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Species Composition and Diversity During Secondary Succession of Coniferous Forests in the Western Cascade Mountains of Oregon

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ABSTRACT. Species diversity and community composition were studied at 23 sites on similar western hemlock/Douglas-fir forest habitats, in undisturbed old-growth stands and stands at 2, 5, 10, 15, 20, 30, and 40 years after clearcutting, broadcast burning, and planting with Douglas-fir. Vegetation was sampled with three 5 × 60 m transects at each site. Invading herbs, then invading and residual shrubs, and finally conifers dominated through the first 30 years. Late seral species, which account for 99% of cover in old-growth stands, are nearly eliminated immediately following disturbance, but account for almost 40% of vegetative cover after 5 years, 66% after 10 years, 83% after 20 years, and 97% at 40 years. After an initial drop following disturbance, species diversity trends weakly upward with heterogeneity peaking at 15 years and richness at 20 years. This initially high diversity (higher than that of old-growth stands) is short-lived. After the tree canopy closes, species diversity declines reaching its lowest values at 40 years. Only two species were eradicated after disturbance, both mycotrophs. Pacific Northwest old-growth forests are relatively poor in species, but moderately high in heterogeneity values. FOR. SCI. 34(4):960–979.

ADDITIONAL KEY WORDS. Old-growth forests, disturbance, Pacific Northwest.

THE THEORETICAL AND PRACTICAL IMPORTANCE of secondary succession has long been recognized by forest ecologists and managers, and successional sequences have been documented throughout North America. Several investigators have suggested and/or shown empirically that species diversity fluctuates during secondary succession, but the patterns and relationships are less than certain. This uncertainty has caused concern among land managers charged with a governmental policy of maintaining diversity in forest ecosystems (Cooley and Cooley 1984). This paper documents changes in plant species diversity and composition on a chronosequence of plots 2 to 40 years after logging, burning, and planting with Douglas-fir (*Pseudostuga menziesii* [Mirb.] Franco), reveals some unexpected trends, and discuss implications for Pacific Northwest forests.

The concept and measurement of diversity can be applied to attributes of

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ecosystems such as processes, structure, or species (Franklin 1984). Species diversity can be viewed at three spatial scales: (1) the landscape or cover type level (gamma diversity), (2) the between-stand level, for instance, along an environmental gradient (beta diversity), and (3) the within-stand or habitat level (alpha diversity) (Whittaker 1975). This paper deals specifically with plant species diversity at the alpha level, that is, the number and relative abundance of species within a particular habitat type.

Some ecologists have predicted that diversity will increase through succession (Odum 1969, Harger and Tustin 1973), and others have observed such increases (Tagawa 1964, Monk 1967, Holland 1971, Brunig 1973, Nicholson and Monk 1974). Still others have predicted that diversity might decrease during a successional sequence (Whittaker 1965, Pielou 1966a). Habeck (1968) found that diversity steadily decreased after initial postfire establishment in cedar-hemlock forests in the Northern Rocky Mountains. Margalef (1963, 1968), Whittaker (1965), and Horn (1974) suggest a pattern of increase and then decrease during forest succession. Much empirical evidence suggests this third pattern is common (Loucks 1970, Auclair and Goff 1971, Whittaker 1972, Shafi and Yarranton 1973, Bazzaz 1975, Johnson et al. 1976, Pett 1978, Bormann and Likens 1979, Hibbs 1983). Peet (1978) reports a decline and then an increase in species diversity with stand age along the Colorado Front Range, and suggests that there may be more than one peak in diversity during succession, depending on site characteristics. Most recently, Norse et al. (1986) have proposed a model for an "idealized forest" in which early and late successional species account for two periods of relatively high diversity, in young and mature/old-growth forests, respectively. Finally, Drury and Nisbett (1973) suggest that "diversity is an ecological phenomenon independent of succession."

These differing views and observations suggest that the relationship between diversity and succession depends on many variables, the most important of which may be type of community (e.g., terrestrial, aquatic, plant, animal), geographic location, and circumstances of disturbance and succession (e.g., type, intensity and frequency of disturbance, patch size, propagule dispersal, seed bank viability). To understand this relationship, even locally, patterns of diversity during succession should be studied in a variety of habitats and locations under a variety of disturbance regimes.

