

Forest dynamics in the Bitterroot Canyons, Montana

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Both shade-tolerant and shade-intolerant tree species may dominate young stands in canyon-bottom forests of the Bitterroot Range. Subsequent dynamics depend on growth characteristics of the colonizing species. Thus, much of the compositional variation arises at stand establishment (initial floristic composition) rather than through a replacement process (relay floristics). *Taxus brevifolia*, however, may require shelter from other species for establishment. Vertical similarity increases with stand age towards a maximum value of about 75%. Although the importance of *Taxus brevifolia* and *Thuja plicata* tends to increase with stand age, convergence on a common climax composition is thwarted by insularity of the canyon bottoms and an average fire cycle (60 years) that is shorter than the normal longevity (120–140 years) of the shortest lived major tree species (*Pinus contorta*).

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Dans les forêts croissant au fond des canyons du massif Bitterroot (Montana), les jeunes peuplements peuvent être dominés aussi bien par des espèces qui tolèrent l'ombre que par des espèces qui ne la tolèrent pas. La dynamique subséquente dépend des caractéristiques de croissance des espèces colonisatrices. Ainsi, une grande partie de la variation dans la composition des forêts apparaît au moment de l'établissement des peuplements (composition floristique initiale), plutôt que par un processus de remplacement (composition floristique de relais). Le *Taxus brevifolia*, cependant, peut avoir besoin d'être abrité par d'autres espèces pour pouvoir s'établir. La similarité verticale augmente avec l'âge des peuplements, jusqu'à une valeur maximale d'environ 75%. Bien que l'importance du *Taxus brevifolia* et du *Thuja plicata* ait tendance à augmenter avec l'âge des peuplements, la convergence vers une composition climacique commune est empêchée par la nature insulaire du fond des canyons, et par le fait que la périodicité moyenne des feux (60 ans) est plus courte que la longévité normale (120–140 ans) du *Pinus contorta*, l'espèce dont la longévité est la plus basse parmi les principaux arbres.

[Traduit par le journal]

Introduction

This paper addresses the first in a series of questions posed by McIntosh (1981, p. 23) that need to be answered for an understanding of vegetation dynamics. Is succession orderly, directional, and predictable? We ask this question of a set of fire-disturbed insular canyon-bottom forests in western Montana.

Directionality in dynamics towards a common equilibrium species composition is also known as convergence. We distinguish between two types of convergence: convergence on different sites and convergence on identical sites. This distinction separates markedly different equilibrium outcomes. Convergence from different sites is necessary for the development of discrete community types, assuming a continuous range of site variation. In this case, many different sites map onto a single species composition, while convergence on identical sites results in a one-to-one mapping of site characteristics to species composition. If neither form of convergence occurs, there is a one-to-many mapping of sites to equilibrium species composition. Elsewhere we evaluated how tightly site characteristics map onto near-equilibrium species composition in the Bitterroot Canyon forests (McCune and Allen 1985). The present paper elaborates how the uncoupling of site factors and vegetation develops by describing the dynamics occurring with increasing time since fire. The primary data are age structure and species composition from stands of varying age taken at a single point in time.

Ecologists have sought temporal order in attributes of vegetation that may be more tractable and universal than species composition (e.g., see Odum 1969). In addition to describing dynamics of species composition, we assess trends in several higher level attributes of the vegetation: vertical similarity,

shade tolerance, growth rates, and size of the dominants at maturity.

Study area

The climate, geomorphology, and soils of the Bitterroot Canyons are described and a map is given in McCune and Allen (1985). Briefly, the canyons are deep, parallel glaciated gorges through a large body of granite forming the Bitterroot Range in western Montana. Much of the study area lies within the Selway–Bitterroot Wilderness. Areas logged or otherwise disturbed by humans were excluded.

The canyon bottoms contain complex mosaics of forests, wet meadows, talus, outcrops, and thin-soil grasslands, locally controlled by the geomorphology. Only low-elevation canyon-bottom forests are included here. These mesic forests are disturbed primarily by fire (McCune 1983). *Pinus contorta* and *Larix occidentalis* are the dominant shade-intolerant species. *Abies grandis*, *A. lasiocarpa*, *Picea engelmannii*, *Taxus brevifolia*, and *Thuja plicata* are common on moist sites, while *Pinus ponderosa* and *Pseudotsuga menziesii* predominate in drier forests (nomenclature of Hitchcock and Cronquist 1973). Tree distributions are markedly uneven across canyons (McCune and Allen 1985; Arno 1970); tree species that are common in some canyons are completely absent in others.

