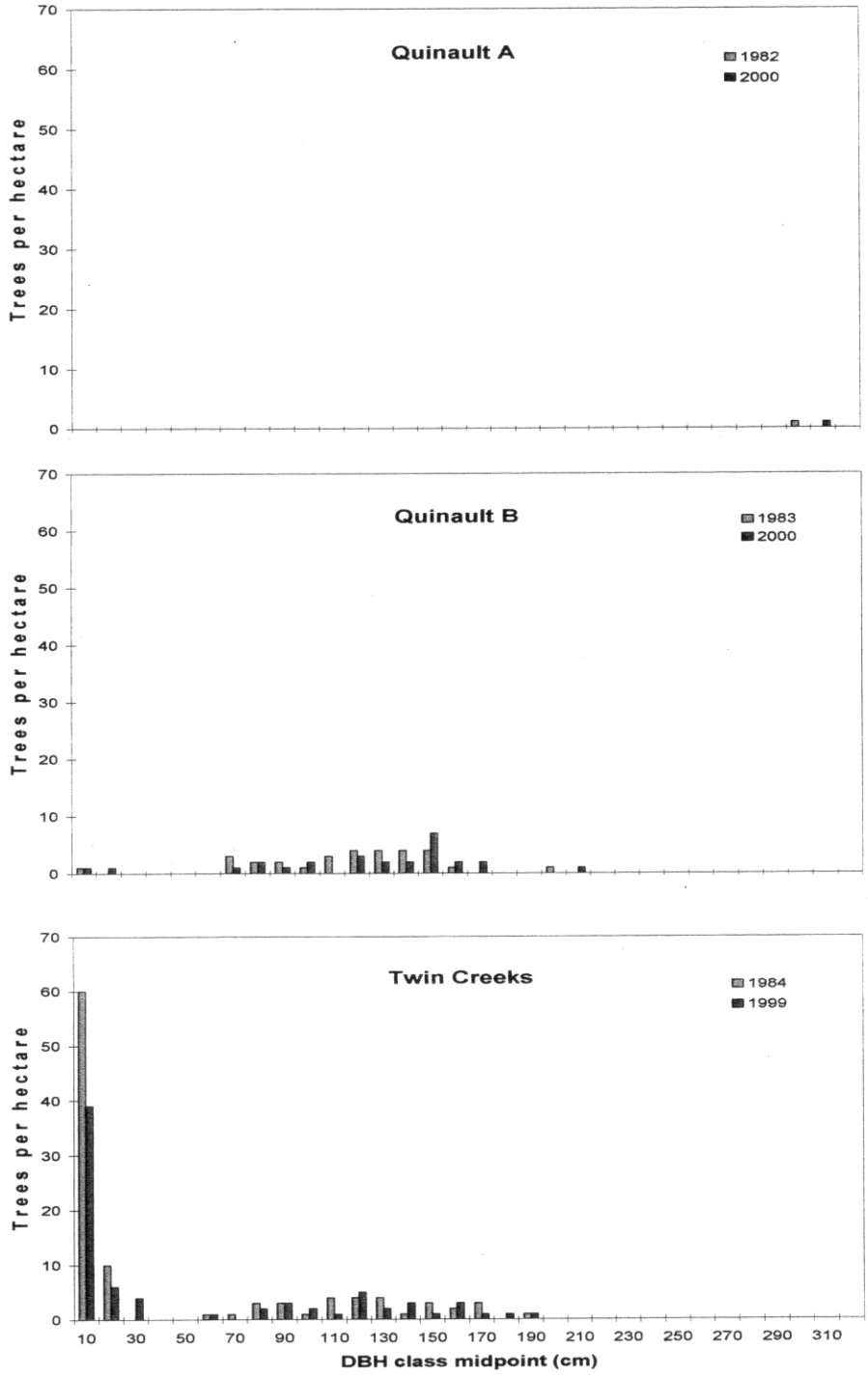

Figure 5B. Diameter distribution of Sitka spruce at the Quinault A, Quinault B, and Twin Creeks study sites at the beginning and end of each study.

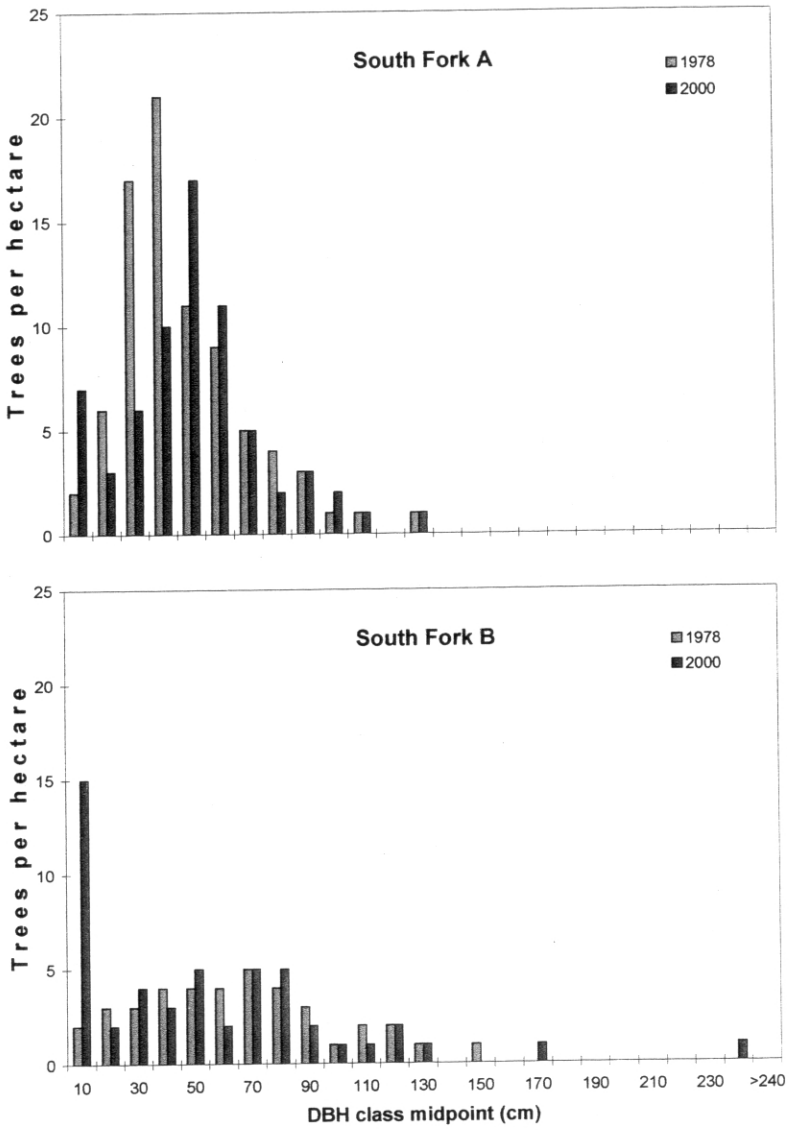

Figure 6A. Diameter distribution of western hemlock at the South Fork A and South Fork B study sites at the beginning and end of each study.

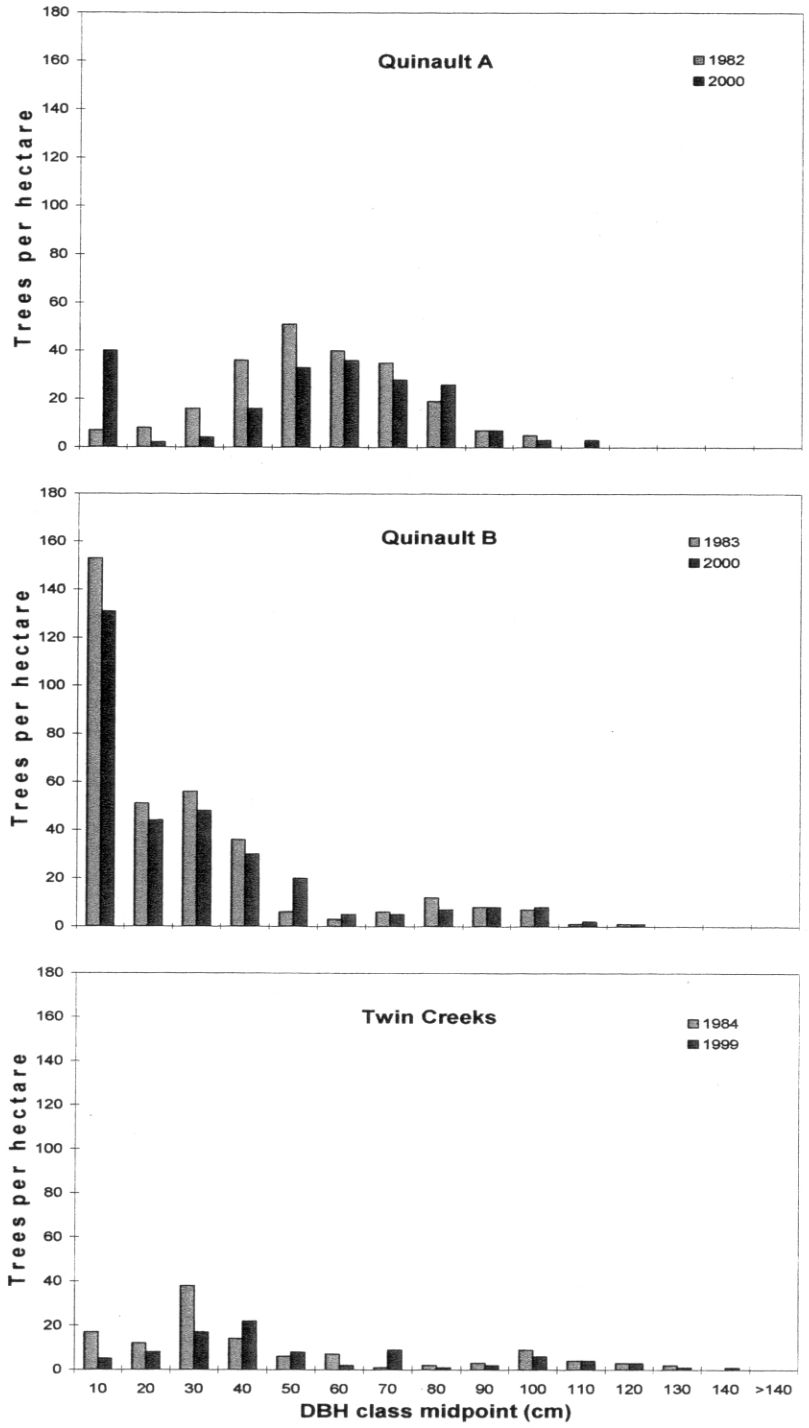

Figure 6B. Diameter distribution of western hemlock at the Quinault A, Quinault B, and Twin Creeks study sites at the beginning and end of each study.

MORTALITY

Mortality rates and distributions

Annual mortality rates varied irregularly by stand and species (Table 6). Total rates ranged from 0.5 to 2.7% (South Fork B and Twin Creeks, respectively). Intermediate rates (average= 1.8%) were reached at the remaining study sites. For species, annual mortality rates for Sitka spruce were higher than those for western hemlock at South Fork and Twin Creeks in the entire period of observation (1978-2000 and 1984-1999, respectively). That also happened at South Fork A and Twin Creeks during all their remeasurement periods. Conversely, annual mortality rates for western hemlock were higher than those for Sitka spruce at both of the Quinault study sites and during the entire period of observation and remeasurement periods (1982-2000 and 1983-2000, respectively).

