Chapter 14

Aspects of Succession in the Coniferous Forests of the Pacific Northwest

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Introduction

Many forest phenomena achieve ultimate expression in the coniferous forests of coastal northwestern America. Coniferous species dominance is, in itself, unusual in a moist temperate region (Waring and Franklin 1979). Nearly every arboreal genus represented attains a size and life span at or near the generic maximum. Except for some *Eucalyptus* forests in Australia, biomass accumulations and leaf areas routinely exceed levels encountered in any other forest type. Accumulations of coarse woody debris are similarly large. Time scales are expanded by species longevity, infrequent disturbances, and relatively slow vegetative regrowth.

In this chapter we shall explore aspects of succession in the northwestern forests found from the crest of the Cascade Range to the Pacific Ocean. Emphasis is on newer findings since general descriptions of successional sequences are already available (e.g., Franklin and Dyrness 1973). These include the persistent effects of the pioneer species, the variable nature of seres as revealed in age structure analyses, and importance of coarse woody debris. Our objectives are to: (1) provide contrasts with succession in temperate deciduous forests as well as with conifer forests in boreal and arid regions; (2) contrast recent understanding about succession in the Pacific Northwest with previous concepts; (3) examine the role of coarse woody debris in forest succession; and (4) suggest some problems northwestern forests present in successional modeling.

Regional Setting

The coastal Pacific Northwest is a mountainous region dominated by the Cascade Range, Olympic Mountains, Coast Ranges, and Siskiyou Mountains of Washington and Oregon (Heilman et al. 1979). Topography is

typically mountainous and rugged. Gentle intermountain regions, such as the Puget Trough and Willamette Valley, are not extensive. Forests extend from essentially sea level to 1600 m or more. Soils are typically youthful but moderately fertile and commonly surprisingly deep due to depositional processes.

The climate of the region favors forest development (Waring and Franklin 1979). Winters have mild temperatures and heavy precipitation. Summers are warm and relatively dry. This regime is believed to be a major factor in the dominance of conifers over deciduous hardwoods. Climate does vary substantially with geography and elevation. The mildest climates are in the coastal *Picea sitchensis* zone. The coolest environments are in the subalpine zones above 800–1200 m elevation, where winter snowpacks of up to 3 or 4 m may be developed.

Synecological studies in the region have shown that moisture and temperature are the primary environmental controls on plant community composition (Zobel et al. 1976). Both vary sharply over short distances in the broken mountain topography. Consequently, similar contrasts occur in the composition and structure of forest communities.

General Features of the Forests

Forests in the Pacific Northwest differ markedly in composition, structure, and function from the deciduous forests that dominate most mesic segments of the world's temperate zones. There are relatively few major tree species, and most are conifers (Table 14.1). Productivity can be very high as a record of 36.2 metric tons ha^{-1} yr^{-1} in a 26-year-old *Tsuga heterophylla* stand indicates (Fujimori 1972). Nevertheless, forest recovery following disturbance (as measured by leaf area, for example) typically requires several decades, and is substantially slower than deciduous forests (Bormann and Likens 1979a). Live above-ground biomass accumulations in old-growth forests (>250-year-old) forests average 700–900 metric tons/ha, and stands with over 1000 metric tons/ha are not uncommon (Franklin and Waring 1980). Leaf areas (one side only) range from 10 to 13 m^2/m^2 in one sample of stands (Franklin and Waring 1980). Gholz (1979) reports a maximum value of 20.2 m^2/m^2 in a *Picea sitchensis-Tsuga heterophylla* stand.

Several general successional sequences have been described in coastal Pacific Northwest forests (Franklin and Dyrness 1973). A typical sere in the *Tsuga heterophylla* zone would be

Pseudotsuga menziesii ⟶ *Tsuga heterophylla* ⟶ *Tsuga heterophylla*
                                    Thuja plicata

In the *Picea sitchensis* zone a normal sere would involve

$$\begin{array}{c} \textit{Picea sitchensis} \\ \textit{Tsuga heterophylla} \end{array} \longrightarrow \textit{Tsuga heterophylla}$$

.ft 1 *Alnus rubra* stands could conceivably occur as the first stage in either of these seres although its successional replacement by conifer stands is still unproven. A sere for the lower subalpine in the Cascade Range is

$$\begin{array}{c} \textit{Pseudotsuga menziesii} \\ \text{and/or} \\ \textit{Abies procera} \end{array} \longrightarrow \begin{array}{c} \textit{Tsuga heterophylla} \\ \textit{Abies amabilis} \end{array} \longrightarrow \textit{Abies amabilis}$$

Throughout most of the region under consideration *Tsuga heterophylla* and *Abies amabilis* are viewed as the major potential climax species based upon a variety of evidence, including size class analyses. Special habitats provide exceptions, such as the dry sites where *Pseudotsuga menziesii* or *Libocedrus decurrens* appear to be self-perpetuating. Some species of moderate shade tolerance, such as *Thuja plicata* and *Chamaecyparis nootkatensis*, typically reproduce poorly in old-growth stands. This may indicate subclimax status, or they may behave similarly to *Sequoia sempervirens*, which manages a stable age class distribution despite an apparent sparsity of reproduction at any one time (Stephen Viers 1979, pers. comm.).