Methods

Two sets of tree species composition data were collected. (i) Transects through each major canyon using the point–quarter method (Cottam and Curtis 1956), stratified by size class, provided data on vertical structure and on species composition in relation to stand age and topographic position. (ii) Thirteen stands were intensively sampled for an analysis of the relative influence of historical factors and site factors on species composition in near-equilibrium forests (McCune and Allen 1985).

Point–quarter samples were taken at 25-m intervals between the elevations 1260 and 1400 m on each canyon-bottom transect. Transects were on nearly level landforms (benches and floodplains) and were frequently interrupted by excluded sites (outcrops, talus, wetlands, major trails, and creeks). Within each quadrant at each point the distance to the nearest individual in each of three layers ("seed-

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lings," <1.5 m tall; "saplings," >1.5 m tall and <10 cm diameter at breast height (DBH); "trees," >10 cm DBH) and the basal area at breast height of the nearest individuals in the two larger size classes were measured.

Points were grouped into stands while sampling, a stand being fairly homogeneous in history and site characteristics, at the scale of trees. Stand boundaries were noted along transects as changes in landform, species composition, or age of the dominant trees. Stands were aged (McCune 1983) and classified by topographic position (floodplain, low bench, midbench, high bench).

Seedlings in the point-quarter transects were randomly sampled to determine the relationship between height and age by species. Ages were estimated by counting terminal bud scale scars where possible; otherwise, rings were counted microscopically on basal stem sections made with a razor blade. Since the sample was taken under a closed canopy or beneath gaps, the shade-intolerant species *Pinus contorta* and *Larix occidentalis* were poorly represented and therefore not analyzed. The remaining sample sizes ranged from 26 (*Picea*) to 145 (*Abies grandis*).

Data analysis

Transect stands were ordinated to examine successional and topographic trends. Only the 32 stands having at least six transect points were included. The ordinations are perpendicularized Bray-Curtis stand ordinations using the variance-regression method of end-point selection (Beals 1984), the quantitative version of Sørensen's index as a dissimilarity measure (Bray and Curtis 1957; Mueller-Dombois and Ellenberg 1974), and the program BCORD (W. M. Post, unpublished). Despite recent criticism, Bray-Curtis ordination has repeatedly been shown to be a superior method of ordinating ecological data, particularly with perpendicularization of axes and improved methods of end-point selection (Beals 1984).

Successional trends, as suggested by vertical differences in tree species composition, were examined by ordinating each stand-layer combination in species space (Goff and Zedler 1972). Dissimilarities were based on relative densities to avoid excessive weight upon scattered large trees. Vertical compositional trends were shown by connecting the sequence of layers (tree → sapling → seedling) in each stand with vectors. For clarity, separate vector diagrams from the single ordination were made for three stand age-classes (48–100, 101–150, and >150 years).

Another ordination of samples in species space showed tree species composition in relation to topography and stand age. We used average relative density across the three layers in each stand to emphasize species well represented in all three layers, the species most likely to persist in the stand. Topographic class (floodplain, low bench, midbench, and high bench) and stand age were superimposed on this ordination to evaluate the relationship of these factors to tree composition.

Transition matrices

Transition matrices between tree strata were calculated as the probabilities of finding one species in a lower layer than another species, based on transect stands with six or more sample points, using the eight most common tree species. Probabilities were derived from stand averages of relative density in whole layers, rather than tree-level data as used by Horn (1975). To accommodate mixed species composition, in both understory and overstory, the proportion of species *j* beneath species *i* is weighted by the relative density of species *i* in the overstory. Where *N* is number of stands; $D_{i,k,s}$ is relative density of species *i* in layer *k* and stand *s*; and $p(j_{k-1}|i_k)$ is probability of finding species *j* in the next lower layer *k* - 1, given species *i* in layer *k*, then for each pair of layers *k* and *k* - 1,

$$p(j_{k-1}|i_k) = \frac{\sum_{s=1}^N (D_{i,k,s} \cdot D_{j,k-1,s})}{\sum_{s=1}^N D_{i,k,s}}$$

Elements of these transition matrices can be interpreted either directly (as the probabilities of finding one species in a lower layer than another) or indirectly (as the probabilities of one species replacing

another). The latter interpretation requires the assumption that proportions of species in the understory estimate probabilities of replacing individuals in the overstory, an assumption that is inappropriate if strictly applied (McIntosh 1980; Horn 1981). Since we were unwilling to make this assumption, we did not perform Markov analyses of the transition matrices.