The lowest annual mortality rate for Sitka spruce was obtained at Quinault B (0%), but only a single spruce was present. In contrast, the highest mortality rate occurred at Twin Creeks (3.6%). In this latter case, there was a strong influence from the high annual mortality rate reached during the last measurement interval (5.4% between 1995 and 1999). The lowest annual mortality rate for western hemlock, however, occurred at South Fork B (0.5%), whereas the highest rates occurred at Quinault B and Twin Creeks (2.0 and 1.9%, respectively. Western hemlock and Sitka spruce mortality at Twin Creeks were quite high and similar during the last measurement interval (5.2 and 5.4%,

respectively, between 1995 and 1999), which in turn resulted in an increase in the annual mortality rate of these species for the total period of observation (1984-1999).

Mortality was strongly related to tree size at the study sites, particularly for Sitka spruce (Figures 7A and B; 8A, B, and C). Most mortality for Sitka spruce occurred in the smallest diameter class (10 cm) of its diameter range (10 to 210-cm diameter classes), whereas mortality for western hemlock was more evenly distributed across its diameter range (10 to 150-cm diameter classes).

Mortality was highly variable among remeasurement intervals, depending on species and study site. For example at South Fork A, absolute mortality of Sitka spruce in the 10-cm diameter class at the end of the first and second remeasurement intervals was 4 trees per hectare, but increased to 18 and 23 trees per hectare at the end of the third and fourth remeasurement intervals, respectively (Figure 7A). In contrast, absolute mortality for western hemlock at Quinault B in the same diameter class was very high at the end of the first remeasurement interval with 48 trees per hectare, then decreased to 17 trees per hectare before increasing again to 23 trees per hectare at the end of the second and third remeasurement intervals, respectively (Figure 8B).

Table 6. Estimated annual mortality rates (%) for the total stand, Sitka spruce and western hemlock by study site in each remeasurement interval and for the total period of remeasurement.

Study site	Remeasurement interval				Total period of measurement
South Fork A	**1978-1984**	**1984-1989**	**1989-1995**	**1995-2000**	**1978-2000**
Total stand	1.2	0.7	2.8	2.4	1.7
Sitka spruce	1.6	0.8	3.3	2.6	2.2
Western hemlock	0.9	0.7	1.9	1.7	1.3
South Fork B	**1978-1984**	**1984-1989**	**1989-1995**	**1995-2000**	**1978-2000**
Total stand	0.0	0.4	0.9	1.5	0.5
Sitka spruce	0.0	0.4	1.2	1.4	0.6
Western hemlock	0.0	0.8	0.0	2.5	0.5
Quinault A	**1982-1989**		**1989-1995**	**1995-2000**	**1982-2000**
Total stand	1.8		1.4	2.1	1.8
Sitka spruce	0.0		0.0	0.0	0.0
Western hemlock	1.8		1.4	2.1	1.8
Quinault B	**1983-1989**		**1989-1995**	**1995-2000**	**1983-2000**
Total stand	2.6		1.3	2.2	1.9
Sitka spruce	0.0		1.1	1.4	0.8
Western hemlock	2.8		1.3	2.2	2.0
Twin Creeks	**1984-1989**		**1989-1995**	**1995-1999**	**1984-1999**
Total stand	1.7		1.6	5.8	2.7
Sitka spruce	2.7		2.8	5.4	3.6
Western hemlock	0.9		0.7	5.2	1.9

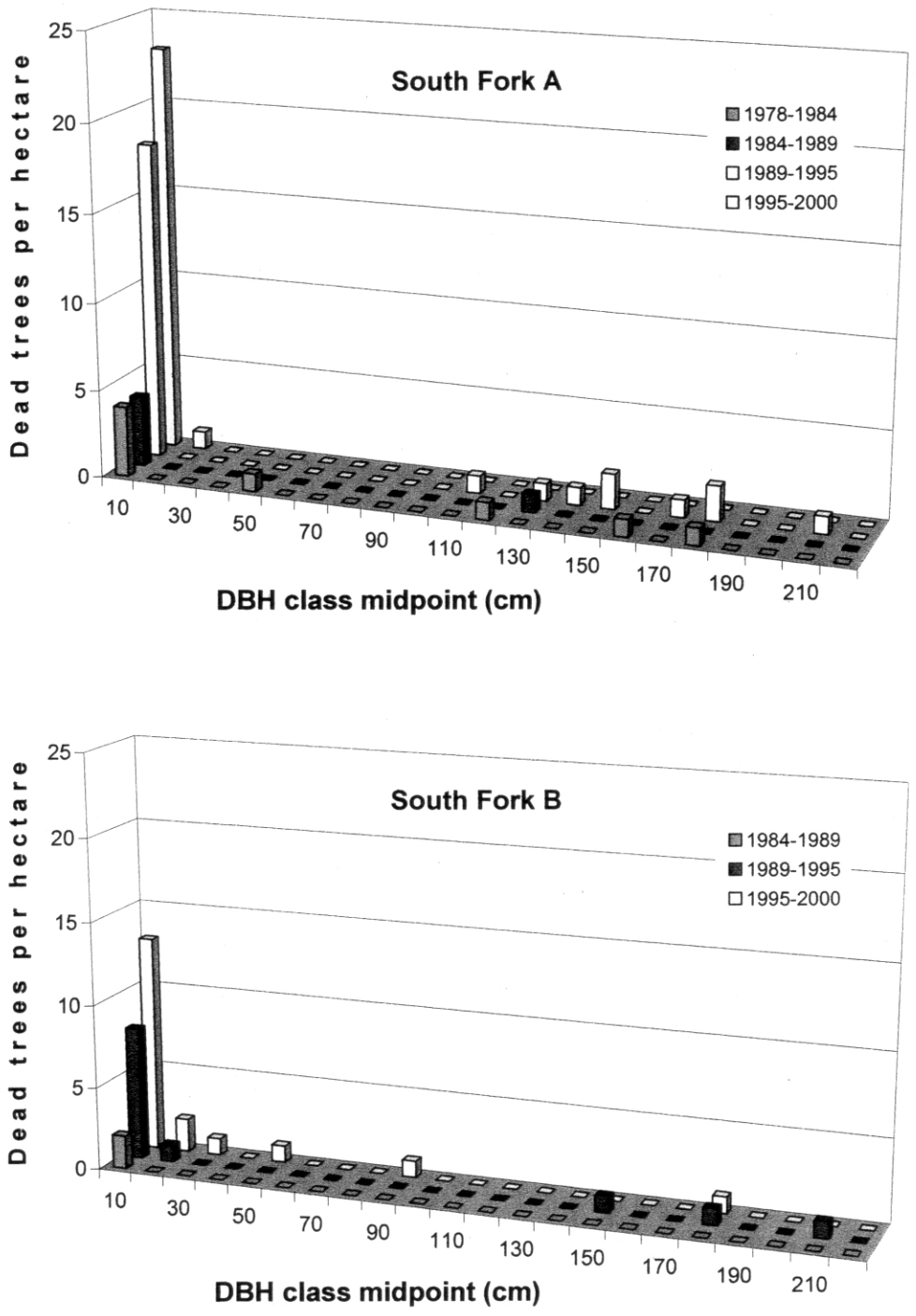

Figure 7A. Change in absolute mortality distribution by diameter class and period of remeasurement for Sitka spruce at the South Fork A and South Fork B study sites.

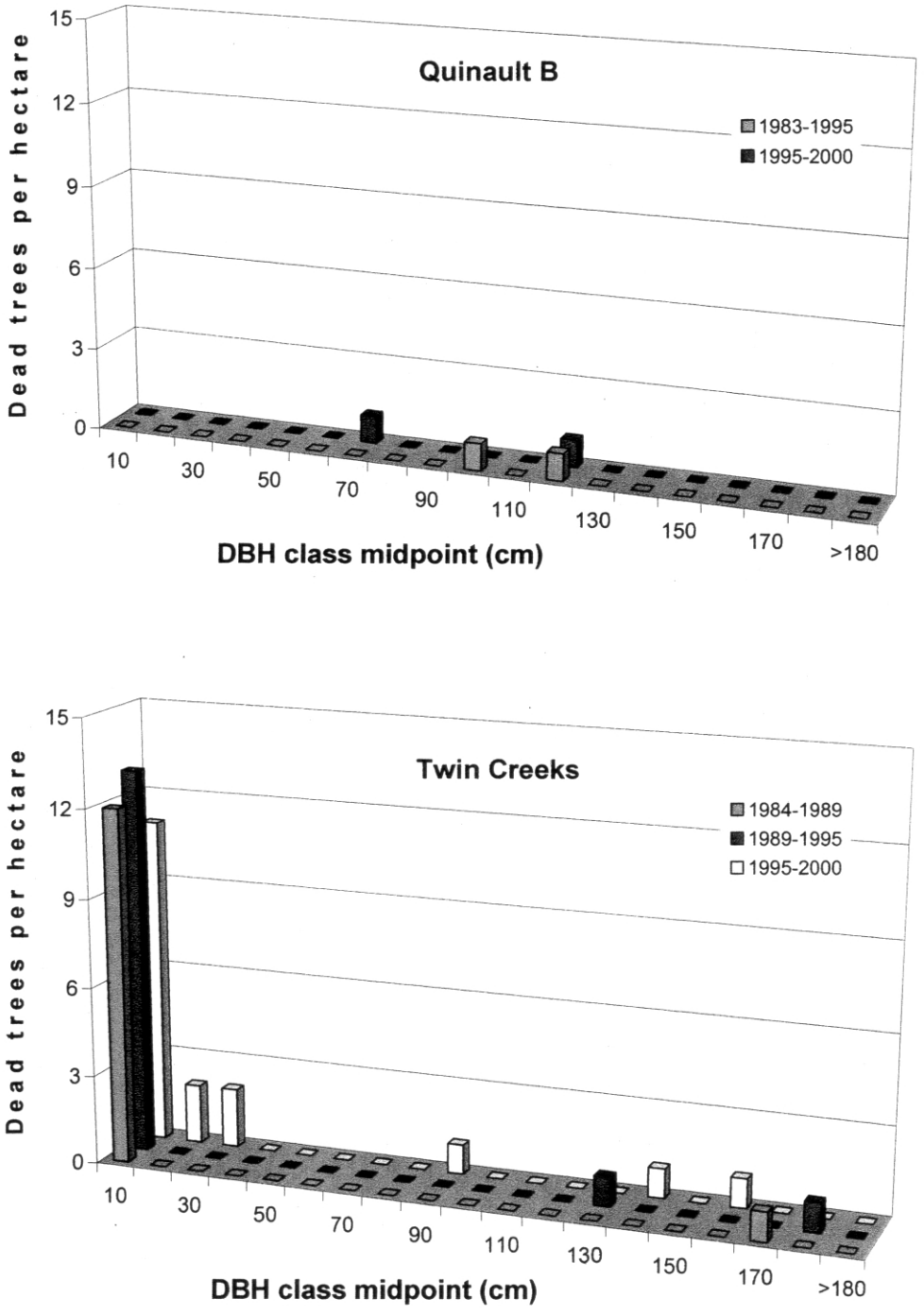

Figure 7B. Change in absolute mortality distribution by diameter class and period of remeasurement for Sitka spruce at the Quinault B and Twin Creeks study sites.