Most tree species in the Pacific Northwest play multiple successional roles. In this discussion it is important to distinguish ecological roles from species' shade tolerances. Species colonizing a site early in a sere are playing a pioneer role. Species apparently capable of perpetuating themselves on a site in the absence of disturbance are playing a climax role. Although shade tolerance is often equated with a climax role and intolerance with a pioneer role, this need not be the case. Several intolerant species can form a stable type of climax if environmental conditions exclude their more tolerant associates. A prime northwestern example is the development of self-perpetuating stands of *Pseudotsuga menziesi* on habitats that are too dry for *Tsuga heterophylla* or *Abies grandis*. In other cases, environmental conditions need only favor the less tolerant associate, such as snowpack favoring reproduction of *Abies amabilis* over that of *Tsuga heterophylla* (Thornburgh 1969).

Similarly, essentially any of the shade-tolerant species can and do play pioneer roles on most sites where they are also climax. *Tsuga heterophylla* is conspicuous early in seres on cut-over forest lands in the *Picea sitchensis* zone. So is *Abies amabilis* on many high-elevation burns. This can be due to an absence of seed source for faster-growing intolerant species. In other cases, the growth rate of the tolerant species may be adequate to stay with or even exceed that of the intolerant species.

Table 14.1. Typical and maximum ages and dimensions attained by forest trees on better sites in the Pacific Northwest.[a]

Species	Typical			Maximum	
	Age (yr)	Diameter (cm)	Height (m)	Age (yr)	Diameter (cm)
Abies amabilis	400+	90-110	45-55	590	206
Abies grandis	300+	75-125	40-60	—	217
Abies procera	400+	100-150	45-70	>600	270
Acer macrophyllum	300+	50	15	—	250
Alnus rubra	100	55-75	30-40	—	145
Chamaecyparis lawsoniana	500+	120-180	60	—	359
Chamaecyparis nootkatensis	1000+	100-150	30-40	3500	297
Libocedrus decurrens	500+	90-120	45	>542	368
Picea sitchensis	500	180-230	70-75	>750	525
Pinus lambertiana	400	100-125	45-55	—	306
Pinus monticola	400+	110	60	615	197
Pinus ponderosa	600+	75-125	30-50	726	267
Populus trichocarpa	200+	75-90	25-35	—	293
Pseudotsuga menziesii	750+	150-220	70-80	1200	434
Quercus garryana	500	60-90	15-25	—	220
Sequoia sempervirens	1250+	150-380	75-100	2,200	501
Thuja plicata	1000+	150-300	60+	>1200	631
Tsuga heterophylla	400+	90-120	50-65	>500	260
Tsuga mertensiana	400+	75-100	35+	>800	221

[a]Based on Franklin and Waring (1980).

Scale in the Pacific Northwest

Many of the unique aspects of coastal Pacific Northwest forests result from an increase in the size and longevity of the tree species in comparison with other temperate and boreal forest regions. Pacific Northwestern tree species are well known for achieving large sizes and long life spans (Table 14.1). Consequently, compositional effects of a disturbance can persist for centuries or even millenia. The long-term persistence of seral species and infrequent catastrophic disturbances often combine to make achievement of climax stands hypothetical. Classical old-growth stands in the Pacific Northwest are actually not climax but, rather, draw much of their character from large seral *Pseudotsuga* (Franklin et al. 1981). This is apparent in stands of *Pseudotsuga* undisturbed for over 1000 years in Mount Rainier National Park (Table 14.2). Climax forests, on the other hand, are almost exclusively dominated by species of smaller stature and shorter life span, such as *Tsuga heterophylla* and *Abies amabilis*, and are not as impressive as those containing the larger, seral species. In forests with such extended seres the potential for direct observation of successional processes is obviously very limited.

The impact of the large, long-lived pioneer species extends to structural as well as compositional aspects of succession. These trees become sources of coarse woody debris—snags and down logs—after dying. These structures are important in many aspects of ecosystem function and composition (Franklin et al. 1980). *Pseudotsuga* produces relatively decay-resistant logs of large size. Between 480 and 580 years are believed necessary to eliminate 90% of an 80-cm diameter *Pseudotsuga* log (Joseph E. Means 1980, pers. comm.). In forests containing these species the accumulations of woody debris are greater and individual pieces are larger and more persistent than would be the case in a climax forest of *Tsuga heterophylla* or *Abies amabilis*. In this way the influence of a large seral tree is extended several centuries beyond the death of the last specimen. While climax composition might be achieved soon after the death of the last *Pseudotsuga* (say, in 1000 years), a stable forest structure based on the climax species could be delayed another 500 years. If one views *Thuja plicata* as a seral species (albeit one that extends the duration of its persistence on a site by some modest reproduction within the stand), many millenia would be necessary to achieve the idealized climax forest. Live trees would persist for several generations, and the large *Thuja* logs are even more resistant to decay than those of *Pseudotsuga*.

In spite of these problems, the climax concept is useful, and climax forests do exist. Forests that compositionally and structurally approximate hypothetical climax conditions are present in both temperate and subalpine regions of the Pacific Northwest. We suspect that these were typically (but not exclusively) developed where the climax species (e.g., *Tsuga heterophylla* or *Abies amabilis*) was the major or sole colonizing

Table 14.2. Pseudotsuga menziesii presence (percentage of plots where it occurs) and basal area and total basal area in three old-growth age classes at Mount Rainier National Park, Washington, on a series of 500- and 1000-m^2 plots located below 1350 m.

