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Successional relationships and a comparison of biological characteristics among six northwestern conifers[1]

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TURNER, D. P. (Environmental Research Center, Washington State University, Pullman, Wa 99164-4430). Successional relationships and a comparison of biological characteristics among six northwestern conifers. Bull. Torrey Bot. Club 112:421–428. 1985—For six coniferous tree species of mid-altitude forests in the northern Rocky Mountains, a comparison of their biological characteristics and usual roles in succession does not reveal the pattern of specialization for early or late successional roles found among some species of the northeastern deciduous forests. Early successional species among these conifers have lower shade tolerance and greater annual extension growth than late successional species, but for seed weight, seed longevity, age to first seed production, crop frequency and maximum longevity, there is not a consistent relationship between rank and successional role. This failure to conform to the predictions of classical r-K selection may be explained in part by the disturbance regime, the site-specific nature of successional roles, and aspects of the abiotic environment related to climate in the northwestern United States.

Key words: succession, niche differentiation, disturbance regime
Nomenclature is that of Hitchcock and Cronquist 1973.

Early and late stages of succession differ in a variety of environmental characteristics (Odum 1969, Vitousek and White 1981) and plant species show a corresponding specialization for early and late successional roles (Marks 1975, Bazzaz 1979, Govindaraju 1984). Consequently, secondary succession in temperate forest ecosystems commonly involves a change in species composition or dominance in the overstory. The changes that occur in succession at a particular site can be viewed as a gradient along which species segregate (Pickett 1976, Whittaker and Woodwell 1978).

Alternative states of many plant characteristics have been argued to be adaptive in contrasting successional environments. The arguments follow from the pattern of environmental changes associated with succession, particularly the changes in plant density and the availability of resources. A number of models have been developed to describe this range of selection regimes and to predict the biological characteristics of species in each environment. The r-K continuum of MacArthur and Wilson (1967) is the prototype for such models. Its limitations, particularly its one dimensionality, have inspired others to propose alternatives (e.g., Grime 1979, Caswell 1982). Optimality models (Stearns and Crandall 1981) have also been used to generate predictions of the characteristics expected in tree species which colonize light gaps.

In this paper I examine the distribution of biological characteristics among six coniferous species of mid-altitude forests in the northern Rocky Mountains. The objective is to test the hypothesis that the species which dominate early successional environments have a suite of characters which differentiate them from their late successional counterparts.

Methods. Six coniferous species were chosen whose successional status has been widely studied (Haig *et al.* 1941, Habeck 1968, Daubenmire and Daubenmire 1968, Franklin and Dyrness 1973). The early successional (ES) species are lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*) and western larch (*Larix occidentalis*); the corresponding late successional (LS) or climax species are grand fir (*Abies grandis*), western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). The

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three climax species are listed in the order in which they would be encountered along an altitudinal gradient in the northern Rocky Mountains (Daubenmire and Daubenmire 1968). Data for leader extension growth was collected in the field, while that for seed weight, seed longevity, age to first seed production, crop frequency and maximum longevity was taken from the literature. For three of the characters, a ranking of the species taken from a literature review by Minore (1979) is used rather than quantitative data because of variations in the characters as a function of location and experimental design. Although there are problems associated with comparing data from many sources, notably that ecotypes may exist, this method is useful for identifying broad-scale patterns among the species.

The study site, located in the Priest River Experimental Forest in northern Idaho (48′18″N 116′47″W), had been clear cut in 1967. Elevation was approximately 1400 m and the surrounding area was a *Tsuga heterophylla/Pachistima myrsinites* habitat type (Daubenmire 1973). Nine coniferous species had colonized the site but *Picea engelmanii*, *Abies lasiocarpa* and *Pseudotsuga menziesii* were relatively few in number and were not included in the study. Annual leader extension growth was determined after terminal buds had formed in the fall of 1981. For twenty randomly chosen individuals of each species, which were two to three meters in height, the distance on the leader from the previous year's bud scar to the newly formed bud was measured. *Thuja plicata* does not have annual buds but the termination of the previous year's growth is indicated by the extent of woody bark on the stem (Parker 1979). Use of saplings in a clearcut site minimized the effects of competition.