In the Pacific Northwest, there has been concern that logging of late-successional, old-growth forest ecosystems may decrease plant species diversity on a local and regional scale and adversely affect rare, threatened, or endangered species (Franklin 1984, Norse et al. 1986). Some plant ecologists in the region have noticed, however, a net increase in numbers of species after clearcutting and burning (Dyrness 1973, Zamora 1982, Franklin 1984). This increase and accompanying changes in community composition in seral forest ecosystems have been accepted intuitively, but lack adequate documentation beyond one to two decades of forest succession.

Previous studies of secondary succession following clearcut logging and burning west of the Cascade Mountains have described only broad successional stages (Kienholtz 1929, Ingram 1931, Issac 1940) or have not gone beyond early successional stages (Morris 1958, Yerkes 1960, Mueller-Dombois 1965, Steen 1966, West and Chilcote 1968, Dyrness 1973). All these studies have focused on compositional changes.

Although plant species diversity and community composition have been tabulated for a variety of coniferous habitats in the Northwest (del Moral 1972, del Moral and Fleming 1979, Zobel et al. 1976), few forest ecologists in northwestern North America have studied diversity and composition for chronosequences of a decade or longer, and only one of these studies was made after clearcut logging and burning in coniferous forests (Zamora 1982). Reiners et al. (1971) measured species diversity and community composition in a primary successional sequence on sites previously occupied by glacial ice at Glacier Bay, Alaska. Alaback (1982) documented changes over 700 years in vegetative structure and biomass in a wide variety of environmental conditions in coastal spruce-hemlock forests in southeastern Alaska. Zamora (1981) determined understory structure and species richness up to 27 years after clearcutting and burning in the *Abies grandis/Pachistima myrsinites* habitat type of north central Idaho. No studies of succession west of the Cascade Mountains of Oregon have examined both richness and evenness components of plant species diversity beyond initial stages of secondary succession while holding variation in elevation, aspect, slope, community type and treatment to a minimum.

The objective of our study was to document these changes in diversity as well as in composition over a 40-year chronosequence of similar sites that had been clearcut logged, broadcast burned, and planted with Douglas-fir seedlings. These first 40 years encompass a period of rapid structural and compositional change, from bare ground through herb, shrub, and early closed tree canopy stages. Although this period is relatively short with respect to a full successional sequence of 600–1000 years in these coniferous forests, it may be the most dynamic phase (see Bormann and Likens 1979), and hence of much ecological interest.

On a more practical level, 40 years represents 40%–60% of the rotation time of a managed forest in the Pacific Northwest. Hence, knowledge of the effects of clearcutting and broadcast burning on the plant community should help those concerned with plant species diversity to understand the consequences of the most common silvicultural treatment in this region.

STUDY SITES

Data were collected from June through August 1980 in the western Cascade Mountains of Oregon on the H. J. Andrews Experimental Forest and on surrounding USDA Forest Service lands and privately owned timber lands. This region of the western Cascades of Oregon is characterized by deeply dissected terrain with generally well-developed soils on Tertiary volcanic substrate. From 200 to 400 cm of precipitation fall annually in this area, most of it between October and April. Summers are relatively dry (Franklin and Dyrness 1973).

Coniferous forests of two age classes, 400+ and 125 years, predominate over this area (Teensma 1986, Morrison and Swanson in press). At lower to middle elevations, the older stands are dominated by western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and Douglas-fir, and the younger by Douglas-fir. Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) and noble fir (*Abies procera* Rehd.) dominate in both age classes at higher elevations. This study was carried out at low to middle elevations in the *Tsuga heterophylla/Rhododendron macrophylum/Gaultheria shallon* habitat type (Dyrness et al. 1974). This relatively abundant type occurs in warm and moderately dry environments (Zobel et al. 1976) on approximately 20% of the landscape of Andrews Experimental Forest.