For inferences about shade tolerance, transition matrices were adjusted to equal species abundances by dividing each $p(j_{k-1}|i_k)$ by the overall abundance of species *j* in all canyons, then standardizing totals to 1.0 for each species *i*. Assuming a linear effect of species abundance on probability of establishment, this procedure yields transition matrices as if all species were equally abundant, thus focusing on differences in aptitude for establishment and survival. This correction is critical for inferences about shade tolerance where local abundance varies greatly (e.g., *Thuja*, *Taxus*, or *Larix* are absent in some canyons).

Shade-tolerance rankings

Two measures of shade tolerance were compared with the classical subjective evaluation of shade tolerance (Baker 1949). First, the slope of the regression of ln(seedling height) on ln(age) in closed forests (r^2 ranged from 0.43 to 0.88) is a measure of aptitude for suppression, an important feature of shade tolerance. In general, the more shade tolerant the species, the slower its growth rate (Spurr and Barnes 1980; Bormann and Likens 1979; Horn 1971). The second measure ranks species by comparing transition probabilities after adjustment for overall abundance. For example, since 21% of the saplings under *Abies grandis* are *Taxus* and 2% of the saplings beneath *Taxus* are *Abies*, *Taxus* is ranked as more shade tolerant than *Abies*.

Results

Stand ordinations

The ordination of stands in species space (Fig. 1A) effectively represents the compositional variation, accounting for 70% of the variation in the dissimilarity matrix. Overlays of stand age (Fig. 1B) and topographic class (Fig. 1C) show relationships to species composition. The general trends accord with those given in other accounts of mesic lowland forests in western Montana (e.g., Antos and Habeck 1981). Departures from the general trends allow us to probe the limitations of the concepts of succession and site determinism.

Dominance (Fig. 1A) is related to stand age (Fig. 1B). As expected, the relatively shade intolerant species *Pinus contorta* and *Pseudotsuga* are more likely to dominate young stands than are tolerant species. Note, however, that four young stands (<100 years) are dominated by the relatively shade tolerant *Abies* spp. The reverse exception also occurs: some older stands are composed largely of long-lived, relatively intolerant species (*Pseudotsuga* or *Larix*). However, these stands are uncommon and are missing from the quantitative sample.

Dominance of *Pinus contorta* and *Pseudotsuga* is more common on higher (presumably warmer and drier) benches (compare Fig. 1A with Fig. 1C), while *Picea*, *Abies* spp., and *Taxus* may dominate on floodplains or benches. Of the four young stands dominated by shade-tolerant species, three were on low benches, one on a midbench. This midbench stand, 85 years old and dominated by *Abies grandis*, exemplifies an anomaly that was observed occasionally but is represented by only one stand in this analysis: a young stand dominated by a shade-tolerant species on a site that appears suitable for an intolerant species (*Pinus contorta*).

Successional vectors

The ordination of stand-layer combinations in tree species space (Fig. 2) shows the magnitude and direction of differences in species composition, both between stands and between