Age class (yr)	Number of plots	Pseudotsuga presence (%)	Basal area	
			Pseudotsuga	All species
350-600	114	67	26.9	98.4
750-1000	55	69	20.1	91.8
1000	9	33	11.9	73.9

species following the last disturbance. Forests dominated by climax species, with only a minor component of typical seral species, are even more common.

Disturbance frequency is a final area of contrast in scale between the Pacific Northwest and most other temperate and boreal forests. We hesitate to suggest that the geographic scale of the disturbances is necessarily any greater in the Pacific Northwest, despite the evidence for fire episodes that covered hundreds of thousands of hectares. Hurricanes and typhoons destroy vast reaches of temperate forests and wildfires destroy similar areas of boreal forests at a time in other parts of the world. The disturbance pattern in the Pacific Northwest is one of infrequent, holocaustic forest fires, however. A study of fire history over the last 1000 years indicates a natural fire rotation averaging 434 years within Mount Rainier National Park (Hemstrom 1979). Limited data from elsewhere in the region suggest that natural fire rotations of several centuries are typical. There are, of course, variations associated with habitat, topographic settings, or geographical locale (e.g., rain shadow of a mountain range). Natural fire rotation may also decline with latitude. The pattern of infrequent catastrophic, as opposed to frequent, light, burns is quite consistent, however.

Several other aspects of catastrophic fire in the Pacific Northwest are relevant to successional studies. Major fire episodes appear to correlate with climatic conditions. This is suggested by correspondance of fire episodes at Mount Rainier with reconstructed dry climatic periods (Hemstrom 1979). It is also suggested by the occurrence of similar forest age classes over large, but geographically isolated, segments of the region. In addition, fuel loadings are almost always heavy in these forests. This is not an environment in which fire suppression leads to unnaturally heavy fuel accumulations. Related to this is the fact that wildfires in these forests rarely consume much of the wood. Trees die and become snags and down logs, but several subsequent fires are necessary to consume a

majority of this woody debris. Even the tree foliage often escapes burn-
ing. Numerous examples of reburn, at least during historic times, sug-
gests that young stands (e.g., 25–75 years) are more susceptible to burn-
ing than later forest stages.

Revised Concepts about Succession in *Pseudotsuga* Forests

General descriptions of succession in northwestern *Pseudotsuga* forests
have been extant for many decades (e.g., Isaac 1943; Munger 1930,
1940). *Pseudotsuga* is described as rapidly occupying burned sites, fol-
lowed by reinvasion of the more shade-tolerant and fire-sensitive *Tsuga
heterophylla* and *Thuja plicata*. Establishment of the *Tsuga* and *Thuja* con-
tinue indefinitely under the canopy of the *Pseudotsuga*. Ultimately these
species replace *Pseudotsuga*, which are lost to wind throw, pathogens, or
other agents of mortality.

Such descriptions were largely anecdotal accounts rather than quantita-
tive analyses, however. They were based on observations of forest restab-
lishment following extensive wildfires in the mid-1800s and the Yacholt
(1902) and Tillamook (1933) burns. Later stages of succession were in-
ferred from species size-class patterns in mature and old-growth stands.
Modern successional studies have also, by necessity, relied heavily on
inferences drawn from size-class analyses. The great sizes and ages
achieved by trees limited the usefulness of tree coring and direct observa-
tion on sample plots.

Age structure analyses and historical reconstructions of *Pseudotsuga*
forests are now underway, however, utilizing sites scheduled for timber
cutting. Quantitative data on succession are accumulating rapidly and pro-
viding new insights, many of which run counter to previous dogma.

One surprising discovery from age structure analyses is the wide range
of ages in dominant *Pseudotsuga* in at least one age class of old-growth
(400–500-year-old) forests. This phenomenon was observed on Experi-
mental Watershed No. 10 at the H. J. Andrews Experimental Forest. This
10-ha watershed is located at 400-600 m elevation on the western slopes
of the central Oregon Cascade Range. In its pristine state the watershed
was occupied primarily by old-growth forests of *Pseudotsuga, Tsuga
heterophylla, Thuja plicata, Pinus lambertiana,* and *Castanopsis chrysophylla*
(Hawk 1979). Prior to logging, all trees greater than 5 cm diameter at
breast height were mapped, measured, and tagged. Followinging logging
in 1975, approximately 600 of 2800 trees, including a large proportion of
the dominant *Pseudotsuga*, were relocated and aged from ring counts on
stumps.

Watershed No. 10 appears to have been burned sometime around

1800, based on a younger generation of *Pseudotsuga* (Fig. 14.1) and sparsity of *Tsuga* over 200 years old. The most notable feature of the age structure is the broad range of ages in the old-growth *Pseudotsuga*, however (Fig. 14.2). This age structure indicates a very slow reestablishment of the new forest, following the catastrophic disturbance(s) that destroyed the forest present on the site over 500 years ago.