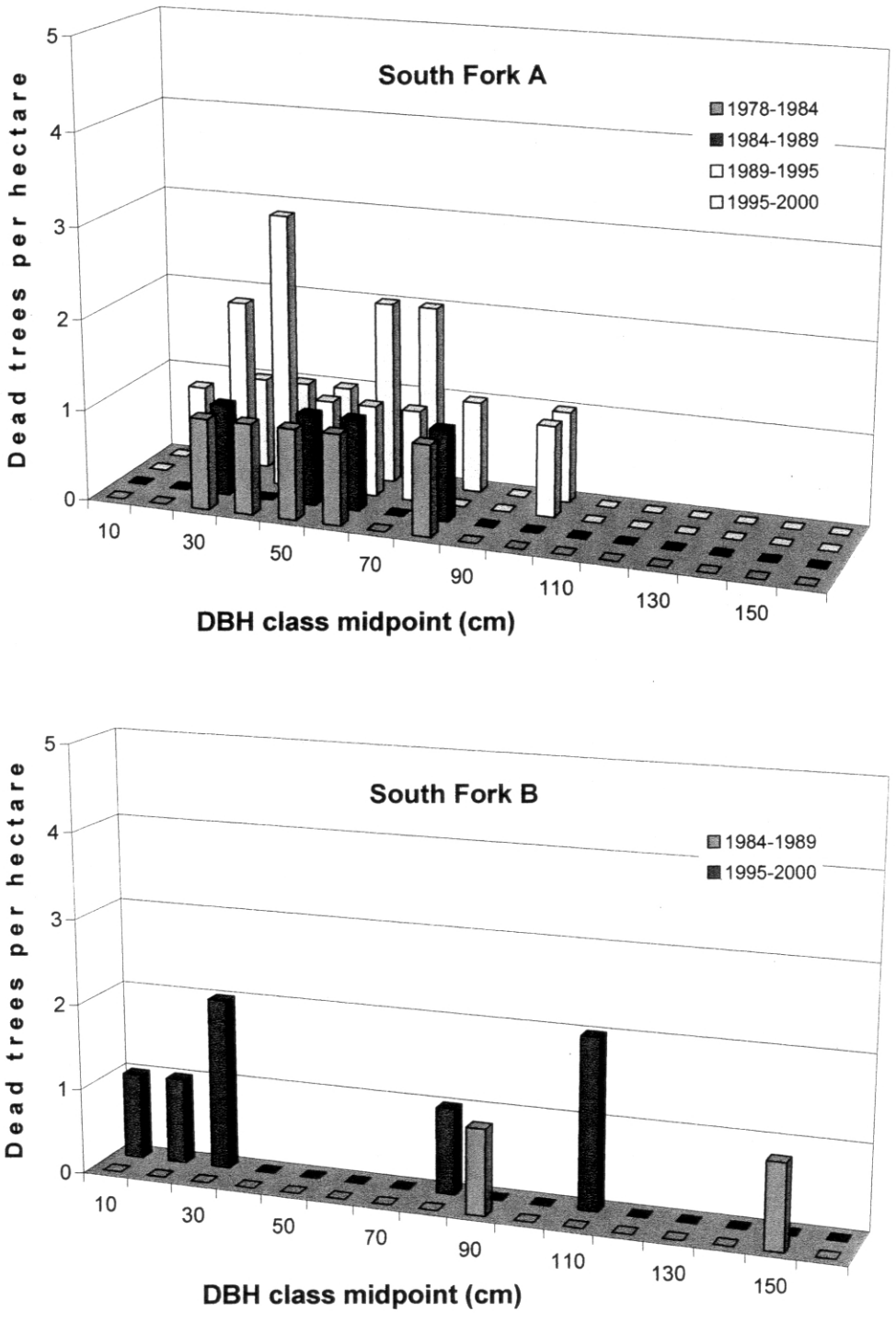

Figure 8A. Change in absolute mortality distribution by diameter class and period of remeasurement for western hemlock at the South Fork A and South Fork B study sites.

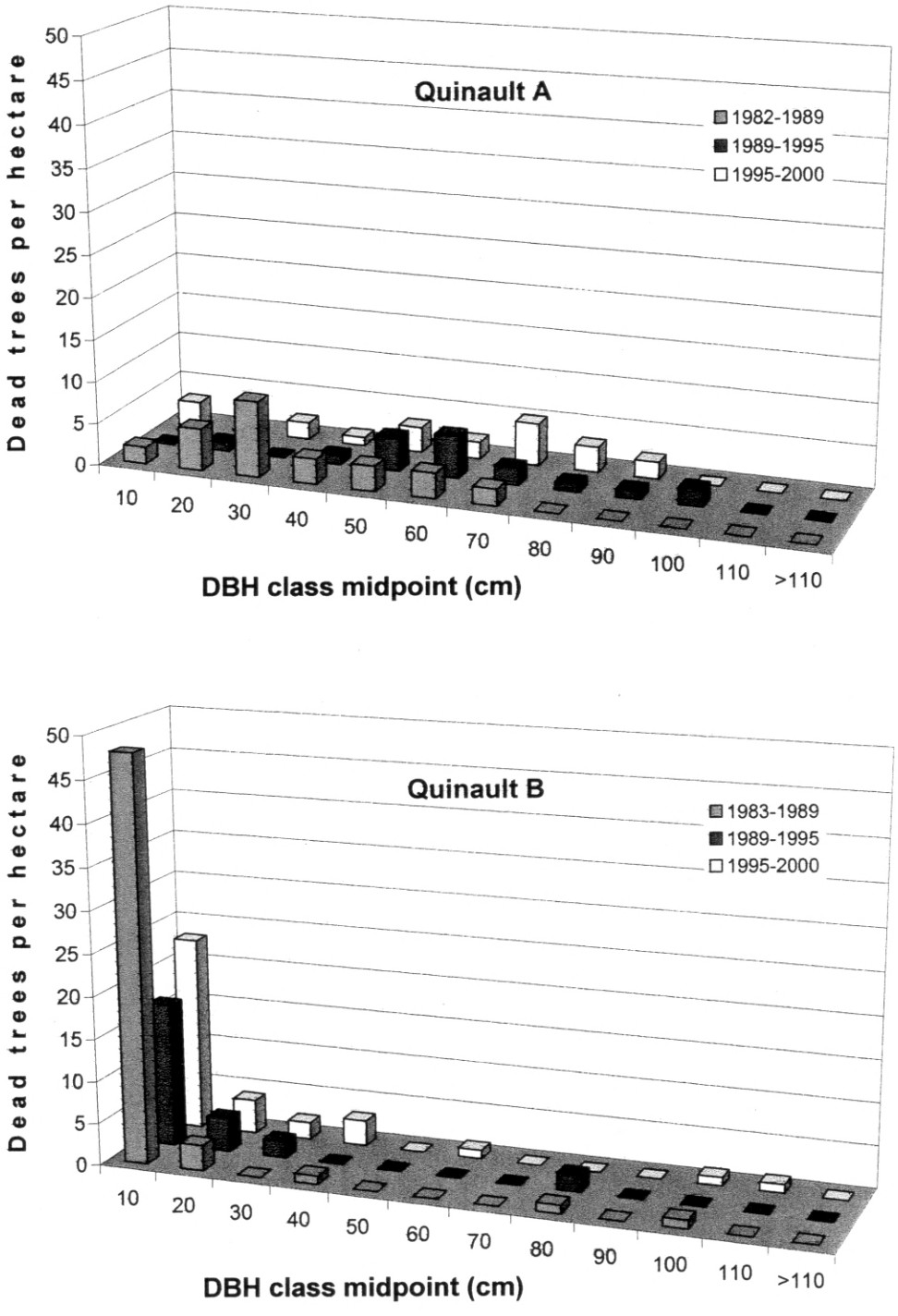

Figure 8B. Change in absolute mortality distribution by diameter class and period of remeasurement for western hemlock at the Quinault A and Quinault B study sites.

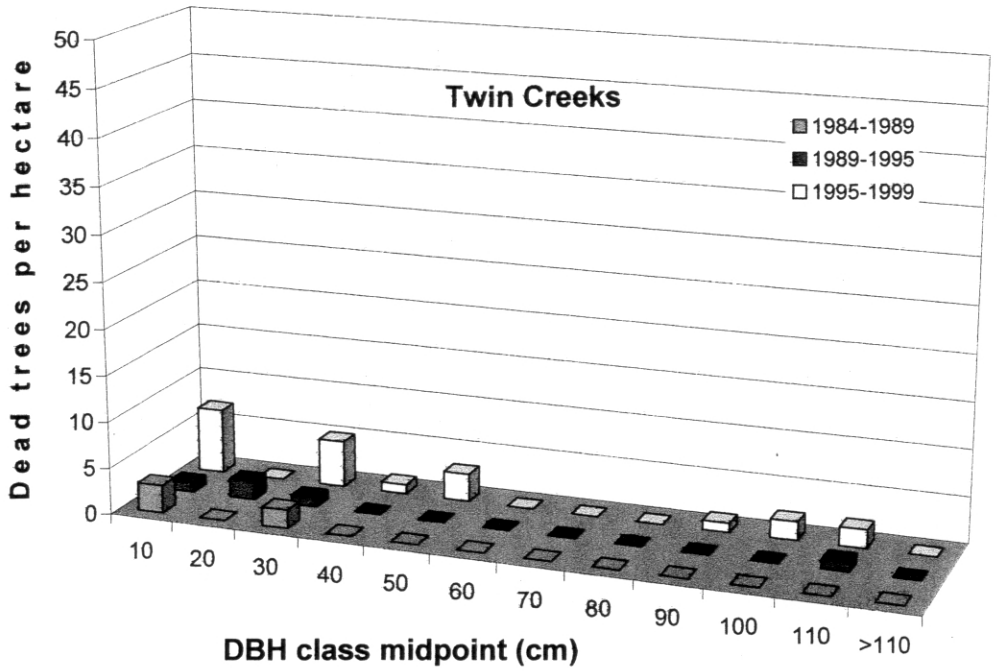

Figure 8C. Change in absolute mortality distribution by diameter class and period of remeasurement for western hemlock at the Twin Creeks study site.

Agents of Mortality

Among all the study sites over the entire period of observation, a total of 387 trees died, of which 142 were Sitka spruce and 240 were western hemlock (Table 7). Without including the unknown category, suppression was the leading cause of Sitka spruce mortality (24 trees/ha). Most of these suppressed trees were in the 10-cm diameter class (Figure 7), thus there were small losses in volume (Table 8). Crushing was the second most common cause of death for spruce, followed by windthrow and windbreak. Similar to death by suppression, most of the crushed spruces were small, whereas the trees killed by windthrow and windbreak were in the larger diameter classes ($\geq$130 cm DBH). In this latter case, the losses in volume were large (Table 8). The number of spruce killed by snow and insects was insignificant. However, the relative importance of mortality agents varied among study sites. For example, at Quinault A and B, no trees died by suppression, while the remaining study sites the number of trees that died by this cause ranged between 6 and 10 (Table 7). At Quinault A, the only living spruce was large and healthy.

The most common cause of known mortality in western hemlock was snow loading (46 dead trees/ha), which were all in the 10-cm diameter class at the Quinault B study site. This mortality resulted in little loss of volume (Table 8). Suppression and crushing were the second most common identifiable cause of death for hemlock (25 dead trees/ha each). Similar to Sitka spruce, most of the hemlocks killed by suppression and crushing were small (10- to 20-cm diameter class), which resulted in low loss in volume (Table 8). The

remaining agents of mortality for western hemlock were butt or root rots, windthrow, and windbreak (16-19 dead trees/ha; no mortality was assigned to insects). The mortality agents for western hemlock were very different among study sites. For example, all snow loading mortality (primarily small trees) occurred at Quinault B, while most of windbreak mortality (larger trees) occurred at Quinault A; as a result, losses in volume were greater than at Quinault A (Table 8, Figure 8).

The relative importance of these agents of mortality also changed over the period of study at the study sites. For example, crushing and windthrow were the leading causes of Sitka spruce mortality at South Fork A during the period 1990-1995, whereas that for this same species and study site unknown and suppression were the most common causes of mortality during the period 1996-2000 (Figure 9A). Similarly, for western hemlock mortality at South Fork A, crushing was the leading cause during the period 1978-1984, and windthrow was the most common cause during the interval 1990-1995 (Figure 9B).

Table 7. Total number of dead trees for whole stand, Sitka spruce, and western hemlock by agent of mortality in the study sites.