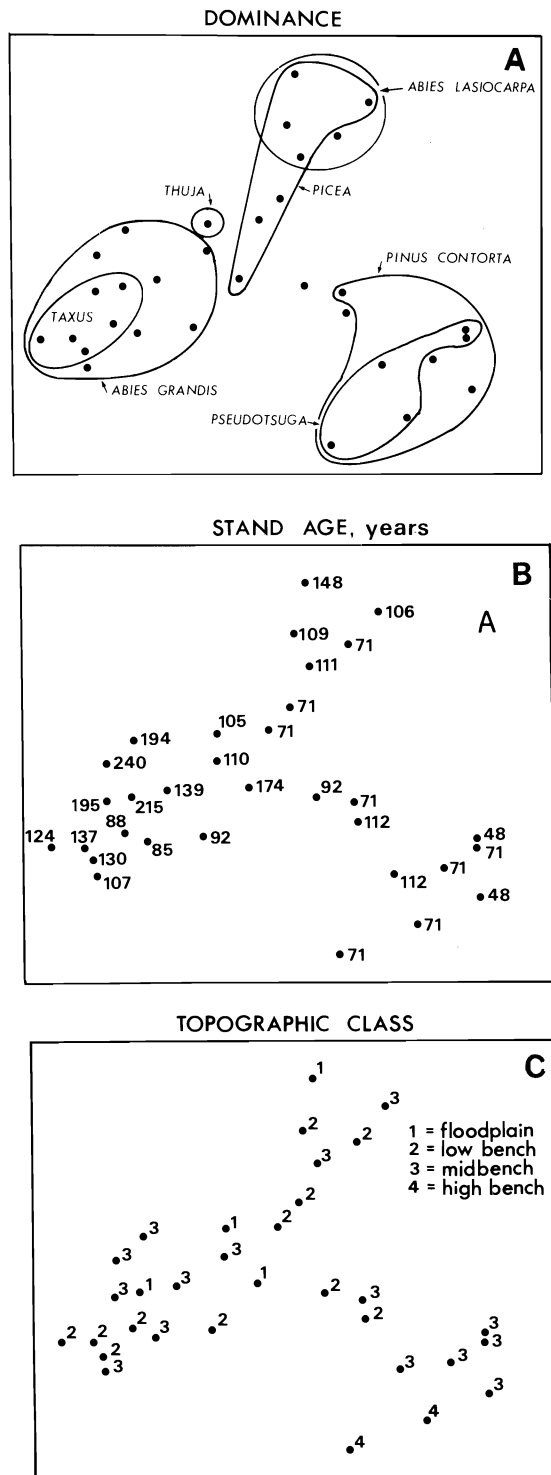


FIG. 1. Ordination of transect stands in tree species space. (A) Dominant species, (B) stand age, and (C) topographic class are superimposed on this ordination. Overlapping areas of dominance in Fig. 1 indicate shared dominance. The two stands not enclosed by loops had no clear dominant or codominants.

layers within stands. This ordination accounted for 59% of the variation in the 96×96 dissimilarity matrix. The vectors connecting adjacent layers in Fig. 2 represent the differences in composition between layers: the longer the vector, the greater the difference between layers. However, to the extent that the composition of lower layers has predictive value for future species compositions, the vectors indicate the rate and

direction of compositional change through time.

Figure 2 comes from a single ordination, but the stands are segregated by age-class into three diagrams, to contrast dynamics in stands of different ages. Generally the magnitude of the vertical differences in species composition decreased with stand age, as shown by the decreasing vector lengths from Fig. 2A to Fig. 2C.

Pinus contorta was always being replaced by shade-tolerant species (note the long vectors consistently pointing away from *Pinus*). The vectors from *Picea* to *Abies lasiocarpa* suggest that *Picea* is often seral to *Abies*. Strong, consistent trends within the *Abies grandis* – *Taxus* region of the ordination are absent. However, the delayed establishment of *Taxus* is shown by the scarcity of vectors leading to *Taxus* in the youngest stands (Fig. 2A) as compared with older stands.

Shade tolerance

Compositional dynamics depend on the relative abilities of the available species to survive and reproduce beneath a canopy. This ability in the vernacular is "shade tolerance"; bear in mind, however, that tolerance of shade is only one of a suite of adaptations for survival beneath a canopy.

The classical subjective evaluation of shade tolerance (Baker 1949) compared reasonably well with two independently derived measures of shade tolerance (Table 1). *Abies lasiocarpa* and especially *Picea engelmannii*, however, were less tolerant in our study area than the classical rating suggests. Species ranks based on transition probabilities (Tables 1 and 2) were similar to ranks based on growth rates (Table 1), suggesting that either method can be useful as a measure of shade tolerance.

Discussion

This discussion of forest dynamics is limited to low-elevation, mesic forests in the canyon bottoms of the Bitterroot Range. Stands are initiated almost entirely by fire with a pre-1911 yearly point probability of burning of 2×10^{-2} (McCune 1983). Disturbances by avalanches out of their chutes and rockfall are infrequent (yearly point probability $\approx 10^{-5}$ for each).

Life-history profiles of the major tree species (Table 3) are a useful reference throughout the following four-part discussion of compositional dynamics: establishment, canopy development, canopy breakup, and climax recognition.

Establishment

Establishment history was inferred from stands older than 40 years, using age structure and compositional data (large recent disturbances were lacking). Most young stands were largely even-aged, dating from a single wave of colonization after a fire. Since any of the major species, shade tolerant or not (excluding *Taxus*), may dominate these young stands, considerable compositional variation arises in stand establishment.

Analysis of young stands lacking shade-intolerant species suggests that tree establishment is only partly determined by site factors. Intolerants do fail in some cases because of site characteristics: *Pinus contorta* dominance is usually restricted to midbenches and high benches, being generally unsuccessful on wetter sites where *Picea* is likely to dominate (Fig. 1). Yet there are young stands of shade-tolerant species on benches, sites that appear to be suitable for *Pinus contorta* (Fig. 1). If so, *Pinus* may have failed because of a local scarcity of seed or early mortality through a historical factor (insects, disease, rodents, etc.).