Vegetation was sampled in three 450-year-old stands and on 20 sites that had been clearcut, broadcast burned, and planted with Douglas-fir seedlings approximately 2, 5, 10, 15, 20, 30 and 40 years before sampling. Forty years was the sampling limitation because there were no older clearcuts on the

TABLE 1. Site characteristics of selected study areas on Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon *habitat types in and around the H. J. Andrews Experimental Forest.*

Age (yr)	Site no.	Year of treatment			Aspect (°)	Slope (%)	Elev. (m)	Area (ha)
		Clearcut	Burned	Planted				
Old-growth	1	.... *uncut*			334	15	610	—
(400+)	2	.... *uncut*			312	15	730	—
	3	.... *uncut*			314	15	530	—
2	1	76	78	79	300	35	610	8.1
	2	77	78	82	20	35	970	7.3
	3	76	78	81	324	30	820	4.4
5	1	75	75	76	340	30	1030	15.4
	2	75	76	81	328	30	730	10.9
	3	75	75	76	24	35	670	6.5
10	1	71	71	n.a.[1]	322	30	880	12.1
	2	68	69	n.a.	330	30	970	15.8
15	1	65	65	66/67	340	25	760	28.3
	2	67	67	68	330	30	850	25.1
	3	65	65	73	50	35	790	15.8
20	1	59	60	61/63	342	25	820	16.2
	2	59	59	60/63	350	30	670	11.3
	3	59	60	61/64	276	30	610	11.3
30	1	49	n.a.	n.a.	300	10	820	16.2
	2	51/52	52	53	330	25	640	8.9
	3	51	51	56	34	20	820	19.4
40	1	40/41	43	n.a.	0	10	460	247
	2	36/39	36/39	n.p.[2]	310	25	550	151
	3	36/39	36/39	n.p.	310	25	500	150

[1] n.a. = not available.
[2] n.p. = not planted, natural regeneration

desired habitat type with reliable treatment histories or documentation. For all but one of the age classes, three sites were selected for uniformity of aspect, slope, elevation, habitat type and treatment (Table 1). Criteria of uniformity could be met on only two sites of the 10-year age class.

We acknowledge limitations of studying succession with multiple-site spatial chronosequences rather than single-site temporal chronosequences. As Oliver (1982) states: "For a group of stands of different ages to be a true chronosequence, they should be on similar soils and sites; have similar climates and climatic histories, originate after similar previous disturbances, and have similar species and spatial and age distributions." We addressed this problem by reviewing thousands of sites cataloged on the USDA Forest Service's Total Resource Inventory (TRI) system for the Blue River Ranger District in addition to stand maps for clearcuts on the Andrews Experimental Forest. We found 104 sites that appeared to meet our criteria for uniformity: NW-N-NE facing; midslope; 15–30% slope; 500–1000 m elevation; similar logging (clearcut, high lead) and burning (medium intensity, during autumn) treatments; and *Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon* habitat type. Most sites had inadequate documentation of planting density and stocking levels. These 104 sites were field-checked, and 20 sites were selected from them. The 40-year sites on privately owned land were identified from stand maps provided by the land owners, similarly field-checked and selected to best meet our criteria.

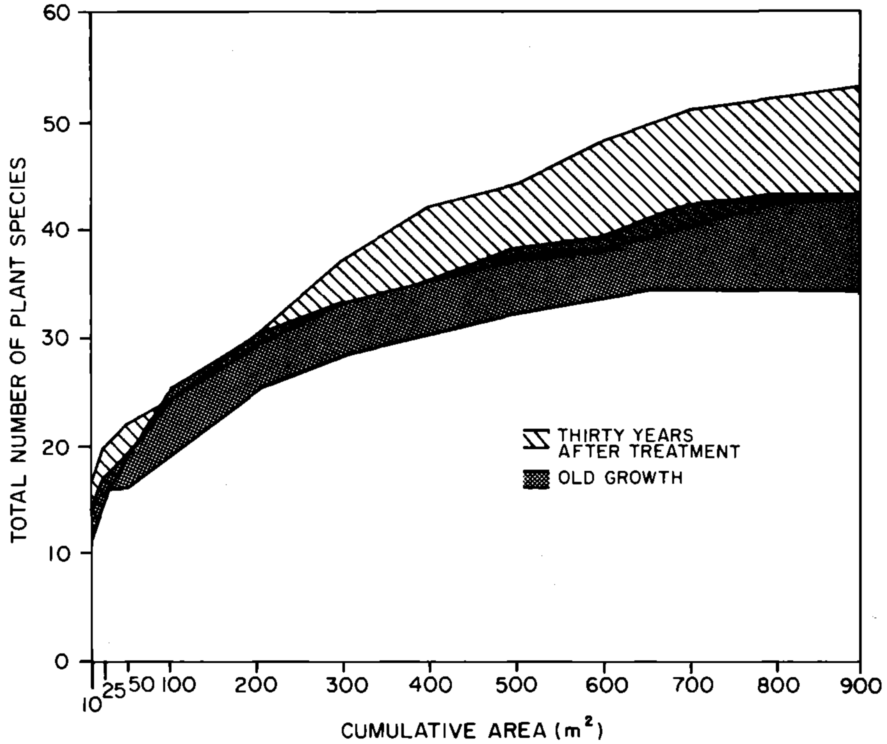

FIGURE 1. Species/area curves for richest and poorest sites in two age classes. Transects from all sites fell within the shaded and/or hatched ranges shown.