Whole stand	South Fork A	South Fork B	Quinault A	Quinualt B	Twin Creeks	Total	(%)
Unknown*	25	18	28	29	50	150	(38.8)
Suppression	11	7	5	15	11	49	(12.7)
Windthrow	14	4	4	2	3	27	(7.0)
Windbreak	6	1	15	2	1	25	(6.5)
Crushing	16	2	4	14	4	40	(10.3)
Snow loading				46	2	48	(12.4)
Butt or root rots	5	2	8	7	3	25	(6.5)
Insects	1	1				2	(0.5)
Other	7	3	1	3	7	21	(5.4)
Total	85	38	65	118	81	387	(100)
Sitka spruce	**South Fork A**	**South Fork B**	**Quinault A**	**Quinualt B**	**Twin Creeks**	**Total**	**(%)**
Unknown*	20	13		1	25	59	(41.5)
Suppression	10	6			8	24	(16.9)
Windthrow	8	3				11	(7.7)
Windbreak	3	1		2	1	7	(4.9)
Crushing	12	2			1	15	(10.6)
Snow loading					2	2	(1.4)
Butt or root rots	2	1		1	2	6	(4.2)
Insects	1	1				2	(1.4)
Other	6	3			7	16	(11.3)
Total	62	30	0	4	46	142	(100)
Western hemlock	**South Fork A**	**South Fork B**	**Quinault A**	**Quinualt B**	**Twin Creeks**	**Total**	**(%)**
Unknown*	5	5	28	28	21	87	(36.3)
Suppression	1	1	5	15	3	25	(10.4)
Windthrow	6	1	4	2	3	16	(6.7)
Windbreak	2		15			17	(7.1)
Crushing	4		4	14	3	25	(10.4)
Snow loading				46		46	(19.2)
Butt or root rots	3	1	8	6	1	19	(7.9)
Insects						0	(0)
Other	1		1	3		5	(2.1)
Total	22	8	65	114	31	240	(100)

* Includes missing trees

Table 8. Total volume of dead trees (m^3) in the study sites for the whole stand, Sitka spruce, and western hemlock by agent of mortality.

Whole stand	South Fork A	South Fork B	Quinault A	Quinualt B	Twin Creeks	Total	(%)
Unknown*	46.2	40.9	78.7	53.0	313.1	531.9	(38.0)
Suppression	1.1	0.1	1.8	0.7	0.4	4.1	(0.3)
Windthrow	184.6	22.8	14.1	14.7	4.8	241.0	(17.2)
Windbreak	109.6	28.6	64.4	30.8	46.5	279.9	(20.0)
Crushing	10.0	0.1	11.2	3.6	1.6	26.5	(1.9)
Snow loading	--	--	--	0.9	0.0	0.9	(0.1)
Butt or root rots	90.2	50.7	46.7	32.6	52.9	273.1	(19.5)
Insects	0.0	0.0	--	--	--	0.0	(0.0)
Other	14.8	28.4	0.0	0.1	0.1	43.3	(3.1)
Total	456.4	171.5	216.9	136.4	419.4	1,400.5	(100)
Sitka spruce	**South Fork A**	**South Fork B**	**Quinault A**	**Quinualt B**	**Twin Creeks**	**Total**	**(%)**
Unknown*	27.5	1.6	--	20.5	110.5	160.1	(21.1)
Suppression	0.1	0.1	--	--	0.2	0.4	(0.1)
Windthrow	165.0	17.9	--	--	--	182.9	(24.1)
Windbreak	85.7	28.6	--	30.8	46.5	191.6	(25.2)
Crushing	0.2	0.1	--	--	0.0	0.3	(0.0)
Snow loading			--	--	0.0	0.0	(0.0)
Butt or root rots	82.0	42.5	--	4.7	52.3	181.5	(23.9)
Insects	0.0	0.0	--	--	--	0.0	(0.0)
Other	14.3	28.4	--	--	0.1	42.7	(5.6)
Total	374.7	119.1	--	56.0	209.6	759.4	(100)
Western hemlock	**South Fork A**	**South Fork B**	**Quinault A**	**Quinualt B**	**Twin Creeks**	**Total**	**(%)**
Unknown*	18.7	39.3	78.7	32.5	95.2	264.4	(50.7)
Suppression	1.0	0.0	1.8	0.7	0.2	3.7	(0.7)
Windthrow	19.6	4.9	14.1	14.7	4.8	58.1	(11.1)
Windbreak	11.3	--	64.4	--	--	75.7	(14.5)
Crushing	9.8	--	11.2	3.6	1.6	26.2	(5.0)
Snow loading	--	--	--	0.9	--	0.9	(0.2)
Butt or root rots	8.2	8.2	46.7	27.9	0.6	91.6	(17.6)
Insects	--	--	--	--	--	0.0	(0.0)
Other	0.5	--	0.0	0.1	--	0.6	(0.1)
Total	69.1	52.4	216.9	80.4	102.4	521.1	(100)

* Includes missing trees.
-- No mortality in this category.

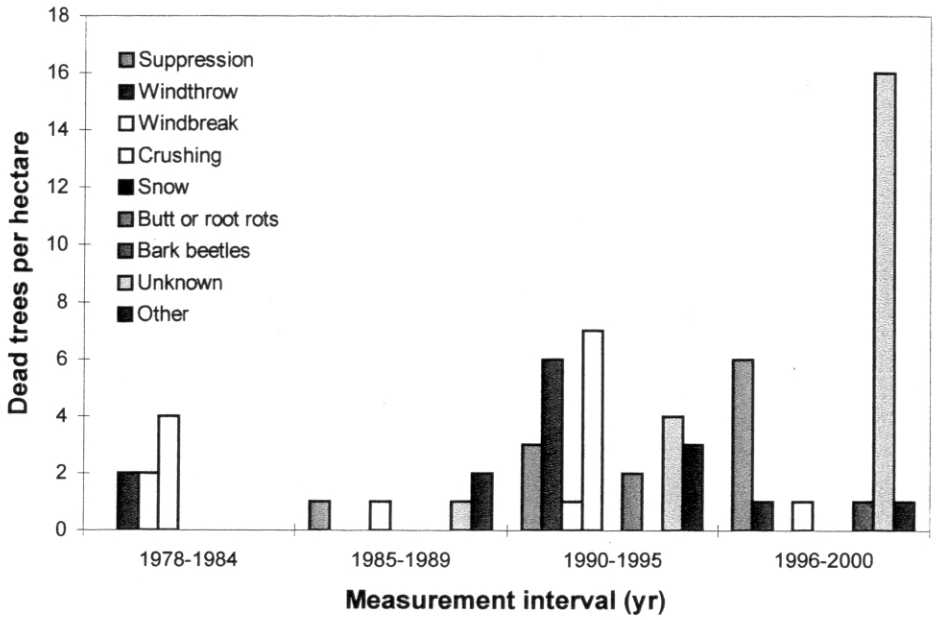

Figure 9A. Variation of mortality causes for Sitka spruce by measurement interval at the South Fork A study site.

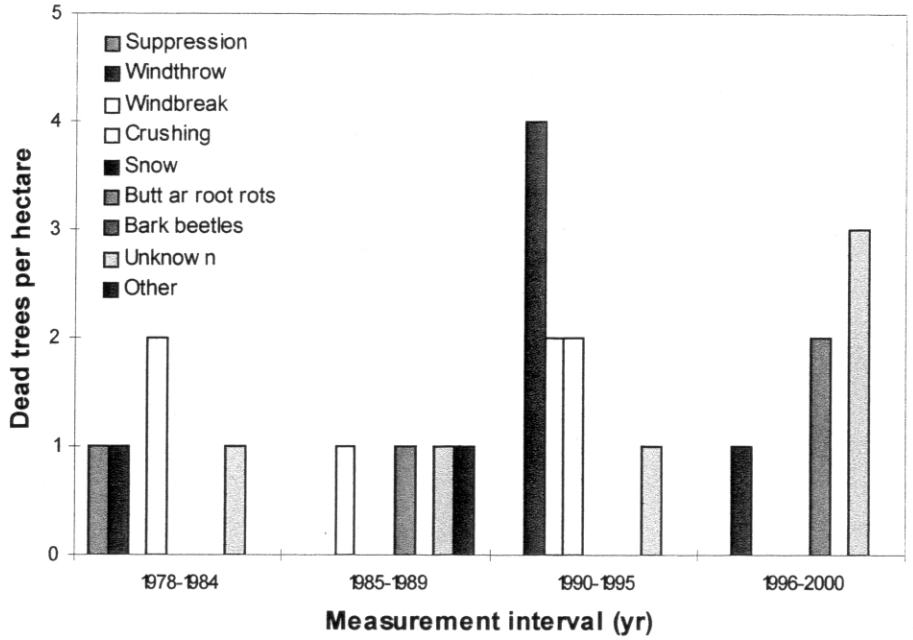

Figure 9B. Variation of mortality causes for western hemlock by measurement interval at the South Fork A study site.

BIOMASS TRENDS

Trends in the rate of accumulation of bole biomass, net primary production of boles, and loss of bole biomass through mortality varied considerably among the five study sites, both for the total stand and for species (Figures 11-13). For the total stand, bole biomass stocks were greater at the older study sites (554 to 764 Mg ha^{-1} at South Fork A and South Fork B) than at the younger study sites (374 to 528 Mg ha^{-1} at Quinault A, Quinault B, and Twin Creeks) (Figure 10a). Furthermore, over the entire period of measurement, the rate of accumulation of bole biomass was positive in just two of the five study sites (South Fork B and Quinault B) (Table 9), which resulted in a leveled or upward general trend of bole biomass accumulation over the years (Figure 10a).

Trends in bole biomass accumulation also showed large fluctuations over time. For example, at South Fork A, bole biomass for the total stand accumulated at an irregular rate that fluctuated from -10.0 Mg ha^{-1} $year^{-1}$ during the first interval (1978-1984) to 2.5 Mg ha^{-1} $year^{-1}$ during the most recent interval (1995-2000), while at Quinault B, total bole biomass accumulated at a relatively more constant rate that fluctuated from 4.0 Mg ha^{-1} $year^{-1}$ in the first interval to 0.7 Mg ha^{-1} $year^{-1}$ in the most recent interval (Figure 10a).

Net primary production of boles (NPPB) for the total stand generally increased with time at the older study sites and was relatively constant at all but one of the younger sites

(Twin Creeks) (Figure 10b). In this latter case, NPPB increased significantly in the most recent interval. For example, at South Fork B, NPPB was 0.7 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 262 years (1984), and 19.1 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 278 years (2000). At Quinault A, NPPB was 3.6 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 217 years (1989), and 3.7 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 228 years (2000).

Loss of bole biomass through mortality for the total stand generally increased with time at all but one site (South Fork A) (Figure 10c). For example at Quinault A, tree mortality increased linearly from 2.2 Mg ha^{-1} $year^{-1}$ in the first interval (1982-1989) to 7.0 Mg ha^{-1} $year^{-1}$ in the most recent interval (1995-2000).

Trends of bole biomass stocks for Sitka spruce were similar to the trends followed by the total stand, reaching the highest stocks at the older study sites (460 to 675 Mg ha^{-1} at South Fork A and South Fork B) and the lowest stocks at the younger study sites (between 78.9 and 317.4 Mg ha^{-1} at Quinault A, Quinault B, and Twin Creeks) (Figures 10a and 11a). The rate of accumulation of tree bole biomass varied considerably as well. For example at South Fork A, bole biomass accumulated at a rate that fluctuated over time, from -10.4 Mg ha^{-1} $year^{-1}$ in the first interval (1978-1984) to 4.1 Mg ha^{-1} $year^{-1}$ in the most recent interval (1995-2000), whereas at Quinault A total bole biomass accumulated at a relatively more constant rate, from 0.2 Mg ha^{-1} $year^{-1}$ in the first interval (1982-1989) to 0.1 Mg ha^{-1} $year^{-1}$ in the most recent interval (1995-2000).