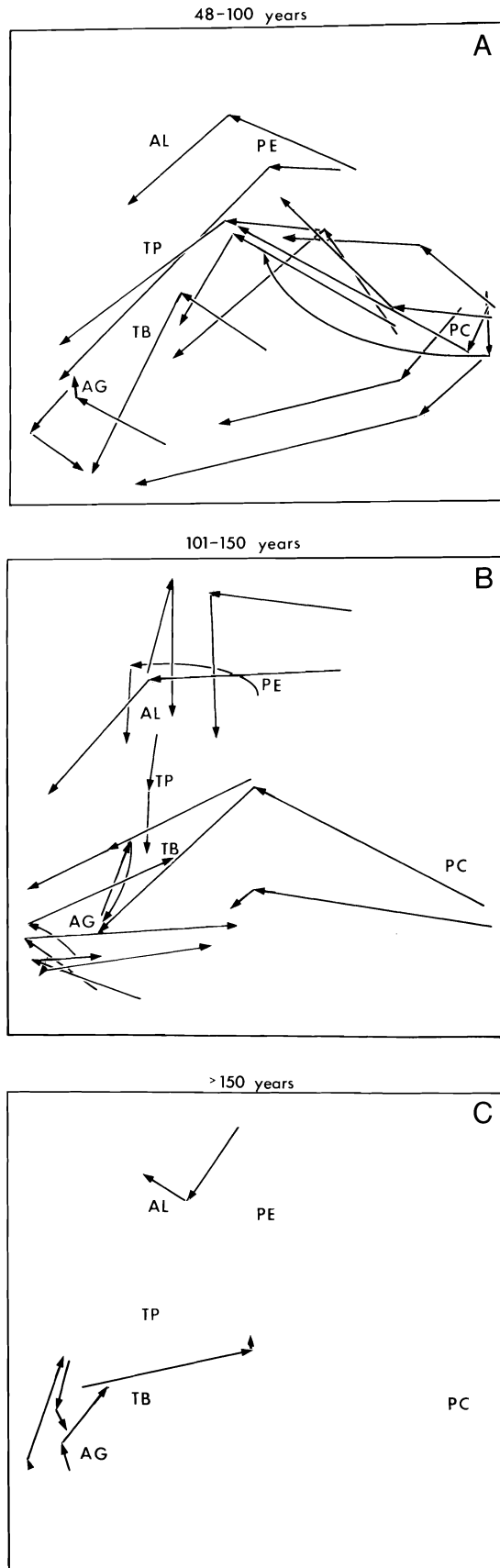


FIG. 2. Ordination of stand-layer combinations in tree species space. Vectors connect successively lower layers (tree, sapling, and seedling). Separate diagrams are given for three stand age-classes: (A) 48–100 years, (B) 101–150 years, and (C) >150 years. Letters

Local seed abundance can be influenced by differential mortality from incomplete burns or insect or pathogen outbreaks or by the composition of nearby forests. Where a burn kills only part of a mixed-species canopy, *Pinus contorta* reproduction is usually slight because of its shade intolerance, and regeneration is apt to reflect the proportions of shade-tolerant survivors. If the burn completely clears a section of canyon bottom, colonization is likely to reflect the adjacent vegetation. Less well adapted species from nearby slopes (*Picea*, *Abies lasiocarpa*, *Pseudotsuga*) may establish in lieu of (or with) better adapted species. This may explain the occasional dominance of *Picea* and *Abies lasiocarpa* on high benches where *Abies grandis* would be expected.

Insularity of the canyon-bottom communities intensifies the effects of such historical factors on establishment since for many species the number of seed-bearing trees within normal dispersal range of a freshly disturbed site is relatively small. Local anomalies may persist through fires, since scattered survival is favored by topographic irregularity and a broken forest cover. The result is "compositional drift" (Auclair and Cottam 1971), that is, similar sites diverging in composition because of their isolation.

In contrast with the ability of all other tree species to establish immediately after a disturbance, age structures suggest that *Taxus* does not usually appear until after a canopy has formed (based on increment coring along transects; see also age structures in McCune and Allen (1985, Fig. 2)). Slow reentry of *Taxus* may relate to its sensitivity to and complete removal by fire, a possible requirement of shelter for establishment, and seed dispersal limitations. Bird dispersal of *Taxus* seeds allows long-range dispersal, but cannot match the seed rain from nearby wind-dispersed conifers.