These results were so unexpected that confirmation was needed from age structure analyses in other stands before they were accepted. Much of Watershed No. 10 was relatively droughty and covered by a mosaic of
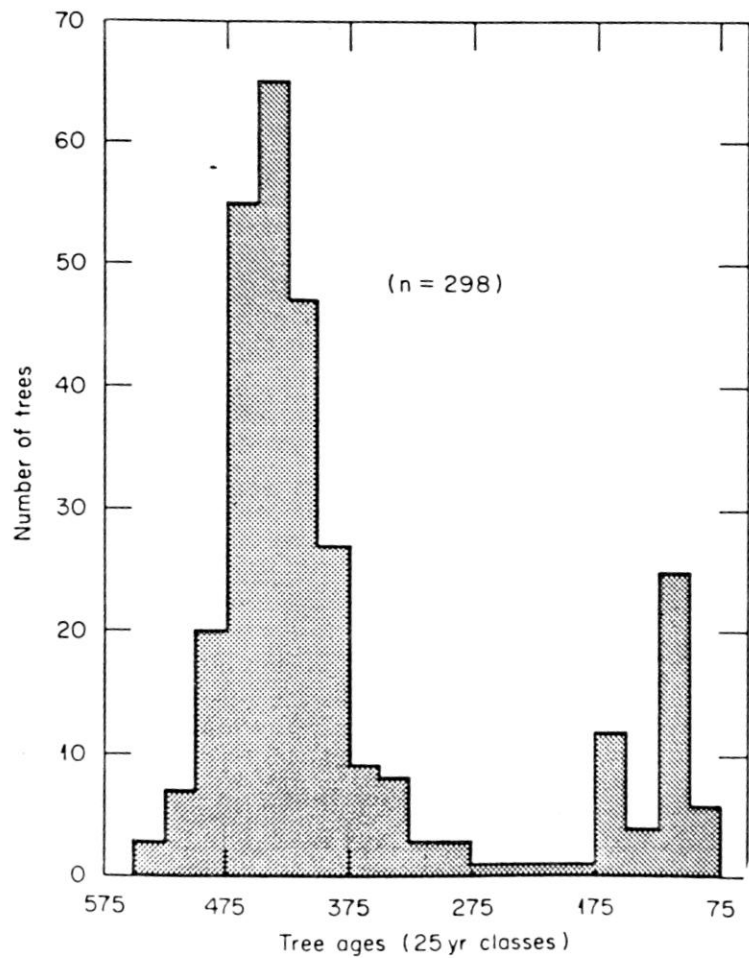

Figure 14.1. Age-class distribution of all *Pseudotsuga menziesii* by 25-year age classes on Watershed No. 10 at the H. J. Andrews Experiment Forest, western Oregon Cascade Range.
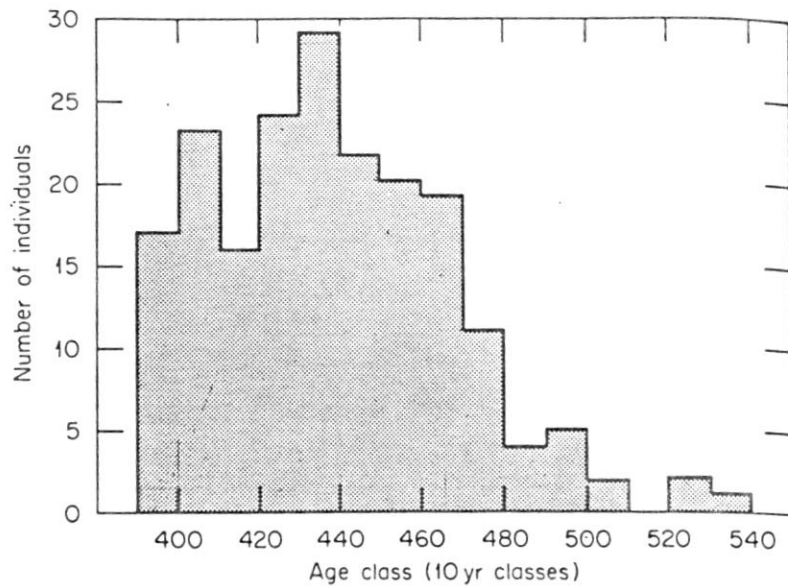
Figure 14.2. Age-class distributions of the old-growth *Pseudotsuga menzesii* on Watershed No. 10 at the H. J. Andrews Experimental Forest, western Cascade Range.