Results. BIOLOGICAL CHARACTERISTICS AND ROLES IN SUCCESSION. In this clearcut site, early successional western larch and lodgepole pine had significantly greater annual extension growth than the other species (Table 1). The tallest conifers on the site were western larch, which were as much as a meter taller than their neighbors. Western white pine (ES) ranked third in extension growth but was not significantly different from western hemlock, which led the other two late-successional species. A similar pattern of greater extension growth by ES species among a group of Pacific northwest conifers was reported by Williams (1968).

Table 1. Annual leader extension growth for six coniferous species in a clearcut at the Priest River Experimental Forest (n = 20). ES = early successional, LS = late successional.

Species	Successional Status	Extension Growth (cm)	SE (cm)
Larix occidentalis	ES	42.1^{ab}	1.8
Pinus monticola	ES	38.7^{ac}	2.0
Pinus contorta	ES	45.3^{b}	1.7
Abies grandis	LS	30.2^{d}	1.3
Thuja plicata	LS	31.1^{d}	0.9
Tsuga heterophylla	LS	36.8^{c}	1.5

[a] Different superscripts indicate significantly different means ($p < .05$, LSD test).

Shade intolerance is also associated with early successional status (Table 2). The species ranked as least shade tolerant by Minore (1979) are the three ES species. The higher shade tolerance of white pine relative to lodgepole pine and western larch correlates with its lower extension growth (Table 1). Among the LS species, the greater shade tolerance of western hemlock and western red cedar relative to grand fir may be explained, in part, as an adaptation to the greater basal areas, hence deeper shade, attained in stands where these species are climax dominants. Basal area averaged 50.6 m^2 ha^{-1} for the *Abies/Pachistima* habitat type, 90.1 m^2 ha^{-1} for the *Tsuga/Pachistima* habitat type and 169.2 m^2 ha^{-1} for the *Thuja/Pachistima* habitat type in climax stands from throughout the northern Rocky Mountains (compiled from Daubenmire and Daubenmire 1968).

For the remaining characters, successional status was not a consistent predictor of rank (Table 2). Seed weight varies from 40 seeds per g in grand fir to 911 seeds per g in red cedar, but these are both LS species. Seed longevity is lowest in grand fir and greatest in lodgepole pine but the species' ranks in between do not conform to a pattern. Phenological characters are likewise inconsistent. Two of the ES species generally produce seeds before they are twenty years old but the other, western larch, is like the three LS species and produces seed somewhat later. Western white pine and lodgepole pine were the only species with cones in 1981

Table 2. Biological characteristics for six conifers of mid-altitude forest in the northern Rocky Mountains.

	Shade Tolerance[a] (rank)	Seed Weight[b] (#/g)	Seed Longevity[c] (rank)	Age to First Seed Production[b] (years)	Crop Frequency[b] (years)	Maximum Longevity[d] (years)
Early successional species						
Larix occidentalis	1	315	2	25	5	700+
Pinus contorta	2	297	5	4–8	1	250+
Pinus monticola	3	59	4	7–20	3–7	400+
Late successional species						
Abies grandis	4	40	1	20	3	300+
Thuja plicata	5	911	3	20–30	3–4	1000+
Tsuga heterophylla	6	572	3	15–25	2–8	400+

[a] Ranking by Minore (1979). Low ranks are less shade tolerant.

[b] Schopmeyer (1974)

[c] Ranking by Minore (1979). Low ranks have less longevity. Species with the same rank cannot be differentiated on the basis of this character.

[d] Franklin and Dyrness (1973).

at the time the extension growth data were collected. Crop frequency is characterized by periodic mast years in all the species except lodgepole pine. Minore (1979) ranks lodgepole pine and western white pine together as having more frequent crops than the three LS species, which in turn are ranked above western larch. Western larch has a long potential life span (700+ years), exceeded only by western redcedar, a LS species, at 1000+ years. Lodgepole pine and grand fir are grouped together at the low end of the longevity spectrum with potential ages of 250+ and 300+ years respectively.

For comparison with the western coniferous species, ten tree species of the northeastern deciduous forests are included in Table 3.

Discussion. For five of the seven characters considered there is no consistent relationship between where the species are ranked and their successional roles. This result does not follow the predictions of either classical r-K selection theory or of the optimality model of Stearns and Crandall (1981).

The poor correlation among characteristics in these conifers of the northern Rocky

Table 3. Biological characteristics of ten tree species of the northeastern deciduous forests.