Canopy development

For the first 100–150 years after stand establishment, vegetation dynamics appears to be mainly an expression of different growth rates, since most middle-aged stands are still even-aged and contain intolerant species (Fig. 2). Much of the rich variation in community composition appears, therefore, to originate at establishment rather than through a replacement process ("initial floristic composition" rather than "relay floristics") (Egler 1954).

Intolerant species, when present, will usually overtop shade-tolerant species which die or persist in suppression until release by death of intolerant species. Where intolerant species fail to establish, the tolerant species grow faster than in the usual stands of mixed tolerant and intolerant species.

Species replacements failed to alter significantly the initial composition in most cases because, historically, most stands burned before the first canopy was lost. The normal longevity of the shortest lived major species, *Pinus contorta*, is about 120–140 years in the canyons, in contrast with an average historical fire cycle of about 60 years, about 10% of the stands surviving to 140 years (McCune 1983). However, as the occasional long-lived stand loses its first colonizers, the importance of initial establishment, though still strong, begins to wane.

indicate regions of relative dominance: AG, *Abies grandis*; AL, *Abies lasiocarpa*; PE, *Picea engelmannii*; PC, *Pinus contorta*; TB, *Taxus brevifolia*; and TP, *Thuja plicata*. For example, the lower right-most vector in Fig. 2 represents a stand dominated by *Pinus contorta* in the tree and sapling layers, but *Abies grandis* in the seedling layer. Only stands with six or more transect sample points are included.

TABLE 1. Relative aptitude for survival beneath a canopy (shade tolerance) at low elevations in the Bitterroot Canyons. Classical ratings are based on Baker (1949)

Species	Classical rating	Seedling height-growth rates in shade (ln dm/ln years)		Ranking by transition probabilities	
		Slope	Rank	Sapling/seedling	Tree/sapling
<i>Thuja plicata</i>	Very tolerant	0.73	1	2	2
<i>Taxus brevifolia</i>	Very tolerant	0.92	2	1	1
<i>Abies grandis</i>	Tolerant	0.98	3=4	3=4	3
<i>Abies lasiocarpa</i>	Very tolerant	0.98	3=4	3=4	4
<i>Pseudotsuga menziesii</i>	Intermediate	1.12	5	5	6
<i>Picea engelmannii</i>	Tolerant	1.52	6	6	5
<i>Pinus contorta</i>	Intolerant	—	—	7	7=8
<i>Larix occidentalis</i>	Intolerant	—	—	8	7=8

NOTE: —, no data available.

TABLE 2. Transition matrices adjusted for overall abundance and standardized by row totals. Elements of the matrices are probabilities of finding column species under row species, for the designated pair of layers

Trees		Saplings							
		1	2	3	4	5	6	7	8
<i>Abies grandis</i>	1	0.303	0.116	0.009	0.152	0.008	0.106	0.214	0.092
<i>A. lasiocarpa</i>	2	0.135	0.305	0.008	0.268	0.003	0.076	0.146	0.059
<i>Larix occidentalis</i>	3	0.153	0.154	0.084	0.194	0.032	0.151	0.138	0.094
<i>Picea engelmannii</i>	4	0.119	0.271	0.000	0.304	0.003	0.055	0.084	0.164
<i>Pinus contorta</i>	5	0.052	0.204	0.033	0.120	0.234	0.253	0.011	0.093
<i>Pseudotsuga menziesii</i>	6	0.169	0.169	0.032	0.154	0.046	0.270	0.033	0.127
<i>Taxus brevifolia</i>	7	0.018	0.002	0.000	0.007	0.000	0.006	0.963	0.004
<i>Thuja plicata</i>	8	0.021	0.013	0.000	0.020	0.000	0.015	0.126	0.805

Saplings		Seedlings							
		1	2	3	4	5	6	7	8
<i>Abies grandis</i>	1	0.259	0.147	0.000	0.116	0.007	0.123	0.272	0.076
<i>A. lasiocarpa</i>	2	0.140	0.444	0.000	0.119	0.003	0.157	0.071	0.066
<i>Larix occidentalis</i>	3	0.185	0.303	0.040	0.044	0.000	0.284	0.094	0.050
<i>Picea engelmannii</i>	4	0.180	0.374	0.000	0.117	0.001	0.120	0.102	0.106
<i>Pinus contorta</i>	5	0.085	0.307	0.028	0.070	0.018	0.447	0.039	0.006
<i>Pseudotsuga menziesii</i>	6	0.221	0.221	0.009	0.057	0.020	0.302	0.073	0.097
<i>Taxus brevifolia</i>	7	0.037	0.028	0.000	0.021	0.001	0.016	0.769	0.128
<i>Thuja plicata</i>	8	0.052	0.012	0.000	0.006	0.000	0.013	0.269	0.648