METHODS

Three sites of each age class (only 2 for the 10-year age class) were sampled with three belt transects 60 m × 5 m per site. The transects were placed in clearcuts 50 m above or below logging roads, 20 m from the edge of the cut, and marked with a wooden stake and flagging. All transects run perpendicular to the slope. Species present were noted in six 5 m × 10 m subplots per transect, and cover values were estimated visually to the nearest percentage up to 10% and to the nearest 5% thereafter on 3 larger 5 m × 20 m subplots. This technique was practiced for 1 month to ensure consistency. Sampling excluded grasses, mosses, and lichens. Nomenclature follows Hitchcock and Cronquist (1973).

Cover values of the three 5 m × 20 m subplots were averaged to give a value for each transect. Mean cover values for each species were calculated from the nine transects in each age class. Species/area curves for transects rise rapidly until about $100m^2$, after which their rate of increase steadily declines up to 900 m^2 (Figure 1). It is likely that a few more species would be added after 900 m^2, but it is unlikely this would greatly change the observed patterns or our interpretations.

Plant species were separated into six classifications established by Franklin and Dyrness (1973) and Dyrness et al. (1974) according to growth-form and their occurrence in late-successional and seral communities: conifers, deciduous trees, residual shrubs, invading shrubs, residual herbs, and invading herbs (Table 2). Residual herbs and shrubs are those species that have persisted on the site from the original unlogged stand. Changes in

TABLE 2. Mean cover values of plant species on old-growth stands and on Douglas-fir plantations (n = 3 for all age classes except 10 yr where n = 2).

Species	Undisturbed old-growth	Interval since clearcutting, broadcast burning, planting						
		2 yr	5 yr	10 yr	15 yr	20 yr	30 yr	40 yr
Conifers								
Abies procera Rehder	0	0.01	0	2.78	0.22	0	0	0
Pseudotsuga menziesii (Mirbel) Franco	21.48	0.16	2.25	5.66	32.73	60.37	63.7	76.85
Thuja plicata Donn	14.87	0.16	1.76	2.87	7.23	15.89	3.48	0.61
Tsuga heterophylla (Raf.) Sarg.	39.22	0.16	0.73	4.67	9.96	6.26	5.55	4.24
Deciduous trees								
Acer macrophyllum Pursh	0	0.004	0.76	0	0.05	4.0	2.96	0
Alnus rubra Borg.	0	0	0.01	0	0.04	0.74	0.07	0.75
Castinopsis chrysophylla (Dougl.) DC.	1.42	0.09	0.05	0.22	2.52	0.63	0.56	3.85
Populus trichocarpa T. & G.	0	0.04	0	0	0	0	0	0
Residual tall shrubs								
Acer circinatum Pursh	6.53	1.61	1.48	1.06	9.70	6.36	17.38	8.16
Corylus cornuta Marsh.	0.002	0.13	0	0	0	0	0	0
Cornus nuttallii Aud.	0.85	0.04	0.13	0	0.04	0.52	0.17	1.69
Rhododendron macrophyllum G. Don	13.23	0.44	2.46	5.39	10.93	2.63	5.50	6.81
Taxus brevifolia Nutt.	9.56	0.05	0.18	0.16	1.51	0.66	2.26	0.49
Vaccinium alaskaense Howell	0	0	0	0.03	0.11	0	0	0
Vaccinium membranaceum Dougl.	0.053	0	0.12	0.53	1.64	0.23	0.17	0.003
Vaccinium parvifolium Smith	1.31	0.65	0.61	0.79	3.72	1.15	2.92	1.34
Invading tall shrubs								
Amelanchier alnifolia Nutt.	0	0	0	0	0	0.001	0	0
Arctostaphylos canescens Eastw.	0	0	0.1	0	0.11	0.52	0	0
A. columbiana Piper	0	0	0.04	0	0.15	0	0.02	0
A. nevadensis Gray	0	0	0	0.06	0.11	0	0	0
Ceanothus integerrimus H. & A.	0	0	0.005	0	0	0	0	0
Ceanothus sanguineus Pursh	0	0.04	2.10	0	5.59	3.19	1.70	0
Ceanothus velutinus Dougl.	0	0	0.005	0	10.19	1.26	0	0
Holodiscus discolor (Pursh) Maxim.	0	0.05	0.11	0.001	0.51	0.15	0.04	0