	Shade Tolerance[a]	Leader Extension Growth (cm)[a]	Duration of Extension Growth (Days to >90% of Seasonal Growth)[a]	Seed Weight (#/g)[b]	Age to First Seed Production (years)[b]	Maximum Longevity (years)[a]
Early successional species						
Betula papyrifera	intolerant	n.a.	112	3036	15	140–200
Populus grandidentata	very intolerant	70–100+	60	334	10–20	70–100
Populus tremuloides	very intolerant	100+	60	7920	10–20	70–100
Prunus pennsylvanica	n.a.	100+	90	31	2	30–60
Late successional species						
Acer rubrum	tolerant	40–50	40	50	4	80–250
Acer saccharum	very tolerant	25–40	30	15	30	300–400
Betula lutea	intermediate	43+	60	n.a.	n.a.	150–300
Fagus grandifolia	very tolerant	25–40	30	3.5	40	350+
Fraxinus americana	intermediate	60+	30	29	20	260–300
Quercus rubra	intermediate	n.a.	30	0.3	25	200–400

[a] Marks (1975)

[b] Schopmeyer (1974)

n.a. = not available

Mountains also contrasts with the pattern in the northeastern deciduous forests described by Marks (1975). Biological characteristics for ten tree species of the northeastern deciduous forest were described (Table 3) and early successional species were generally less shade tolerant, had a greater duration and amount of leader extension growth and had lower maximum longevity. The magnitudes of the differences between extension growth in ES and LS species were much greater than those found in the western conifers (Tables 1 and 3). Data from the literature (Table 3) suggest these eastern ES species also have smaller seeds and earlier age of first reproduction than the LS species. Pin cherry (*Prunus pennsylvanica*) is exceptional in being an ES species with heavy seeds. Unlike the other species, however, its seeds are bird dispersed and so must have a thick seed coat to survive passage through the digestive tract of the bird. *Acer rubrum* is unusual among late successional species in having an early age of first reproduction. It also has the smallest seeds of the six LS species listed. In contrast to Marks (1975), Fowells (1965) considered *Acer rubrum* a pioneer to subclimax species; thus, it might be expected to have characteristics intermediate between those of ES and LS species.

The arguments for the adaptive significance of these characters for ES and LS species generally follow from r-K theory (MacArthur and Wilson 1967, Pianka 1970) and can be summarized as follows: Environments predominantly characterized by r-selection occur at two spatial scales, one in which catastrophic disturbances generate large open areas and one in which more local disturbances, such as treefalls, generate small openings. Small seeds allow for ready wind dispersal into disturbed areas of both kinds and great seed longevity increases the likelihood of encountering a small scale disturbance. Large seeds fuel early growth in low-light environments associated with K-selection or attract high quality seed dispersers. Early and frequent seed production permit maximum exploitation of both newly colonized large sites and periodically available small sites. Such seed production, however, requires energy that will generally increase fitness more if used for vegetative growth in the highly competitive environment of K-selected species. Low shade tolerance, which is typically associated with a relatively high photosynthetic capacity (Bazzaz 1979), and indeterminant extension growth are coupled to promote rapid growth in high light environments. Lower maximum longevity is perhaps a consequence of the rapid growth rate of ES species, in that fewer resources are allocated to biochemical and morphological defenses against grazers and pathogens. The high power/low efficiency metabolism (Odum and Pinkerton 1955) of the ES species may also render them competitively inferior as resource availability drops during canopy closure, a factor also potentially limiting longevity.

The lack of a consistent pattern in the characteristics of ES and LS species in the northwestern coniferous forest, but its presence in the tree species of the northeastern deciduous forests suggests that specialization for successional roles is greater in the latter than the former. It cannot be assumed that community composition and dynamics remain constant over evolutionary time frames (Davis 1981); thus, the nature of selective forces imposed by neighbor species cannot be inferred. There are, however, several ways in which the climate is related to the selection regime that may, in part, explain the interregional differences in how biological characteristics are distributed among the species. These include the effect of climate on the disturbance regime, the greater importance of adaptations relating to climate among the conifers, and the effect of climate on determining successional roles among the conifers (Fig. 1).

THE DISTURBANCE REGIME. In the northwestern coniferous forest the disturbance regime is characterized by periodic fires (see Martin 1982 for a literature review) and insect outbreaks (Amman and Baker 1972). Dry summers enhance the likelihood of fire while the tendency towards even size-class distributions raises susceptibility to insects and pathogens. The frequency, intensity, and size of these disturbances is a function of many interrelated factors but their effect is to create large areas in which secondary succession is initiated. In a review of patch dynamics, Pickett and Thompson (1978) found that disturbance patches tended to be larger in coniferous ecosystems than in those dominated by deciduous species.