older and younger forests because of the wildfire around 1800; perhaps the age range in forests of comparable age would be less variable elsewhere. Subsequent age structure analyses were conducted to test this hypothesis. One was in a heavily stocked old-growth forest at about 900 m (Joseph E. Means 1980, pers. comm.), also on the H. J. Andrews Experimental Forest, and in several clear cuts on the Wind River Experimental Forest in the southern Washington Cascade Range. The results confirm a wide age range in dominant *Pseudotsuga* in forests established 400–500
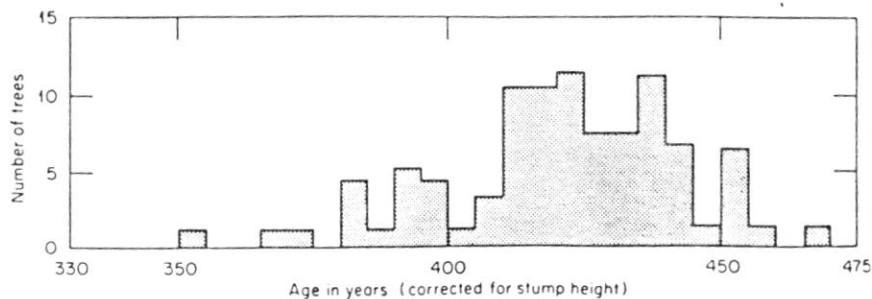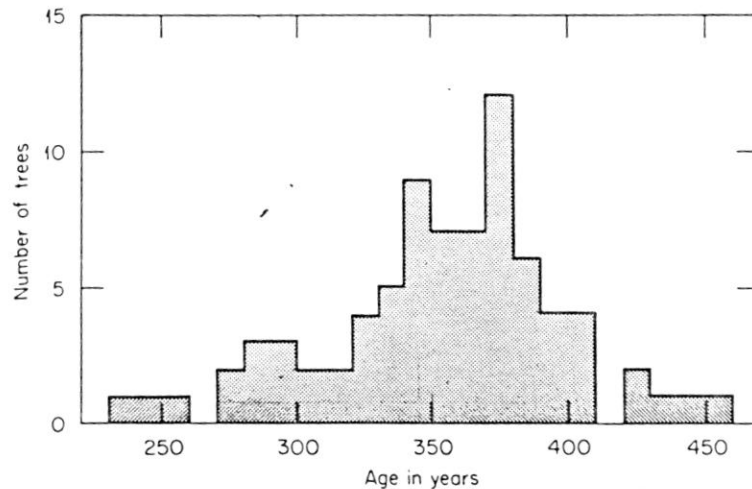

Figure 14.3. Age-class distribution of *Pseudotsuga menziesii* in an old-growth stand located at about 900 m on the H. J. Andrews Experimental Forest, western Oregon Cascade Range (courtesy Joseph E. Means).
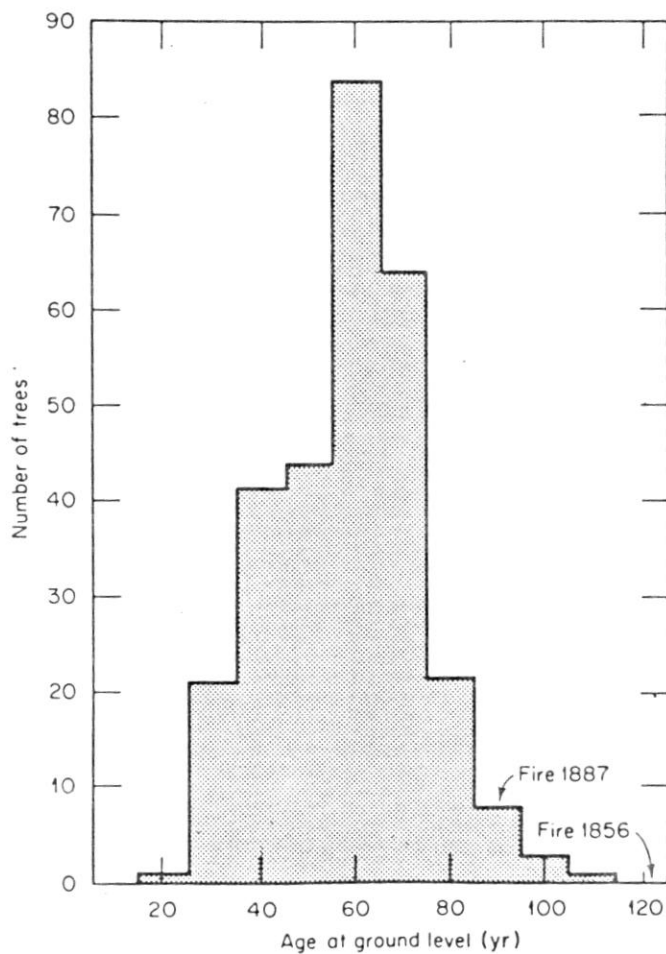
Figure 14.4. Age-class distribution of *Pseudotsuga menziesii* in old-growth stands located around the periphery of the T. T. Munger Research Natural Area in the Wind River Valley, southern Washington Cascade Range.

years ago. *Pseudotsuga* occurred only as dominants in this stand and covered an age span of about 140 years (Fig. 14.3). Stands at Wind River had the widest range of *Pseudotsuga* ages yet encountered — 230–460 years (Fig. 14.4).

A number of hypotheses have been proposed to explain these results. Slow recolonization is an obvious possibility. The disturbance episode that occurred around 500 years ago was certainly extensive, covering hundreds of thousands of hectares in the Cascade Range. The episode may also have been exceptionally severe involving repeated wildfires. Such circumstances could result in a lack of seed source. The age distributions resemble those proposed for such a scenario by Harper (1977a). Multiple disturbances are a second possibility. Young *Pseudotsuga* forests are particularly susceptible to wildfire during their first 75–100 years. Partial reburns during this time can provide opportunities for establishment of additional *Pseudotsuga* cohorts. This has been documented in young *Pseudotsuga* stands (Mark Klopsch 1980, pers. comm.) but is very hard to verify in old-growth stands, where there are fewer trees and greater errors in aging. Surface erosion on steep sites or climatic damage early in stand history could also contribute to the wide age range in dominant, old-growth *Pseudotsuga*. Another possibility is competition from shrub or hardwood trees, such as *Ceanothus* and *Alnus*. They could delay conifer establishment or suppress early growth of conifer seedlings and saplings. There is very little evidence for the suppression phenomenon in early growth patterns of the dominant conifers, however.