Net primary production for Sitka spruce varied a little more than net primary production for the total stand (Figures 10b and 11b). For example at South Fork B, Sitka spruce NPPB was 0.5 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 262 years (1984), and 14.2 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 278 years (2000), whereas at Quinault A NPPB for this same species was very low and relatively constant over time: 0.2 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 217 years (1989), and 0.1 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 228 years (2000).

Loss of bole biomass through mortality for Sitka spruce mortality varied even more among study sites than did total stand mortality (Figures 10c and 11c). For example at Quinault A, there was no tree mortality over the total study period (1982-2000), whereas at South Fork B loss of bole biomass started in the third interval (1989-1995) at a rate of 6.1 Mg ha^{-1} $year^{-1}$ and decreased to a rate of 3.1 Mg ha^{-1} $year^{-1}$ in the most recent interval (1995-2000).

Accumulations of bole biomass for western hemlock were different from those for the total stand or Sitka spruce (Figures 10a, 11a, and 12a). The highest stocks occurred at the youngest study sites (between 154 and 313 Mg ha^{-1} at Quinault A, Quinault B, and Twin Creeks) and the lowest stocks occurred at the oldest study sites (78 - 99 Mg ha^{-1} at South Fork A and South Fork B). The rate of accumulation of tree bole biomass varied considerably as well. For example at South Fork A, bole biomass accumulated at a rate that fluctuated over time from 0.4 Mg ha^{-1} $year^{-1}$ in the first interval (1978-1984) to –0.6

Mg ha^{-1} $year^{-1}$ in the most recent interval (1995-2000), whereas at Twin Creeks bole biomass accumulated a rate that fluctuated from 1.7 Mg ha^{-1} $year^{-1}$ in the first interval (1984-1989) to -5.2 Mg ha^{-1} $year^{-1}$ in the most recent interval (1995-1999).

NPPB for western hemlock also varied considerably compared to NPPB for the total stand or Sitka spruce (Figures 10b, 11b, and 12b). Western hemlock rates were relatively more constant at all but one (South Fork B) of the study sites. For example at Quinault A, western hemlock NPPB was 3.3 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 217 years (1989), and 3.6 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 228 years (2000), whereas at South Fork B, NPPB was low during the first intervals and then significantly increase in the more recent interval: 0.2 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 262 years (1984) and 4.8 Mg ha^{-1} $year^{-1}$ in the interval that ended at age 278 years (2000).

Loss of bole biomass through mortality for western hemlock differed even more than loss of bole biomass through mortality for the total stand and Sitka spruce (Figures 10c, 11c, and 12c). For example at South Fork A, mass of dead boles increased slightly from 0.8 Mg ha^{-1} $year^{-1}$ in the first interval (1978-1984) to 2.2 Mg ha^{-1} $year^{-1}$ in the most recent interval (1995-2000), whereas at Twin Creeks, mass of dead boles increased strongly from 0.1 Mg ha^{-1} $year^{-1}$ in the first interval (1984-1989) to 7.6 Mg ha^{-1} $year^{-1}$ in the most recent interval (1995-1999).

Table 9. Annual rates of accumulation in bole biomass (Mg ha^{-1} $year^{-1}$) at the five study sites during the entire study period.

Study site	Sitka spruce	Western hemlock	Total stand
South Fork A	-6.1	0.1	-6.2
South Fork B	1.9	0.6	2.5
Quinault A	0.4	-0.9	-0.5
Quinault B	1.4	0.1	1.5
Twin Creeks	-2.9	-0.7	-6.7
Average, all sites	-1.1	-0.2	-1.9

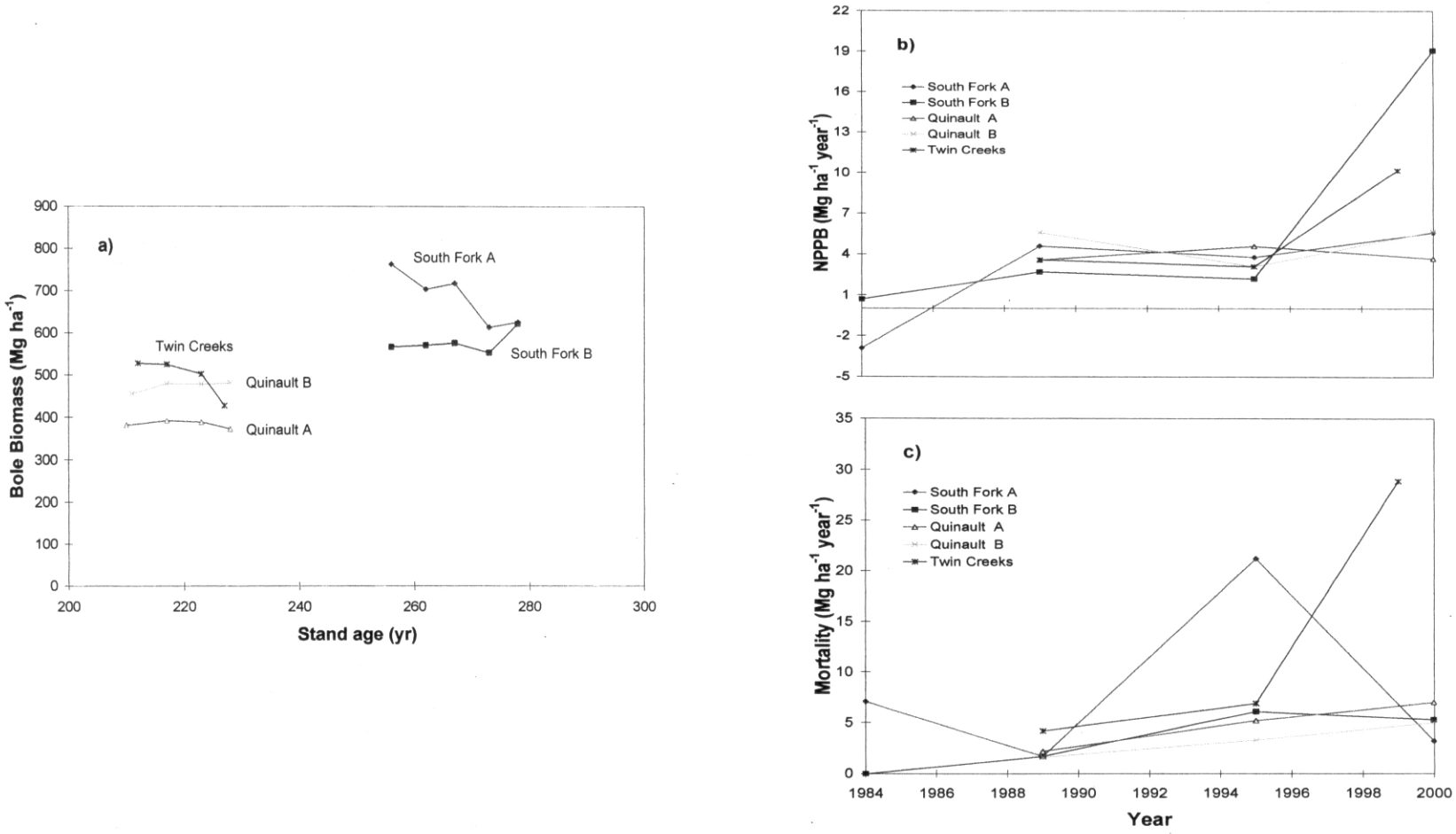

Figure 10. Changes in bole biomass (a), net primary production of boles (b) and loss of bole biomass through mortality (c) with time in the total stand at the five study sites.

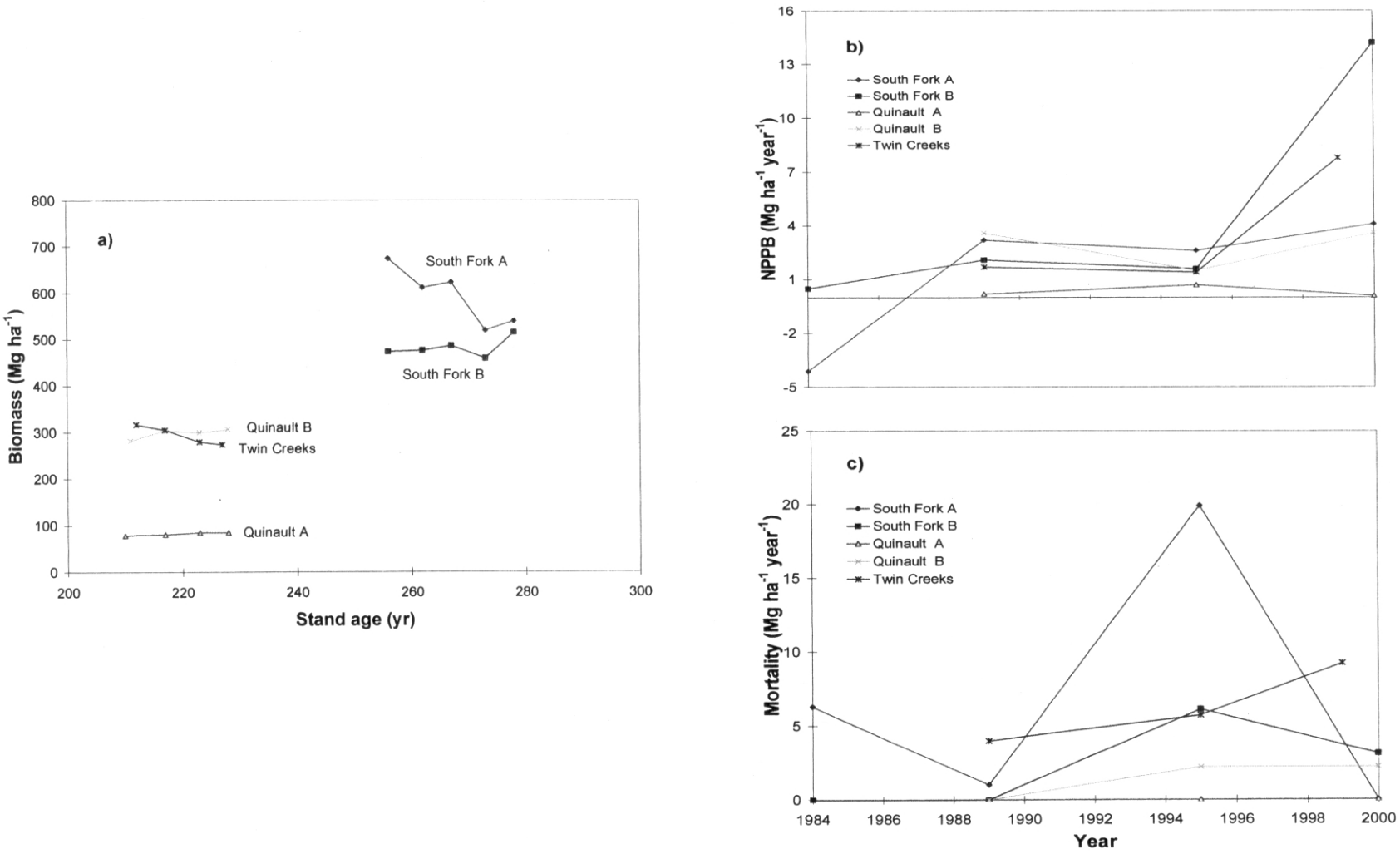

Figure 11. Changes in bole biomass (a), net primary production of boles (b) and loss of bole biomass through mortality (c) with time of Sitka spruce at the five study sites.