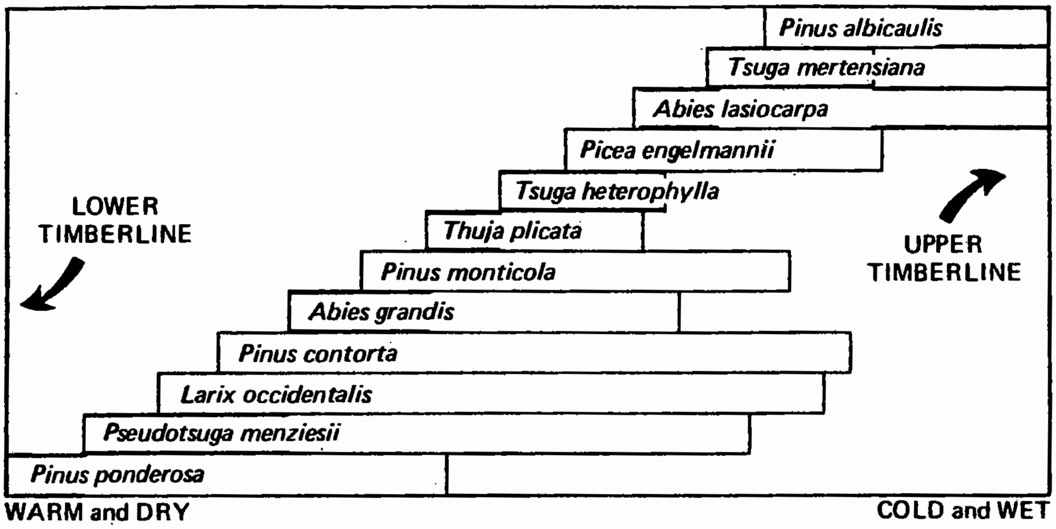

Fig. 1. A qualitative comparison of the ecological amplitudes of coniferous species in eastern Washington and northern Idaho. Darkened lines indicate the portion of its range a species is climax in the face of intense competition (from Daubenmire 1966).

The disturbance regime in the northeastern deciduous forests is quite different (Bormann and Likens 1979, Russell 1983). There, year round precipitation limits fire frequencies and size. Lower relief, along with the less flammable nature of the forests (Mutch 1970), may also slow the spread of fires. Hurricanes and wind storms contribute significantly to the disturbance regime along the east coast, and they act differently from fires or insect epidemics in that usually only isolated individuals or small groups of trees are knocked down (Oliver and Stevens 1977). This pattern of isolated mortality in the larger size classes allows for gap phase replacement and the maintenance of regeneration niches (Grubb 1977) for both ES and LS species within mature stands (Forcier 1975; Barden 1981; Runkle 1981).

Over much of the area in the northern Rocky Mountains where grand fir, western redcedar and western hemlock are the potential climax species, seedlings of both ES and LS species can tolerate the conditions after a catastrophic fire and readily colonize disturbed areas (Daubenmire and Daubenmire 1968, Lyon and Stickney 1976). Thus, the "initial floristics" model of succession (Egler 1954, Connell and Slatyer 1977) often holds. ES species may dominate the early stages of succession because of their faster growth rates (Haig *et al.* 1941). As time elapses, however, these shade intolerant species fail to reproduce locally (Turner and Franz 1985) and they lose dominance to the slower-growing LS species. Commonly another fire or insect outbreak occurs which opens up the area to all species again before competitive equilibrium is achieved (Wright and Heinselman 1973). The rarity of true climax stands in the northwestern forests has been remarked on by several regional ecologists (Munger 1940, Daubenmire and Daubenmire 1968, Habeck and Mutch 1973), and has been attributed primarily to the low probability that the hundreds of years required for a complete secondary succession would be uninterrupted by some kind of catastrophic disturbance.

One consequence of a disturbance regime that limits the occurrence of climax communities is that neither of the primary strategies associated with regeneration in climax stands, that is, gap phase replacement (Watt 1947) and slow growth into the canopy, is selectively favored because climax stands do not commonly persist for more than one generation of the trees. Rather, niche differentiation is based, in part, on the shift in dominance from the ES species with lower shade tolerance and higher growth rates to the slower-growing LS species. Coexistence of ES and LS species occurs because that dominance shift typically is accomplished in the interval between catastrophic disturbances.