We currently suspect that lack of seed source and multiple distur-
bances are both major contributors to the wide age range in *Pseudotsuga*
dominants in 400–500-year-old stands. This has certainly been the case in
some young stands at Mount Rainier National Park, Washington (Hem-
strom 1979). These stands are sufficiently open that recruitment of in-
tolerant *Pseudotsuga* and *Abies procera* is still occurring over 100 years
after the last recorded wildfire (Fig. 14.5).

Other age classes of *Pseudotsuga* forests appear to have had different
developmental histories. Old-growth forests of around 250 years in age

Figure 14.5. Age-class distribution of seral tree species (*Pseudotsuga, Pinus mon-
ticola,* and *Abies procera*) in stands developed following wildfires in the late 1800s
in the Cowlitz River valley, Mount Rainier National Park, Washington. (From
Hemstrom 1979.)

occur at scattered locations in the Cascade Range. These forests have been noted for their relatively high densities of rather uniformly sized *Pseudotsuga* dominants. Tree ages in several stands, were much more tightly clustered than in the older forests (Fig. 14.6). More abundant seed supplies and an absence of reburns would both contribute to the more rapid complete restocking of the site. Age structure analyses of stands on sites of small, single-burn wildfires may reveal even tighter cohorts—comparable to these proposed by Munger (1930, 1940) and Isaac (1943).

Recent data show species composition to be as variable as stocking levels in early stages of forest succession in the Pacific Northwest. Many species play varying successional roles, depending on site and seed source. Shade-tolerant species, such as *Tsuga heterophylla* or *Abies amabilis*, have the potential for direct reestablishment on many disturbed sites. Even more commonly species mixtures, such as *Pseudotsuga* and *Tsuga*, become established on disturbed sites, followed by structural differentiation due to contrasting species growth rates. Dr. Chadwick Oliver and his students at the University of Washington have studied several young forest stands in the Pacific Northwest that follow this pattern, including mixtures of *Pseudotsuga* and *Tsuga heterophylla* (Wierman et al 1979) and *Alnus rubra* and associated conifers (Stubblefield et al 1978).

Analyses of age structure and developmental history are just beginning in the Pacific Northwest, but current work has been revealing. The seres
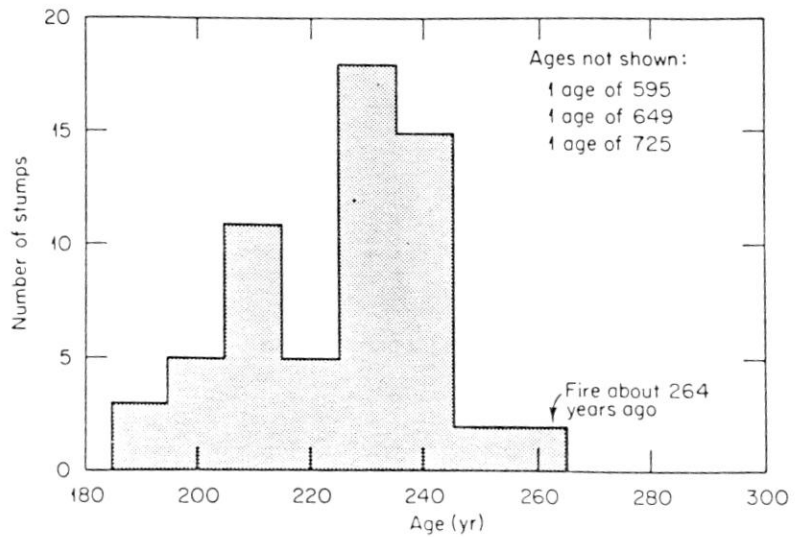

Figure 14.6. Age-class distribution of *Pseudotsuga* in a mature forest near Bagby Research Natural Area, Clackamas River drainage, western Oregon Cascade Range.

following each disturbance episode appear very individualistic. Initial forests have been widely divergent in composition, stocking levels, and times to canopy closure. Forest chronosequences must be interpreted conservatively. For example, a 450-year-old *Pseudotsuga* forest has not necessarily evolved through stages comparable to existing 135–250-year-old stands.

Role of Woody Debris in Forest Succession

Coarse woody debris in the form of snags and down logs is a major structural feature of northwestern forests (Franklin et al. 1981). An average of 194 metric tons/ha was measured in a series of 10 natural stands ranging from 100 to 1000 years in age (Franklin and Waring 1980). Down logs averaged 106.7 metric tons/ha with a range of 60–156 in this data set. The maximum value recorded for down logs was 418.5 metric tons/ha in an intact stand in the Carbon River, Mount Rainier National Park.

Trends in coarse woody debris were weak across the chronosequence of stands due partially to surprisingly high levels in three young (100–150-year-old) stands. Large amounts of dead wood are apparently carried over from previous stand, since massive boles of the fire-killed trees are typically not consumed. This material persists until the replacement stand begins to provide woody debris of comparable size.