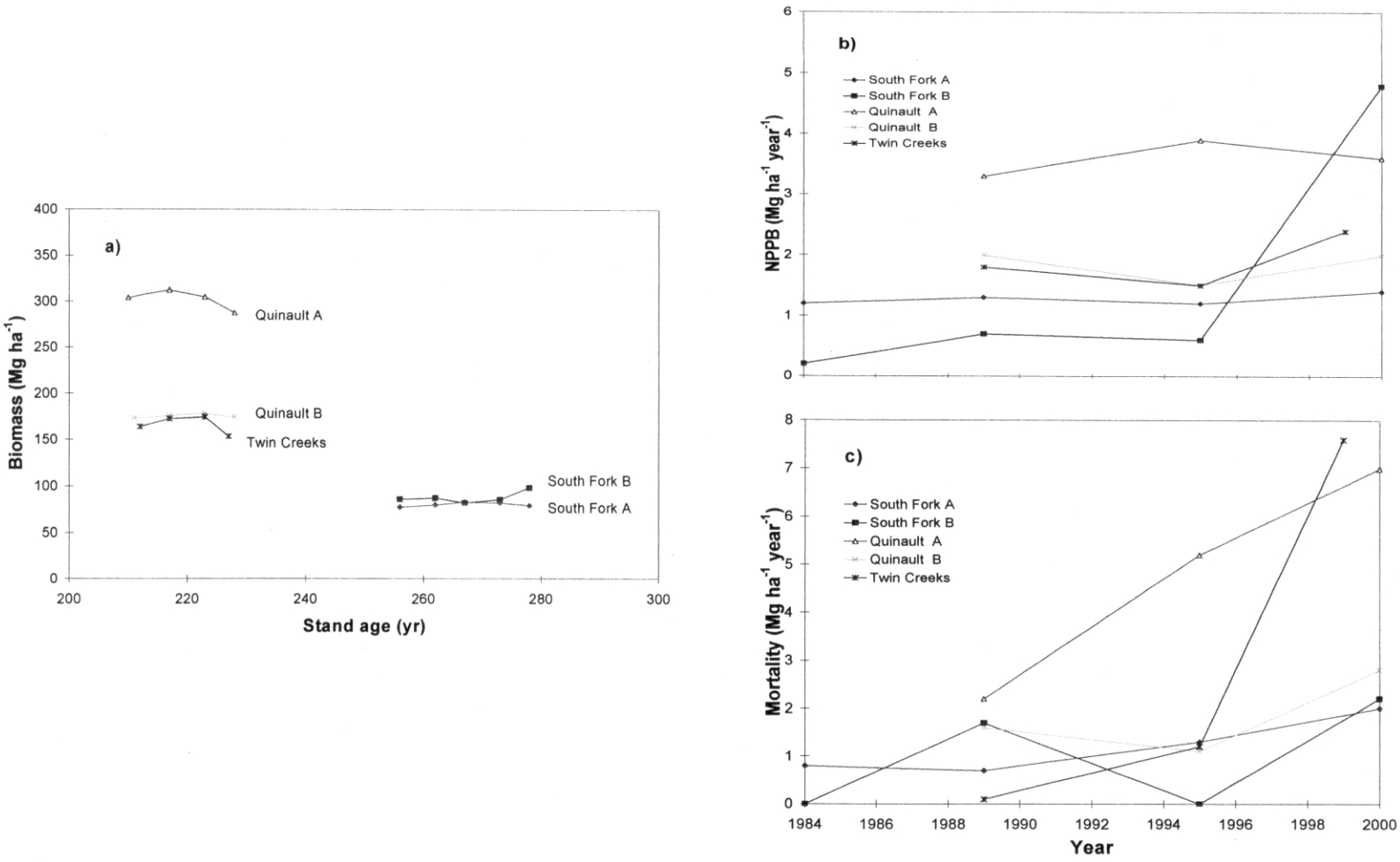

Figure 12. Changes in bole biomass (a), net primary production of boles (b) and loss of bole biomass through mortality (c) with time of western hemlock at the five study site

DISCUSSION

TREE POPULATION DYNAMICS

At the time of plot establishment, tree densities among study sites varied five-fold (75 to 370 trees/ha) and were consistently lower than densities reported by Harcombe et al. (1990) and Greene et al. (1992) for similar forests in the Oregon Coast Range (438 to 463 trees/ha). Differences between these study areas could be attributed to stand age or seral stage; the Coastal Oregon stands are approximately 100 years younger than the Olympic Peninsula stands (140 vs. 240 years on average). Thus, the stands are in a less developed stage with more individuals competing for light and nutrients, particularly the suppressed canopy strata.

According to Franklin et al. (2002) the coastal Oregon stands are near the end of the "maturation stage" (90-160 years), in which the pioneer cohort of trees attains maximum height and crown spread, and the understory begins to reestablish, including shade-tolerant trees. In contrast, the Olympic Peninsula stands are in the middle of the "vertical diversification stage" (160-320 years), in which there significant development of late-successional or old-growth forest attributes, particularly the development of canopy continuity between the ground and upper tree crowns.

At the last remeasurent (15 to 22 years later, depending on the study site), stem densities had increased dramatically at South Fork A and South Fork B (63.3% and 337.3%, respectively) and decreased both slightly and markedly in the remaining study sites (Quinault A and B, and Twin Creeks, respectively). Differences between these two groups of sites could be explained by the tree population dynamics (species composition and diameter distribution changes over time) rather than site characteristics, since overall site characteristics among stands are quite similar.

Sitka spruce presence relative to western hemlock was very similar at plot establishment at South Fork A, South Fork B, and Twin Creeks (71 vs. 77, 36 vs. 36, and 101 vs. 118 stems/ha, respectively), but low at Quinault A and Quinault B (1 vs. 224 and 30 vs. 340, respectively). At the study sites with similar proportion of both species, Sitka spruce stems were mostly in the 10-cm diameter class creating approximately a reverse J-shape curve (negative exponential distribution of density over size class), whereas at the sites with the lower number of Sitka spruce stems were spread out more or less uniformly through the intermediate diameter classes (70-160 DBH classes). At the last remeasurement, the more important change was in the 10-cm diameter class of Sitka spruce, which in the older stands increased significantly in number per hectare as a consequence of the massive ingrowth. At Twin Creeks the number of Sitka spruce in the 10-cm diameter class decreased a little as a result of stem advance in diameter class. Similar results for this type of forest were observed in Southeast Alaska and the Oregon

coast, appearing to confirm the intermediate shade-tolerance of this species (Deal 1987; Greene at al. 1992).

Diameter distributions for western hemlock were more variable than for Sitka spruce for both study sites and remeasurement times. At the time of plot establishment, just the Quinault B study site showed a negative exponential distribution, which is typical of shade-tolerant species that are increasing in density with numerous individuals in the smaller diameter classes (Barnes 1962; Deal 1987). The remaining study sites displayed approximately normal (Quinault B), lognormal (South Fork A), and un-even (Fork B, Twin Creeks) diameter distributions, which reflects not a single pattern of stand dynamics in similar forests. At the last remeasurement, important changes were observed at Fork B and Quinault A with a significant increase of stems in the 10-cm diameter class as a result of ingrowth. The remaining study sites advanced in diameter class but their distributions did not change significantly.

Greene et al. (1992) also observed a negative exponential distribution for western hemlock in a 130-year-old Sitka spruce-western hemlock stand at the Cascade Head Experimental Forest, Oregon. Furthermore, this type of distribution has been observed for other shade-tolerant species, such as *Tsuga canadensis*, *Thuja occidentalis*, and *Acer saccharum*, in the upper Great Lakes region of the United States (Craig et al. 2001).

Thus, some of these Olympic Peninsula sites represent an advanced stage of forest development with a significant number of western hemlock stems in the intermediate and larger diameter classes (South Fork A, Quinault A), which in turn could result in a replacement of Sitka spruce. In fact, some authors state that because of its greater shade tolerance, western hemlock is often considered to eventually replace Sitka spruce (Ruth and Harris 1979; Franklin and Dyrness 1988; Peterson et al. 1997). However, the heavy ingrowth of spruce in the 10-cm diameter class at some study sites (South Fork A and Twin Creeks) appears to also indicate that Sitka spruce could coexist with western hemlock as a climax species. Such co-existence could be attributed to the special conditions found in "rain forest" valleys of the Western Olympic Peninsula, particularly the relatively open nature of many of the stands and the selective grazing of hemlock seedlings by deer (Franklin et al. 1972).

Even though there are some typical trends for species, it should be recognized that diameter distributions are dynamic, and that mortality as well as other factors will change the shape of a distribution.

RATES OF MORTALITY

Tree mortality rates varied among study sites for both the total stand (0.5-2.7 % per year) and the primary species (0.6-3.6% per year for Sitka spruce and 0.5-2.0 % per year for

western hemlock). The rates at some plots were comparable to other Sitka spruce-western hemlock stands in the Pacific Northwest and lower than in other cases. In a 130-year-old stand at the Cascade Head Experimental Forest, Oregon, total annual mortality rate was 2.8% and annual mortality rates of individual species were 1.6 and 3.2% for Sitka spruce and western hemlock, respectively (Greene et al. 1992). For 30-yr to 50-yr stands in southeast Alaska, annualized mortality was 1.2% for Sitka spruce and 1.7% for western hemlock (Deal et al. 1991). The average mortality rate for Douglas-fir stands in the Western Cascade Mountains of Washington and Oregon was 1.1% for mature and old-growth, and 2.0% for young forests (Bible 2001). These forests presented an inverse relationship among them according to the main species in the stands: Douglas-fir annual mortality rates decreased with stand age (2.0-0.7%), while the western hemlock mortality rates increased with stand age (0-0.4%).

At these study sites, despite a small difference in age among them (average: 256 and 211 yr for the older and younger sites, respectively, at the time of plot establishment) there was a greater annual mortality rate in the younger sites (average: 2.1 vs. 1.1%). These differences could be explained by different situations in stand composition and structure among them. The lowest whole stand annual mortality rate was observed at South Fork B (0.5%), the stand of lowest initial density (75 stems/ha) and similar tree proportion of the main species (48% for both Sitka spruce and western hemlock). A greater initial space among large stems promoted a massive ingrowth of spruce that greatly exceeded the relatively few trees that died during the total period of measurement (269 vs 28).

Furthermore, higher light levels through canopy allowed better growth of the hemlock seedlings already present, which in turn led to get a low mortality rate. Worrel and Malcom (1990) also observed this pattern for Sitka spruce stands in northern Britain.

On the other hand, the greatest rate of annual mortality for the total stand was observed at Twin Creeks (2.7%), which was not the stand of highest initial density, but it was the stand with the highest number of Sitka spruce stems comprised in the smallest diameter class (10-cm). This situation probably generated a strong competition for the available resources (especially light) among the suppressed cohort, which contributed to the increase in whole stand annual mortality rate.

Individual annual mortality rates for species were also different among study sites. Sitka spruce annual mortality rate was much higher than for western hemlock at South Fork A and Twin Creeks (2.2 vs. 1.3% and 3.6 vs. 1.9%, respectively), whereas the annual mortality rates of western hemlock were much higher than for Sitka spruce at Quinault B and Quinault A (2.0 vs. 0.8% and 1.8 vs. 0%, respectively). Greene at al. 1992 also observed this situation in the Cascade Head Experimental Forest, Oregon (3.2% vs. 1.6% for western hemlock and Sitka spruce, respectively). Similar to the mortality rates by stand age, the differences among them can be explained by the stand composition and structure.

CAUSES OF MORTALITY

Inferring causes of tree mortality in a natural forest ecosystem is somewhat challenging and sometimes impossible because although tree death can be abrupt, it is more frequently a complex and gradual process with multiple factors contributing (Franklin et al. 1987). Hence, "unknown" was the most important cause of mortality in both this study and others (Edmonds et al. 1993; Hennon 1995; Bible 2001). Wind damage, including "windthrow" and "windbreak," accounted for 13.5% of the whole stand mortality, becoming the second most common cause of mortality in terms of number of dead trees; although some of this may actually have been result of root or butt rots. Wind damage was primarily focused on intermediate and larger trees and resulted in high loss of volume per hectare in the stand (37.2%). Suppression was the third-most common assigned cause of death, accounting for 12.7% of all dead trees. These two agents of mortality combined, wind damage and suppression, accounted for 88% of all dead trees at the Cascade Experimental Forest western hemlock-Sitka spruce stand (Green et al. 1992). The greater percentage at the Cascade Experimental Forest is probably because at that location most of the dead trees could be identified.