Besides the recurrence of catastrophic fires, the geometry of the conifer trees also militates against gap phase replacement. Monopodial trunks make the canopies of individual conifers relatively narrow, probably as a means of shedding snow, and capturing low angle sunlight. Often these trees remain standing after tree death (Franklin *et al.* 1981). When a large conifer does fall, the space it opens up is small and the beneficiaries are more likely to be neighbors in the understory than individuals that seed into the gap.

There is some indication that potential longevity can be related to the fire regimes in these environments. Western redcedar, with the greatest potential longevity, typically occurs in pure stands only where soils remain relatively moist throughout the year (Daubenmire and Daubenmire 1968). Thus, the frequency of catastrophic fire in cedar stands tends to be low, allowing longer life spans and, perhaps, selecting for longer life spans. Western larch, which in contrast is ES, also has great potential longevity, but its evolutionary origin may be quite different. Larch has thick bark and is considered to be the most fire-resistant conifer in the northern Rocky Mountains (Flint 1925). Its range takes it into more xeric environments than any of the six species being compared (Daubenmire 1966) where low intensity ground fires reduce fuel levels and decrease the probability of catastrophic fires (Martin 1982). Thus, a larch tree will survive many such low intensity fires in its long life span. A relatively late age to first reproduction (Table 2) suggests that resources are allocated to height growth early in the life of a larch tree in order to promote survival of ground fires subsequent to establishment. At higher altitudes there are fewer low intensity fires but, as stands age and fuel accumulates, the probability of a catastrophic fire in a dry year increases (Martin 1982). The three to four hundred year potential life span of the remaining species may reflect the low probability of surviving these fires. Windstorms that kill old, tall trees make great potential longevity a less successful trait in the eastern forests for either ES or LS species.

SITE-SPECIFIC ROLES IN SUCCESSION. Another factor that may limit niche specialization based on successional role among the northwestern conifers is the site-specific nature of their roles (Daubenmire and Daubenmire 1968, Franklin 1982). LS species can usually tolerate the environmental conditions in early stages of secondary succession. Due to their shade tolerance they can also seed into latter stages of succession on sites that they didn't originally colonize because local seed sources were absent. Selection is thus not strictly for one successional role.

ES species may also play a LS role. Lodgepole pine is seral over much of its range but on some pumice soils in central Oregon it is the only conifer that can tolerate the conditions and so successfully reproduces while typical LS species cannot (Franklin and Dyrness 1973). Nonpyrogenous climax stands of lodgepole pine have also been reported (Despain 1983). In relatively dry environments characterized by recurrent fires, western larch and lodgepole pine, usually ES species, may form a fire climax (Franklin and Dyrness 1973).

SPECIALIZATION FOR CLIMATIC FACTORS. The relationship of seed size to ecological amplitude among the LS northwestern conifers supports the idea that selection by climatic factors is more important in shaping this character than selection related to successional role (Fig. 1). Where soil drought is common, a large seed size is required to fuel a fast-growing tap root that precedes the descending wave of soil drying occurring most summers (Daubenmire 1968). This may explain the large seeds of grand fir and ponderosa pine (*Pinus ponderosa*), which are climax dominants in drier habitat types than those dominated by cedar and hemlock (Daubenmire 1956). Where snow and litter accumulations are high and the growing season short, a large seed size may be favored to give mechanical strength to the seedlings, as in the *Abies amabalis* zone in the Cascade range (Thornburg 1967). Subalpine fir (*Abies lasiocarpa*) has an average of 766 seeds per g and whitebark pine (*Pinus albicaulis*), which also grows up to timberline, has the largest seeds of any of the northwestern conifers with only 57 per g (Schopmeyer 1974). Western redcedar and western hemlock occupy modal sites for moisture and temperature along the elevational gradient (Daubenmire 1956, Zobel *et al.* 1976) which apparently do not require a large seed. The hemlock and cedar trees which survive to reproduce do so because their seeds were originally deposited in a large disturbed area or on rotting wood safe sites within older stands (Christy and Mack 1984, Turner and Franz 1985). Production of many small seeds rather than few large ones increases the probability of encountering such germination sites.