TABLE 2. *Continued.*

Species	Undisturbed old-growth	Interval since clearcutting, broadcast burning, planting						
		2 yr	5 yr	10 yr	15 yr	20 yr	30 yr	40 yr
Prunus emarginata (Dougl.) Walp.	0	0	0.05	0	0.19	0.49	0.07	0
Ribes lobbii Gray	0	0.008	0.16	0.06	0	0.001	0.11	0
Ribes sanguineum Pursh	0	0.04	0.15	0.02	0.18	0.74	0.04	0.07
Rubus leucodermis Dougl.	0.07	0.31	9.15	0.53	0.17	0.11	0	0
Rubus parviflorus Nutt.	0.001	1.35	1.90	13.12	6.41	16.68	5.79	0.05
Salix sp.	0	0.001	0	0.18	2.18	0.81	6.52	0.6
Sambucus cerulea Raf.	0	0	0	0.002	0.02	0.48	0.19	0.003
Sambucus racemosa L.	0	0.04	0.004	0	0.74	0	0.56	0
Residual low shrubs								
Berberis aquifolium Pursh	0	0	0	0	0	0.018	0	0
Berberis nervosa Pursh	11.52	1.88	5.04	4.22	9.48	6.98	22.18	20.97
Cornus canadensis L.	0	0.004	0	0.03	0.02	0.001	0.03	0
Gaultheria shallon Pursh	7.37	3.18	1.41	10	8.52	9.93	17.74	14.97
Pachistima myrsinites (Pursh) Raf.	0	0.002	0	0	2.24	0	0	0.001
Rhamnus purshiana DC.	0.001	0.001	0	0	0	0.001	0.001	0
Rosa gymnocarpa Nutt.	0.002	0.005	0.001	0	0.10	0.07	0.03	0.70
Rubus nivalis Dougl.	0.02	0.01	0.01	0.01	0.03	0.01	0.08	0.01
Rubus sp.	0.08	0.005	0.12	0.03	0.05	0.01	0.13	0.08
Rubus ursinus Cham & Schlecht.	0.18	2.28	2.18	1.11	9.7	20.52	7.35	0.66
Symphoricarpus mollis Nutt.	0.07	0	0.01	0	0	0.3	0.001	0.53
Vaccinium scoparium Leib.	0	0	0	0	0	0	0	0.001
Residual herbs								
Achlys triphylla (Smith) DC.	0.72	0.41	0.28	0.47	0.01	0.19	0.01	1.25
Adenocaulon bicolor Hook.	0.001	0	0	0	0	0	0.001	0.004
Adiantum pedatum L.	0.04	0	0	0	0.02	0.004	0.04	0
Anemone deltoidea Hook.	0.03	0.003	0.04	0.01	0.15	0.08	0.001	0.05