Canopy breakup

Loss of intolerant species from the canopy results in a period of relatively rapid compositional change. If *Pinus contorta* is dominant, this demise usually occurs 100–150 years after establishment (note lack of *P. contorta* in Fig. 2C). However, with longer lived species in the wave of colonizers, canopy breakup can extend over several centuries (based on age structures of old-growth stands). The occupants of openings are often suppressed shade-tolerant individuals of approximately the same age as the canopy. Gradually the canopy becomes all-aged as latecomers occupy gaps.

From their shade tolerance, one might project that given an unusually long period without fire, *Taxus* and (or) *Thuja* will dominate. However, seed distribution and seedling establishment in the canyons are too inequitable to permit such a uniform result. Also, long periods without fire were extremely rare. Thus the projection appears hypothetical. However, the drastic reduction in fire frequency (McCune 1983) may provide us with an example of forest dynamics with prevention of natural, major disturbances.

With the exception of *Taxus*, shade-tolerant tree species are susceptible to damage by falling debris from the disintegrating canopy. *Taxus*, however, is well adapted to bombardment, exploiting this as a method of propagation (main stems often do not break and will root when pinned to the ground). Thus, large falling debris favors a shift among the tolerant species to *Taxus*.

Local persistence of *Taxus* is apparently favored by its high resistance to insects and diseases. No serious fungal or insect problems were observed for *Taxus* in the Bitterroot Range. Although we saw heavily browsed individuals, *T. brevifolia* is apparently not as severely limited by herbivory as *T. canadensis* in eastern North America (cf. Beals and Cottam 1960). The major limitation on *T. brevifolia* in the canyon bottoms appears to be a high susceptibility to fire. Fire suppression, the current policy in the Bitterroot Canyons, should increase *Taxus* in the canyon bottoms.

Taxus may require shade for establishment, but can it maintain dominance once the original canopy is lost? Because of the great longevity of the shade-tolerant associates of *Taxus*,

TABLE 3. Life-history characteristics of the major tree species (primarily based on this study, Antos and Habeck (1981), Baker (1949), Habeck (1968), Kessell (1979), McCune (1983), Pfister et al. (1977), Fowells (1965), and Wellner (1970))

	Potential longevity (years)	Shade tolerance	Growth rate in open	Fire resistance	Establishment in closed forest	Other important population controls
<i>Abies grandis</i>	>300	High	Moderate	High in old trees, low when young	Usually requires a gap	Chronic and eventually lethal <i>Echinodontium tinctorium</i> , western spruce budworm
<i>Abies lasiocarpa</i>	>150	High	Moderate	Low	Relatively successful, especially in gaps	Western spruce budworm, chronic decay fungi
<i>Larix occidentalis</i>	>600	Low	Fast	High	None	Dwarf mistletoe, larch casebearer
<i>Picea engelmannii</i>	>500	Moderate	Moderate	Low, moderate in old age	Plentiful short-lived seedlings on rotten logs	Windthrow, western spruce budworm
<i>Pinus contorta</i>	>150	Low	Fast	Low, moderate in old age	Rare	Mountain pine beetle, dwarf mistletoe
<i>Pseudotsuga menziesii</i>	>500	Moderate	Moderate	High in old trees, low when young	Occasional seedlings, usually short-lived	Western spruce budworm, dwarf mistletoe
<i>Taxus brevifolia</i>	>250	High	Slow	Easily killed by light ground fire	By seed or layering	Grazing by ungulates
<i>Thuja plicata</i>	>500	High	Moderate	Moderate in old trees, low when young	Mostly by layering, seedlings successful under gaps	Chronic decay fungi, grazing by ungulates