There is no obvious relationship between the ecological amplitudes of the species and their ranking relative to the two characteristics not thus far mentioned—seed longevity and crop frequency. The rankings for seed longevity are based on dry, cold storage, so may not be a good indication of relative longevities under natural conditions. Except for lodgepole pine, which retains seeds on the tree in well-defended cones (Smith 1970), all these conifer species have periodic mast years, perhaps as a predator satiation strategy (Silvertown 1980).

In addition to acknowledging the possibility that natural selection may not tightly regulate some characters, it must be recognized that limited genetic variability within a character, allometric constraints, genetic linkages between characters and coevolved relationships with seed dispersers could all influence the evolutionary history of a given character. Further empirical studies at a variety of levels of organization will be useful in identifying the environmental factors and genetic constraints which have generated the current constellation of characters possessed by each species.

Literature Cited

Amman, G. D. and B. H. Baker 1972. Mountain pine beetle influence on lodgepole stand structure. J. For. 70:204–209.

Barden, L. S. 1981. Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. Oikos 37:205–209.

Bazzaz, F. A. 1979. The physiological ecology of plant succession. Annu. Rev. Ecol. Syst. 10:351–371.

Bormann, F. H. and G. E. Likens 1979. Pattern and process in a forested ecosystem. Springer-Verlag. New York, 253 p.

Caswell, H. 1982. Life history theory and the equilibrium status of populations. Am. Nat. 120:317–339.

Christy, E. J. and R. N. Mack 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. J. Ecol. 72:75–91.

Connell, J. H. and R. O. Slatyer 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111:1119–1144.

Daubenmire, R. 1956. Climate as a determinant of vegetation distribution in eastern Washington and northern Idaho. Ecol. Monogr. 26:131–156.

———. 1966. Vegetation: Identification of typal communities. Science 151:291–298.

———. 1968. Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. Ecology 49:431–438.

———. 1973. A comparison of approaches to the mapping of forest land for intensive management. For. Chron. 49:431–438.

——— and J. B. Daubenmire 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Ag. Expt. Sta. Tech. Bull. 60, Washington State University, 104 p.

Davis, M. B. 1981. Quaternary history of the stability of forest communities, p 132–153. *In* D. C. West, H. H. Shugart and D. B. Botkin [eds.], Forest succession: concepts and application. Springer-Verlag, New York, 517 p.

Despain, D. 1983. Nonpyrogenous climax lodgepole pine communities in Yellowstone National Park. Ecology 64:231–234.

Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition—a factor in old-field vegetation development. Vegetatio 4:412–417.

Flint, H. R. 1925. Fire resistance of northern Rocky Mountain conifers. Idaho For. 7:7–10, 41–43.

Forcier, L. K. 1975. Reproductive strategies and cooccurrence of climax tree speciess. Science 189: 808–809.

Fowells, H. A. (comp.) 1965. Silvics of forest trees of the United States. U.S. Dept. Agr. Handbook 271, 762 p.

Franklin, J. F. 1982. Forest succession research in the northwest: an overview, p 163–173. *In* J. E. Means [ed.], Forest succession and stand development research in the Northwest. For. Res. Lab., Oregon State University, Corvallis, 170 p.

——— and C. T. Dyrness 1973. Natural vegetation of Oregon and Washington. U.S. Dept. Agr. For. Serv. Gen. Tech. Report PNW-8, 417 p.

———, K. Cromack, Jr., W. Denison, A. Mckee, C. Maser, J. Sedell, F. Swanson and G. Juday 1981. Ecological characteristics of old-growth Douglas-fir forests. U.S. Dept. Agr. For. Serv. Gen. Tech. Rep. PNW-118, 48 p.

——— and M. A. Hemstrom 1982. Aspects of succession in the coniferous forests of the pacific northwest, p. 212–229. *In* D. C. West, H. H. Shugart and D. B. Botkin [eds.], Forest succession, concepts and application. Springer-Verlag, New York, 517 p.

Govindaraju, D. R. 1984. Mode of colonization and patterns of life history in some North American conifers. Oikos 43:271–276.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, Chichester, England, 222 p.

Grubb, P. J. 1977. The maintenance of species richness in plant communities. The importance of the regeneration niche. Biol. Rev. 52:107–145.

Habeck, J. R. 1968. Forest succession in the Glacier Park cedar-hemlock forests. Ecology 49:872–880.

——— and R. W. Mutch 1973. Fire-dependent forests in the northern Rocky Mountains. Quart. Res. 3:408–424.