Table 14.3. Densities and total numbers of *Picea sitchensis* and *Tsuga heterophylla* reproduction (stems ≤ 8 m tall) by substrate type and log decay class in a mature forest on a high terrace along the South Fork Hoh River, Olympic National Park, Washington.[a]

	Density (number/m2)		Absolute (number/ha)	
	Picea	*Tsuga*	*Picea*	*Tsuga*
Substrate type				
Picea logs	36.0	15.3	14,500	6170
Tsuga logs	29.9	9.6	15,300	4910
Unknown logs	30.0	7.5	4920	1230
Stumps and root wads	5.1	1.6	550	170
Ground humus	0.08	0.01	700	90
Log decay class				
Early (II)	24.8	15.5	7030	4340
Middle (III)	38.5	10.7	19,000	5250
Late (IV)	28.6	9.2	7800	2500
Very late (V)	28.2	8.2	820	170

[a]From McKee et al. (in press).

Rotten wood seedbeds are very important throughout the coastal *Picea sitchensis* zone (Minore 1972), but nurse logs attain maximum importance in the forests of *Picea sitchensis* and *Tsuga heterophylla* found in the valleys of the western Olympic Mountains. Reproduction in these alluvial forests is essentially confined to log substrates (Table 14.3) (McKee et al. in press). The absence of seedlings on the forest floor contrasts sharply with the dense reproduction crowded onto logs, which occupy only 11% of the area. Logs also vary markedly in their suitability as a seedbed with stage of decay (moderate stages of decay have highest seedling densities) and log species (*Tsuga* logs are poorer seedbeds than those of *Picea sitchensis* or *Pseudotsuga*).

Past patterns in amount and distribution of woody debris may also have strongly influenced the structure of existing mature *Picea-Tsuga* forests in the western Olympic Mountains. Tree densities and stand basal areas and biomass values are less than expected in this climatically favorable forest environment, resulting in relatively open and well lighted stands. The lower densities could result from the fact that suitable seedbeds (logs) were limited at the time of stand establishment and have still not been produced in sufficient numbers to allow development of full stocking. In any case, *Picea sitchensis* reproduces successfully and attains climax status in these relatively open alluvial forests in contrast to its seral role elsewhere in the dense forests typical of the *Picea sitchensis* zone (Franklin and Dyrness 1973).

Long-Lived Seral Species in Succession Modeling

We are interested in developing and utilizing successional models for Pacific Northwestern conifer forests for use in both basic and applied research. The philosophical construct that underlies the JABOWA-FORET family of models appears to us as a concise general statement summarizing our knowledge of succession: vegetational or ecosystem change is a function of life histories of available species interacting with environmental conditions (including disturbances) and with stochastic elements to produce a probabilistic array of alternative outcomes. This construct encompasses the diversity of ecosystems and processes outlined in this book and provides a basis for developing and testing hypotheses. Some of the distinctive features of Pacific Northwest forests require special consideration in a FORET-type model (Shugart and West 1977). Rates and scales rather than types of processes distinguish succession in these forests and require model modification. Specific modeling concerns in the northwestern forests include the following: (1) mortality must be

modeled on an annual time step; (2) plot size is critical; and (3) previous stand history is important.

Long-lived trees complicate the task of developing mortality probability functions. Two to four generations of shorter-lived species may germinate, mature, and die during the life span of one *Pseudotsuga, Thuja plicata*, or *Chamaecyparis nootkatensis*. Annual mortality of these short- and long-lived species is not constant between species nor within species by diameter. There seem to be five patterns of suppression-related mortality (Fig. 14.7):

1. Long-lived early seral species, which undergo high mortality rates in small, suppressed size classes but are able to endure long periods of slow growth in large size classes (e.g. *Pseudotsuga, Pinus ponderosa*) (Fig. 14.7a).

2. Short-lived early seral species, which experience constant annual mortality (e.g., *Alnus rubra*) (Fig. 14.7b).

3. Long-lived early to late seral species, which are relatively shade tolerant and experience little suppression mortality in small or large sizes (e.g., *Chamaecyparis nootkatensis* and *Thuja plicata*) (Fig.14.7c).

4. Long-lived early to mid-seral species, which experience moderate suppression mortality in small sizes, reach minimum suppression mortality at about half their maximum diameter, then experience increasing suppression mortality in large sizes (e.g., *Abies procera*) (Fig. 14.7d).

5. Relatively shorter-lived, mid- to late seral, shade-tolerant species, which experience the least suppression mortality at small sizes and slowly increasing suppression mortality in larger sizes (e.g., *Abies amabilis* and *Tsuga heterophylla*) (Fig. 14.7e).

The current model requires that trees die any year based on their estimated annual mortality probability. Because all species are relatively long-lived and at least a few usually survive to old age in a given stand, annual mortality probabilities are very small (Table 14.4). In addition, fires or wind storms, which occur at intervals of 100–1000 years, cause episodes of mortality. Episodic disturbances must be included to accurately simulate patterns of regeneration and growth in understory trees and inputs of dead wood to the forest floor.