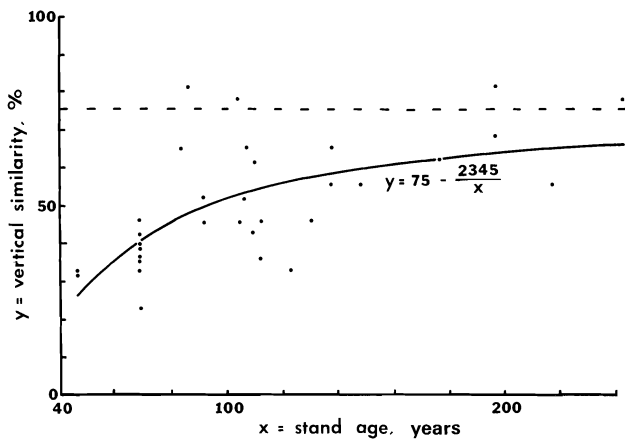


FIG. 3. Vertical similarity as a function of stand age, the hyperbolic model fitted with the least squares method ($r^2 = 0.38$). The broken line is the asymptote for the curve.

complete loss of the original canopy is virtually unseen in nature. However, the forests in lower Bear Canyon are approaching a state of continuous *Taxus* as *Larix* diminishes under attack by dwarf mistletoe (*Arceuthobium laricis* (Piper) St. John) and the scattered *Picea* and *Abies grandis* continue to decline with little regeneration. *Taxus* browns but may survive when an overstory is removed by logging (S. F. Arno, personal communication; J. A. Antos, personal communication), yet this response may reflect intolerance to the microclimatic change rather than intolerance of the new regime. In any event, it seems likely that establishment of conifers other than *Taxus* would occur sporadically and, as they overtopped the *Taxus*, would provide microclimatic shelter, even if in low numbers.

Increasing dominance of the small-statured *Taxus* with time contrasts with the classical concept of increasing size of the

dominants with succession (Clements 1916). The intolerant *Larix*, towering over 50 m, dwarfs *Taxus*, which seldom exceeds 6 m in the Bitterroot Canyons. Similarly, tall seral trees are sometimes replaced by smaller, tolerant species in coastal Pacific Northwest forests (Franklin and Hemstrom 1981).

Climax recognition

Although the climax concept cannot be strictly applied at the scale of individual stands as a stable "end point" of succession (Cowles 1901, p. 81; and many others since), if we relax our criteria for the degree of community stability required to apply the term "climax," then it becomes a more reasonable and useful concept. We use it here simply as a state of relatively stable composition that develops in the absence of major disturbance.

The primary criterion for climax recognition in forests is, in practice, a stable age structure. The understory should be similar to the canopy if, without major disturbance, individuals in the canopy are to be replaced in the existing proportions. Compositional stability generally increases with time in the canyon-bottom forests, vertical differences in composition decreasing with stand age (compare vector lengths among Figs. 2A, 2B, and 2C).

Vertical homogeneity was also evaluated as the average percent similarity between three layers: seedlings, saplings, and mature trees. Vertical homogeneity increases as shade-intolerant species are lost (Fig. 3). The rate of increase declines until about 120–140 years in the canyon-bottom forests (Fig. 3), coincident with the demise of the dominant intolerant species, *Pinus contorta*. Because the maximum vertical homogeneity is well below 100%, we can conclude that the vertical structure suggests continuing compositional flux.

Table 4 summarizes the applicability of some commonly mentioned trends in secondary succession to our study area.

TABLE 4. Applicability of characteristics of succession to forest dynamics in the Bitterroot Canyons

Characteristic	Evaluation
Increasing size of dominants	Notable exceptions: the small tree <i>Taxus brevifolia</i> increases in dominance, the pioneer <i>Larix occidentalis</i> is the tallest species in the canyons
Increasing vertical similarity	Yes, \pm asymptotic at 75% similarity
"Climax" species require preestablishment of others, i.e., "relay floristics"	No, except perhaps <i>Taxus brevifolia</i>
Convergence on similar sites	Moderate within canyons, weak between canyons (McCune and Allen 1985)
Convergence on different sites	Weak to none
Increasing dominance of shade-tolerant species	Yes, except that some young stands are dominated by shade-tolerant species
Intolerant tree species are relatively small and short-lived	Exception: <i>Larix occidentalis</i>
Intolerant tree species are relatively fast growing	Yes. However, the shade-tolerant species <i>Abies grandis</i> and <i>Thuja</i> grow fast when not suppressed

Despite clear competitive advantages of *Thuja plicata* and *Taxus brevifolia*, convergence on a common climax composition in the Bitterroot Canyons is weak. Uneven species distributions appear to influence species composition at establishment. Peculiarities of circumstance during establishment tend to persist in the absence of disturbance; colonizers are long-lived and may be shade tolerant. This unpredictability of forest dynamics is aggravated by insularity of the canyon bottoms.

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