The results of Edmonds et al. (1993) in old-growth forests located in the West Twin Creek and Hoh Lake watersheds of the Olympic Peninsula are consistent with the results of this research; there "suppression-unknown" was the dominant cause of mortality averaging 56%, followed by "disease-insects" and "wind," which accounted for 18.4%

and 7.8%, respectively. In this research "suppression-unknown" combined, accounted for 51.5% of the mortality. Differences in the other causes of mortality, particularly less mortality by "wind" in the Edmonds' findings, were probably due to a more protected site condition in the West Twin Creek and Hoh Lake watersheds.

Among the known causes of mortality for species, wind damage also produced the highest mortality for Sitka spruce and western hemlock (12.6% and 13.8%, respectively). This damage was focused on big trees for Sitka spruce and intermediate-sized trees for western hemlock, which resulted in substantial loss of volume per hectare (49.3% and 25.6% of the species' volume, respectively). Suppression was also a common cause of death for Sitka spruce (16.9%), which was concentrated in the smaller size classes (0.1% of the species' volume). Surprisingly, the third most common cause of death for western hemlock was "snow loading" (19.2%), occurring in the smaller diameter class (0.2% of the species' volume). However, this occurred only at Quinault B as a consequence of a copious amount of heavy, wet snow that fell on small western hemlock trees during the earliest stage of this study (1983-1989) leaving them partially uprooted (Howard Bruner, *personal communication*). The reason why it did not happen in the adjacent study site (Quinault A) could be that the canopy structure is more closed at Quinault A. Bible (2001) found that "root and stem decay" were the primary causes of death for Douglas-fir (19.3%) and "wind or snow" and "suppression" were the primary causes of western hemlock mortality (28% each) in Western Cascade Mountains Douglas-fir forests.

The results of this research seem to support Edmonds and Marra's (1993) view about tree mortality causes in the Pacific Norwest forests. According to them, wind and diseases are the most important disturbance agents in coastal forests, especially in older forests. Storms are common in this area and a large wind storm blew down thousands of hectares on the Olympic Peninsula in 1921. Fire and insects are less important here than they are in the drier inland forests. Diseases strongly interact with wind, making it difficult to determine accurately which was the primary cause of death.

BIOMASS TRENDS

Even though there was not a linear relationship, the five study sites display two general trends in the rate of accumulation of bole biomass: relatively stable at Quinault A, Quinault B, and South Fork B; and negative at the South Fork A and Twin Creek study sites. Thus, these results support, in part, the generally accepted notion that biomass accumulation declines with stand age (Loucks 1970). The fluctuating trend observed at all of the study sites is consistent with the results obtained by Acker et al. (2002) for Douglas-fir old-growth forest in the western Oregon Cascade Range. At Quinault A, Quinault B, and South fork B, the relative constancy of biomass in the study period is likely due to time lags in tree regeneration, asynchronous tree mortality, and little overall decline in net primary production of boles.

A decrease in net primary production of boles and an increase in tree mortality both contributed to the observed decrease in biomass accumulation with stand age (e.g. Twin Creeks during the second measurement interval). Conversely, an increase in net primary production of boles and a decrease in tree mortality both contributed to the observed increase biomass with stand age (e.g. South Fork B during the most recent interval measurement). Constant biomass over time implied a balance between net primary production and mortality (e.g. Quinault B during the second measurement interval). Acker et al. (2002) found similar relationships among these variables in Douglas-fir forests of contrasting age in the western Oregon Cascade Range. Thus, the apparent decrease in biomass accumulation with stand age appears to be the result, in roughly equal parts, of a decrease in production and an increase in mortality. Similarly, above-ground biomass increases only if production of boles exceeds biomass loss via tree mortality.

The higher bole biomass stocks at the older study sites (South Fork A and South B) appear to indicate that most of the younger forests may continue accumulating bole biomass for at least some period. At South Fork A, maximum biomass stock occurred at the beginning of the study (764 Mg ha^{-1} at the age of 254 yr), then systematically diminished, suggesting that biomass in this stand peaked at a younger age. At South Fork B, maximum biomass occurred at the end of the study (554 Mg ha^{-1} at the age of 278 yr), which suggest that this stand may be able to accumulate more bole biomass. At the younger study sites the maximum biomass ranged between 374 and 528 Mg ha^{-1}

(Quinault A sand Twin Creeks, respectively). Harcombe (1990) reported peaks of biomass at 600 to 900 Mg ha^{-1} in the Cascade Head Experimental Forest, which appear to be similar to those observed at South Fork A. Only continued observation can reveal whether live biomass will remain relatively constant or not in these study sites over the long run.

Variation in bole biomass between older study sites was related to the abundance of Sitka spruce, while variation in bole biomass among younger study sites was related to abundance of western hemlock. That is observed in the similar trends of bole biomass displayed for these species and the whole stand at those study sites. This pattern is the result of the relative importance of each species in the stand through the study period. The bole biomass trends observed at the older study sites are consistent with the trends previously found by Harcombe et al (1990) at the Cascade Experimental Forest.

CONSEQUENCES OF TREE MORTALITY FOR ECOSYSTEM PROCESSES

Tree mortality occurs throughout stand life; however, it is more important in two development stages: the "biomass accumulation/competitive exclusion stage" and the "maturation stage" (Franklin et al. 2002). The "biomass accumulation/competitive exclusion" stage occurs in young stands and is characterized by density-dependent tree mortality or self-thinning. At this point, intense intra-tree competition occurs in dense

stands resulting in high mortality, primarily of trees at the low end of the stand diameter distribution. The maturation stage occurs in older stands, when the pioneer cohort of trees attains maximum height and crown spread. At this stage, tree mortality shift from competitive to non-competitive causes. Insects, diseases, and wind become much more important causes of mortality, affecting all sizes of trees (Oliver and Larson 1996; Franklin et al. 2002). The old-growth stands of this study showed that wind and diseases, but not insects, were the main mortality factors. The impact of weather-caused mortality is because of the closeness to the sea and the predominant maritime climate in the study area. Maritime conditions, characterized by relatively low temperatures and heavy precipitation during most of the year also would account for proliferation of fungal pathogens, root rots in particular.

The importance of tree mortality reflects the multiple roles that a tree plays in an ecosystem. At the time that a tree dies, it has only partially fulfilled its potential ecological function. In its dead form, a tree continues to play numerous roles for its surrounding organisms. The impact of this dead individual gradually fades as it is decomposed and its resources are dispersed, but the woody structure may remain for centuries and influence habitat conditions for millenia (Franklin et al. 1987). Tree death substantially increases the basic resources available to other organisms in the ecosystem, such as light, nutrients, and water, which increase with a larger number of dead trees. The dead tree is itself a major new resource for the ecosystem, whether as a snag or as a downed log. Snags and logs provide habitat for plants and animals species, which in turn

enrich the stand composition and structure. Additionally, death of big trees creates canopy gaps, which in many cases is the only possible strategy to ensure regeneration (Ruth and Harris 1979; Peterson et al. 1997). For all the above reasons, tree mortality is an important process in the development of forest ecosystems that deserves further study.

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APPENDICES

Appendix A: Summary statistics for study plots by species and remeasurement year

S. Fork Hoh River Plot 1

Species	Trees per hectare				
	1978	1984	1989	1995	2000
Sitka spruce	78	130	178	212	218
Western hemlock	87	83	81	72	69
Western redcedar	1	1	1	1	1
Douglas-fir	1	1	1	1	1
Total	167	215	261	286	289
Species	Basal area (m^2/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	52.9	53.3	53.8	38.9	40.6
Western hemlock	19.5	19.7	20.5	20.2	18.4
Western redcedar	0.7	0.7	0.7	0.8	0.8
Douglas-fir	1.4	1.4	1.4	1.5	1.5
Total	74.5	75.1	76.4	61.4	61.3
Species	Volume (m^3/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	1,051.1	1,054.6	1,063.9	753.7	785.6
Western hemlock	272.1	278.4	292.7	292.0	267.2
Western redcedar	7.4	8.0	8.3	8.9	9.3
Douglas-fir	18.5	19.1	19.7	20.3	21.2
Total	1,349.1	1,360.1	1,384.6	1,074.9	1,083.3
Species	Biomass (Mg/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	456.2	457.7	461.7	327.1	341.0
Western hemlock	101.7	104.1	109.5	109.2	99.9
Western redcedar	2.4	2.5	2.6	2.8	3.0
Douglas-fir	8.3	8.6	8.8	9.1	9.5
Total	568.6	572.9	582.6	448.2.	453.4

S. Fork Hoh River Plot 2

Species	Trees per hectare				
	1978	1984	1989	1995	2000
Sitka spruce	64	77	98	119	139
Western hemlock	67	64	64	59	59
Western redcedar	1	1	1	1	1
Douglas-fir	1	1	1	1	0
Total	133	143	164	180	199
Species	Basal area (m^2/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	92.4	85.4	87.2	78.4	81.2
Western hemlock	11.1	11.4	11.5	11.1	11.6
Western redcedar	0.2	0.2	0.3	0.3	0.3
Douglas-fir	1.7	1.8	1.8	1.8	0.0
Total	105.4	98.8	100.8	91.6	93.1
Species	Volume (m^3/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	1,897.4	1,766.5	1,808.5	1,641.0	1,703.4
Western hemlock	144.0	150.0	152.3	148.3	158.1
Western redcedar	2.2	2.4	2.6	2.8	2.9
Douglas-fir	23.7	24.6	25.3	25.3	0.0
Total	2,067.3	1,943.5	1,988.7	1,817	1,864.4
Species	Biomass (Mg/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	893.5	766.7	784.9	712.2	739.3
Western hemlock	53.9	56.1	56.9	55.5	59.1
Western redcedar	0.7	0.8	0.8	0.9	0.9
Douglas-fir	10.7	11.1	11.4	11.4	0.0
Total	958.8	834.7	854.0	780.0	799.3

S. Fork Hoh River Plot 3

Species	Trees per hectare				
	1978	1984	1989	1995	2000
Sitka spruce	43	108	195	256	290
Western hemlock	24	27	27	31	28
Western redcedar	1	1	1	1	1
Red alder	2	2	2	2	2
Total	70	138	225	290	321
Species	Basal area (m^2/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	46.5	46.9	49.1	47.9	51.7
Western hemlock	6.5	6.8	4.7	5.0	10.3
Western redcedar	2.4	2.4	2.4	2.5	2.6
Red alder	0.6	0.6	0.6	0.7	0.7
Total	56.0	56.7	56.8	56.1	65.3
Species	Volume (m^3/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	1,021.4	1,018.8	1,053.4	999.5	1,091.9
Western hemlock	100.0	103.4	62.7	67.4	182.1
Western redcedar	30.8	30.8	30.4	31.3	32.9
Red alder	7.0	7.4	7.9	8.4	9.0
Total	1,159.2	1,160.4	1,154.4	1,160.6	1,315.9
Species	Biomass (Mg/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	443.3	442.2	457.2	433.8	473.9
Western hemlock	37.4	38.7	23.4	25.2	68.1
Western redcedar	9.8	9.8	9.7	9.9	10.5
Red alder	2.6	2.7	2.9	3.1	3.3
Total	493.1	493.4	493.2	472.0	555.8