Large trees also place some constraints on plot size for simulated stands. Internal computer storage limits require that number of trees modeled as individuals be relatively small. A plot size for simulated stands large enough to prevent a single large *Pseudotsuga* from completely dominating the stand could contain large numbers of small trees. Raising the minimum recruitment size to compensate results in loss of information about regeneration patterns. In addition, the simulated death of an old-growth *Pseudotsuga* in a small plot causes a sharp increase in available light; gap-phase reproduction becomes possible. In reality, a small open area in a matrix of trees 80 m tall does not receive enough light for suc-
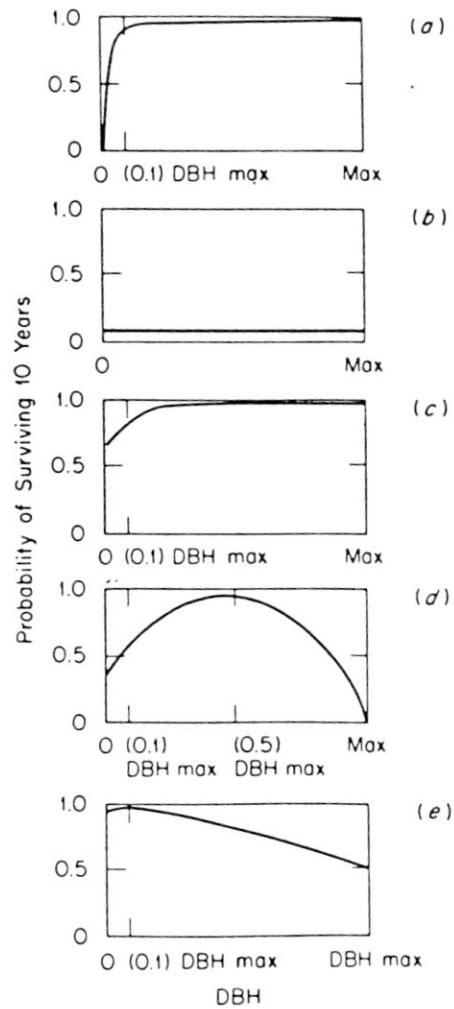
Figure 14.7. Probability of surviving 10 years of suppressed growth, diameter increase <0.1 cm/yr, for five groups of important tree species west of the Cascade Crest, Washington and Oregon. (a) long-lived early seral species; (b) short-lived early seral species; (c) long-lived early to mid-seral species, low suppression mortality; (d) long-lived early to mid-seral species, increasing suppression mortality; (e) long-lived late seral species (dbh, diameter at breast height). Curve a is compiled from McArdle (1949) and a chronosequence of stands in western Washington and Oregon (data on file at Forestry Sciences Laboratory, Corvallis, Oregon).

cessful establishment of intolerant species. Unrealistically high levels of intolerant species regeneration may occur in closed forest situations. Eventually, stand models should be altered to accept larger plot sizes,

Table 14.4. Example of annual mortality in *Pseudotsuga menziesii.*[a]

Age (yr)	P_1[b]	P_{10}[c]
20-50	0.940	0.586
50-100	0.981	0.825
100-150	0.996	0.961
150-250	0.999	0.990
250-450	0.996	0.961
450-750	0.995	0.951
750-1000	0.994	0.942

[a]Compiled from McArdle (1949) and unpublished data on file at the Forestry Sciences Laboratory, Corvallis, Oregon.
[b]Probability of surviving 1 year of diameter growth less than 0.1 cm.
[c]Probability of surviving 10 years of diameter growth less than 0.1 cm/yr.

perhaps by modeling cohorts of small trees and then graduating them into the stand as individuals at a particular diameter.

Finally, stands and disturbance over the previous centuries have an important bearing on the development of future stands by determining the availability of log seedbeds and seed sources. Currently, the model assumes time zero to be bare ground with all species available for establishment. As emphasized by Franklin and Waring (1980), abundant dead wood carries over from one stand to another even though sequences of severe wildfires or other disturbances. Thus, adjustments in the model must be made to account for variable initial conditions that follow natural disturbances. Disturbance intensity and frequency are important determinants of those conditions.

Conclusions

1. The forests of coastal Pacific Northwest differ from forests in other temperate and boreal regions in several respects. Trees can grow very large and old. Leaf areas can reach 20 m^2/m^2, and above-ground, live biomass values can exceed 1500 metric tons/ha.

2. Northwestern forests recover slowly after disturbance. Canopy closure may not occur for 40 years or more. Early seral intolerant trees may have an age range greater than 100 years in one cohort.

3. Due to infrequent, catastrophic disturbance and long-lived seral species, climax conditions rarely occur when intolerant, early seral trees are important in the initial stand.

4. Late seral or "climax" species are often important pioneers.

5. Stand history, as it determines the availability of log seedbeds and seed sources, plays an important role in determining the composition and structure of future stands.

6. The longevity and size of the early seral species pose interesting problems in developing FORET-type successional models, particularly in modeling mortality, determining plot size, and verifying models.

7. The northwestern forests provide the maximum expression of many forest features as well as trends observable in other temperate forest regions. These include size and longevity of species, biomass accumulations, and overall importance of coarse woody debris. General successional theories must take these northwestern phenomena into account and may find their ultimate tests in this region.