Haig, I. T., K. P. Davis and R. H. Weidman 1941. Natural regeneration in the western white pine type. U.S. Dept. Agr. Tech. Bull. 767, 99 p.

Lyon, L. J. and P. F. Strickney. 1976. Early vegetal succession following large northern Rocky Mountain wildfires, p. 355–375. *In* Tall Timbers fire ecology conference, Vol 14, Tall Timbers Research Station, Tallahassee, 675 p.

MacArthur, R. H. and E. O. Wilson 1967. The theory of island biography. Princeton University Press, Princeton, 203 p.

Marks, P. L. 1975. On the relationship between extension growth and successional status of deciduous trees of the northeastern United States. Bull. Torrey Bot. Club 102:172–177.

Martin, R. E. 1982. Fire history and its role in succession, p 92–99. *In* J. E. Means [ed.], Forest succession and stand development research in the Pacific Northwest. For. Res. Lab., Oregon State University, Corvallis, 170 p.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species—a literature review. U.S. Dept. Agr. For. Serv. Gen. Tech. Rep. PNW-87, 72 p.

Munger, T. T. 1940. The cycle from douglas-fir to hemlock. Ecology 21:451–459.

Mutch, R. W. 1970. Wildland fires and ecosystems—a hypothesis. Ecology 51:1046–1051.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Odum, H. T. and R. C. Pinkerton 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. Am. Sci. 43:331–343.

Oliver, C. D. and E. P. Stephens 1977. Reconstruction of a mixed-species forest in central New England. Ecology 58:562–572.

Parker, T. 1979. Natural regeneration of western redcedar in northern Idaho. MS thesis. University of Idaho, Moscow.

Pianka, E. R. 1970. On r– and K– selection. Am. Nat. 104:592–596.

Pickett, S. T. A. 1976. Succession: an evolutionary interpretation. Am. Nat. 110:107–119.

———. 1980. Non-equilibrium coexistence of plants. Bull. Torrey Bot. Club 107:238–248.

——— and J. N. Thompson 1978. Patch dynamics and the design of nature reserves. Biol. Conserv. 13:27–37.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern U.S. Ecology 62:1041–1051.

Russel, E. W. B. 1983. Indian-set fires in the forests of the northeastern United States. Ecology 64:78–88.

Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. Biol. J. Linnean Soc. 14:235–250.

Schopmeyer, C. S. (comp.) 1974. Seeds of woody plants in the United States. U. S. Dept. Agr. Handbook 450, 883 p.

Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol. Monogr. 40:349–371.

Stearns, S. C. and R. E. Crandall 1981. Bet hedging and persistence as adaptations of colonizers, p 371–383. *In* G. G. E. Scudder, J. L. Reveal [eds.], Evolution today. Proc. Second Int. Congr. Syst. Evol. Biol.

Thornburg, D. A. 1967. Dynamics of the true fir-hemlock forests of western Washington. PhD thesis. University of Washington, Seattle.

Turner, D. P. and E. H. Franz 1985. Size class structure and tree dispersion patterns in old-growth cedar-hemlock forests of the northern Rocky Mountains (USA). Oecologia (Berl.): In press.

Vitousek, P. M. and P. S. White 1981. Process studies in succession, p 267–276. *In* D. C. West, H. H. Shugart and D. B. Botken [eds.], Forest succession, concepts and application. Springer-Verlag, New York, 517 p.

Watt, A. S. 1947. Pattern and process in the plant community. J. Ecol. 35:1–22.

Whittaker, R. H. 1975. Communities and ecosystems. Macmillan, New York, 385 p.

——— and G. M. Woodwell 1978. Retrogression and coenocline distance, p. 51–70. *In* R. H. Whittaker [ed.], Ordination of plant communities. Dr. W. Junk D. V. Publishers, The Hague.

——— and D. Goodman 1979. Classifying species according to their demographic strategy. I. Population fluctuations and environmental heterogeneity. Am. Nat. 113:182–200.

Williams, C. B. Jr. 1968. Seasonal height growth of upper-slope conifers. U.S. Dept. Agr. For. Serv. Res. Pap. PNW-62, 7 p.

Wright, H. E. Jr. and M. L. Heinselman 1973. The ecological role of fire in natural conifer forests of western and northern North America. Quart. Res. 3:319–328.

Zobel, D. B., A. Mckee, G. M. Hawk and C. T. Dyrness 1976. Relationship of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecol. Monogr. 46:135–156.