S. Fork Hoh River Plot 4

Species	Trees per hectare				
	1978	1984	1989	1995	2000
Sitka spruce	28	83	130	227	262
Western hemlock	47	47	48	53	65
Western redcedar	0	0	0	0	1
Red alder	1	1	5	5	6
Total	76	131	183	285	334
Species	Basal area (m^2/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	53.8	54.7	55.6	52.8	59.2
Western hemlock	22.1	22.4	23.1	23.9	21.2
Western redcedar	0.0	0.0	0.0	0.0	0.0
Red alder	0.4	0.4	0.5	0.5	0.6
Total	76.3	77.5	79.2	77.2	81.0
Species	Volume (m^3/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	1,162.5	1,177.4	1,190.6	1,120.3	1,284.1
Western hemlock	361.1	365.5	378.9	392.6	346.6
Western redcedar	0.0	0.0	0.0	0.0	0.0
Red alder	5.3	5.8	5.8	6.3	6.9
Total	1,528.9	1,548.7	1,575.3	1,519.2	1,637.6
Species	Biomass (Mg/ha)				
	1978	1984	1989	1995	2000
Sitka spruce	504.5	511.0	516.7	486.2	557.3
Western hemlock	135.1	136.7	141.7	146.8	129.6
Western redcedar	0.0	0.0	0.0	0.0	0.0
Red alder	2.0	2.1	2.2	2.3	2.6
Total	641.6	649.8	660.6	635.3	689.5

Quinault RNA Plot 1

Species	Trees per hectare			
	1982	1989	1995	2000
Sitka spruce	1	1	1	1
Western hemlock	224	212	211	198
Total	225	213	212	199
Species	Basal area (m^2/ha)			
	1982	1989	1995	2000
Sitka spruce	6.9	7.1	7.4	7.4
Western hemlock	58.1	58.3	56.4	52.8
Total	65.0	65.4	63.8	60.2
Species	Volume (m^3/ha)			
	1982	1989	1995	2000
Sitka spruce	181.7	185.8	195.2	196.7
Western hemlock	813.9	835.6	815.8	770.3
Total	995.6	1,021.4	1,011.0	967.0
Species	Biomass (Mg/ha)			
	1982	1989	1995	2000
Sitka spruce	78.9	80.6	84.7	85.4
Western hemlock	304.4	312.5	305.1	288.1
Total	383.3	393.1	389.8	373.5

Quinault RNA Plot 2

Species	Trees per hectare			
	1983	1989	1995	2000
Sitka spruce	30	31	29	27
Western hemlock	340	326	329	309
Cascara	0	0	1	1
Total	370	357	359	337
Species	Basal area (m^2/ha)			
	1983	1989	1995	2000
Sitka spruce	35.3	37.4	36.5	36.7
Western hemlock	33.8	34.2	34.6	33.8
Cascara	0.0	0.0	0.0	0.0
Total	69.1	71.6	71.1	70.5
Species	Volume (m^3/ha)			
	1983	1989	1995	2000
Sitka spruce	651.8	701.0	691.3	708.0
Western hemlock	463.9	470.9	477.8	467.3
Cascara	0.0	0.0	0.0	0.0
Total	1,115.7	1,171.9	1,169.1	1,175.3
Species	Biomass (Mg/ha)			
	1983	1989	1995	2000
Sitka spruce	282.9	304.2	300.0	307.3
Western hemlock	173.5	176.1	178.7	174.8
Cascara	0.0	0.0	0.0	0.0
Total	456.4	480.3	478.7	482.1

Twin Creeks RNA Plot 1

Species	Trees per hectare			
	1984	1989	1995	1999
Sitka spruce	101	96	90	75
Western hemlock	118	114	109	89
Douglas-fir	2	2	2	0
Cascara	0	0	2	0
Total	221	212	203	164
Species	Basal area (m^2/ha)			
	1984	1989	1995	1999
Sitka spruce	39.6	38.3	35.4	34.2
Western hemlock	28.4	29.7	30.1	26.4
Douglas-fir	7.0	7.1	7.2	0.0
Cascara	0.0	0.0	0.0	0.0
Total	75.0	75.1	72.7	60.6
Species	Volume (m^3/ha)			
	1984	1989	1995	1999
Sitka spruce	731.4	703.9	645.5	632.8
Western hemlock	439.1	461.7	467.0	411.3
Douglas-fir	101.1	105.3	107.3	0.0
Cascara	0.0	0.0	0.1	0.0
Total	1,274.6	1,270.9	1,219.9	1,044.1
Species	Biomass (Mg/ha)			
	1984	1989	1995	1999
Sitka spruce	317.4	305.5	280.1	274.6
Western hemlock	164.2	172.7	174.7	153.8
Douglas-fir	46.8	47.4	48.3	0.0
Cascara	0.0	0.0	0.0	0.0
Total	528.4	525.6	503.1	428.4

Appendix B: Diameter distribution tables of Sitka spruce for study plots at plot establishment and last remeasurement

S. Fork Hoh River Plot 1

DBH Class (cm)	Trees per hectare	
	1978	2000
10	47	168
20	0	26
30	0	3
40	0	0
50	1	0
60	0	0
70	0	0
80	1	0
90	0	1
100	1	1
110	1	0
120	2	1
130	6	3
140	8	4
150	1	4
160	2	1
170	3	2
180	2	2
190	0	0
200	1	0
210	2	2
220	0	0
230	0	0
240	0	0
250	0	0
260	0	0
270	0	0
280	0	0
290	0	0
300	0	0
310	0	0
>310	0	0
Total	78	218

S. Fork Hoh River Plot 2

DBH Class (cm)	Trees per hectare	
	1978	2000
10	17	96
20	1	6
30	0	1
40	0	0
50	0	0
60	0	1
70	0	0
80	1	1
90	1	0
100	0	1
110	3	1
120	2	1
130	2	1
140	5	1
150	5	3
160	8	6
170	6	4
180	7	7
190	2	3
200	3	3
210	0	2
220	0	0
230	0	0
240	1	0
250	0	1
260	0	0
270	0	0
280	0	0
290	0	0
300	0	0
310	0	0
>310	0	0
Total	64	139

S. Fork Hoh River Plot 3

DBH Class (cm)	Trees per hectare	
	1978	2000
10	23	197
20	2	53
30	0	20
40	0	3
50	0	1
60	0	0
70	0	0
80	1	1
90	1	1
100	1	0
110	0	0
120	0	1
130	0	0
140	0	0
150	2	1
160	3	2
170	0	0
180	3	0
190	1	3
200	2	1
210	1	1
220	0	1
230	0	0
240	1	2
250	1	0
260	1	2
270	0	0
280	0	0
290	0	0
300	0	0
310	0	0
>310	0	0
Total	43	290

S. Fork Hoh River Plot 4

DBH Class (cm)	Trees per hectare	
	1978	2000
10	5	211
20	0	25
30	0	6
40	0	0
50	0	0
60	1	0
70	0	1
80	0	0
90	2	0
100	0	0
110	0	0
120	1	1
130	1	0
140	1	1
150	3	2
160	1	1
170	1	1
180	3	0
190	5	7
200	1	0
210	1	3
220	0	0
230	0	0
240	1	1
250	0	0
260	0	1
270	1	1
280	0	0
290	0	0
300	0	0
310	0	0
>310	0	0
Total	28	262

Quinault RNA Plot 1

DBH Class (cm)	Trees per hectare	
	1982	2000
10	0	0
20	0	0
30	0	0
40	0	0
50	0	0
60	0	0
70	0	0
80	0	0
90	0	0
100	0	0
110	0	0
120	0	0
130	0	0
140	0	0
150	0	0
160	0	0
170	0	0
180	0	0
190	0	0
200	0	0
210	0	0
220	0	0
230	0	0
240	0	0
250	0	0
260	0	0
270	0	0
280	0	0
290	0	0
300	1	0
310	0	1
>310	0	0
Total	1	1

Quinault RNA Plot 2

DBH Class (cm)	Trees per hectare	
	1983	2000
10	1	1
20	0	1
30	0	0
40	0	0
50	0	0
60	0	0
70	3	1
80	2	2
90	2	1
100	1	2
110	3	0
120	4	3
130	4	2
140	4	2
150	4	7
160	1	2
170	0	2
180	0	0
190	0	0
200	1	0
210	0	1
220	0	0
230	0	0
240	0	0
250	0	0
260	0	0
270	0	0
280	0	0
290	0	0
300	0	0
310	0	0
>310	0	0
Total	30	27

Twin Creeks RNA Plot 1

DBH Class (cm)	Trees per hectare	
	1984	1999
10	60	39
20	10	6
30	0	4
40	0	0
50	0	0
60	1	1
70	1	0
80	3	2
90	3	3
100	1	2
110	4	1
120	4	5
130	4	2
140	1	3
150	3	1
160	2	3
170	3	1
180	0	1
190	1	1
200	0	0
210	0	0
220	0	0
230	0	0
240	0	0
250	0	0
260	0	0
270	0	0
280	0	0
290	0	0
300	0	0
310	0	0
>310	0	0
Total	101	75

Appendix C: Diameter distribution tables of western hemlock for study plots at plot establishment and last remeasurement.

S. Fork Hoh River Plot 1

DBH Class (cm)	Trees per hectare	
	1978	2000
10	2	7
20	6	2
30	17	6
40	20	10
50	10	14
60	12	11
70	8	9
80	7	3
90	3	4
100	1	2
110	0	0
120	0	0
130	1	1
140	0	0
150	0	0
160	0	0
170	0	0
180	0	0
190	0	0
200	0	0
210	0	0
220	0	0
230	0	0
240	0	0
>240	0	0
Total	87	69

S. Fork Hoh River Plot 2

DBH Class (cm)	Trees per hectare	
	1978	2000
10	1	6
20	6	3
30	17	6
40	21	10
50	11	19
60	6	10
70	1	0
80	1	1
90	2	2
100	0	1
110	1	1
120	0	0
130	0	0
140	0	0
150	0	0
160	0	0
170	0	0
180	0	0
190	0	0
200	0	0
210	0	0
220	0	0
230	0	0
240	0	0
>240	0	0
Total	67	59

S. Fork Hoh River Plot 3

DBH Class (cm)	Trees per hectare	
	1978	2000
10	2	6
20	3	2
30	3	4
40	2	1
50	4	6
60	3	1
70	4	2
80	1	4
90	1	0
100	0	0
110	0	0
120	0	1
130	0	0
140	0	0
150	1	0
160	0	0
170	0	0
180	0	0
190	0	0
200	0	0
210	0	0
220	0	0
230	0	0
240	0	1
>240	0	0
Total	24	28

S. Fork Hoh River Plot 4

DBH Class (cm)	Trees per hectare	
	1978	2000
10	1	23
20	3	1
30	2	4
40	6	4
50	4	4
60	5	3
70	5	8
80	7	6
90	4	3
100	1	2
110	4	2
120	3	2
130	1	2
140	0	0
150	1	0
160	0	0
170	0	1
180	0	0
190	0	0
200	0	0
210	0	0
220	0	0
230	0	0
240	0	0
>240	0	0
Total	47	65

Quinault RNA Plot 1

DBH Class (cm)	Trees per hectare	
	1978	2000
10	7	40
20	8	2
30	16	4
40	36	16
50	51	33
60	40	36
70	35	28
80	19	26
90	7	7
100	5	3
110	0	3
120	0	0
130	0	0
140	0	0
>140	0	0
Total	224	198

Quinault RNA Plot 2

DBH Class (cm)	Trees per hectare	
	1978	2000
10	153	131
20	51	44
30	56	48
40	36	30
50	6	20
60	3	5
70	6	5
80	12	7
90	8	8
100	7	8
110	1	2
120	1	1
130	0	0
140	0	0
>140	0	0
Total	340	309

Twin Creeks RNA Plot 1

DBH Class (cm)	Trees per hectare	
	1978	2000
10	17	5
20	12	8
30	38	17
40	14	22
50	6	8
60	7	2
70	1	9
80	2	1
90	3	2
100	9	6
110	4	4
120	3	3
130	2	1
140	0	1
>140	0	0
Total	118	89