Antenaria dimorpha (Nutt.) T. & G.	0	0.03	0	0	0	0	0	0
Asarum caudatum Lindl.	0	0	0	0	0.26	0.57	0.24	0.02
Athyrium felix-femina (L.) Roth.	0.04	0	0	0	0	0.19	0.07	0
Blechnum spicant (L.) Roth.	0.04	0.08	0	0.01	0	0	0	0
Boykinia elata (Nutt.) Greene	0	0.002	0.001	0.01	0.20	0	0	0
Chimaphila sp.	0	0	0	0	0	0	0.001	0.001
Chimaphila menziesii (R. Br.) Spreng.	0.004	0	0	0	0	0.001	0.02	0.01
Chimphila umbellata (L.) Bart.	1.54	0.003	0.001	0.24	0.08	0.004	0.41	0
Clintonia uniflora (Schult.) Kunth.	0	0	0	0.005	0	0	0	0
Coptis laciniata Gray	1.69	0.01	0.47	0.3	0.2	1.04	0.54	0.12
Corallorhiza mertensiana Bong.	0.001	0	0	0	0	0	0	0
Galium aparine L.	0	0.08	0.06	0.14	0.005	0.05	0.35	0
Galium oreganum Britt.	0	0	0	0.001	0	0	0	0.004
Galium triflorum Michx.	0.06	0.062	0.30	0.23	0.40	0.35	0.09	0.09
Goodyera oblongifolia Raf.	0.24	0.001	0.001	0	0.001	0.002	0	0.002
Hieracium albiflorum Hook.	0.01	2.35	4.9	0.39	0.18	0.19	0.009	0.009
Linnaea borealis L.	10.66	0.32	0.85	7.17	7.56	1.67	4.51	0.01
Lilium columbianum Hanson	0	0	0	0	0	0.001	0	0
Lilium washingtonianum Kell.	0	0	0	0	0.02	0	0.003	0
Osmorhiza chilensis H. & A.	0	0	0	0	0	0.002	0.004	0.05
Oxalis oregana Nutt.	3.52	0.85	0.21	18.22	0.93	0	2.78	36.35
Petasites frigidus (L.) Fries	0	0.19	0.37	0	0.08	0.04	0.04	0.001
Polystichum munitum (Kaulf.) Presl	7.86	2.33	9.87	3	8.26	12.87	18.59	11.7
Pterospora andromeda Nutt.	0.003	0	0	0	0	0	0	0
Smilacina stellata (L.) Desf.	0.01	0.003	0.13	0.79	0.001	0.01	0.01	0.23
Syntheris reniformis (Dougl.) Benth	0.003	0.06	0	0	0	0.04	0.001	0
Tiarella unifoliata (Hook.) Kurtz.	0.08	0.21	0.004	0.78	0.003	0.16	0.12	0
Trientalis latifolia Hook.	0.05	0.07	1.46	2.22	2.53	0.5	0.54	0.06
Trilium ovatum Pursh	0.003	0.003	0.006	0.01	0.1	0.02	0.02	0.49
Vancouveria hexandra (Hook.) Morr. & Dec.	0.02	0.01	0.07	0.92	0.003	0.12	0.01	0.89
Vicia americana Muhl.	0	0	0.19	0	1.18	0.98	0	0

TABLE 2. *Continued.*

Species	Undisturbed old-growth	Interval since clearcutting, broadcast burning, planting						
		2 yr	5 yr	10 yr	15 yr	20 yr	30 yr	40 yr
Viola sempervirens Greene	0.36	0.04	0.14	0.14	0.83	0.57	0.23	0.13
Whipplea modesta Torr.	0.02	0.3	0.83	0	0.91	1.33	0.29	0
Xerophylum tenax (Pursh.) Nutt.	0.18	0.32	0.09	0.06	0.68	0.003	0	0.07
Invading herbs								
Actaea rubra (Ait) Willd.	0.001	0	0.005	0	0	0.06	0.002	0
Anaphalis margaritacea (L.) B. & H.	0	0.13	0.4	0.61	0.98	0.75	0.09	0.004
Aster sp.	0.113	0.07	0.02	0.007	0.03	0.003	0	0.001
Circium sp.	0	0	0.42	0	0	0	0	0
Circium arvense (L.) Scop.	0	0.09	0.85	0.001	0.001	0	0	0
Circium vulgare (Savi) Tenore	0	1.81	3.0	0	0.003	0.09	0.003	0
Collomia heterophylla Hook.	0	0.002	0.01	0	0	0	0	0.001
Dicentra formosa (Andr.) Walp.	0	0.17	0.01	0.11	0	0.003	0.1	0.001
Epilobium angustifolium L.	0.11	10.59	33.37	22.55	17.12	2.57	0.07	0.01
E. minutum Lindl.	0	0.44	0.28	0	0.002	0.002	0	0
E. paniculatum Nutt.	0	2.98	1.98	0	0.01	0.03	0	0
E. watsonii Barbey	0	4.0	3.63	0.003	0	0.006	0	0
Equisetum telmateia Ehrh.	0	0	0	0	0	0.01	0	0
Fragaria sp.	0	0	0.03	0.002	0.12	0.001	0	0
Hypericum perforatum L.	0	0.04	0.14	0.006	0.05	0.03	0.07	0.003
Lactuca muralis (L.) Fresen.	0	0.001	3.86	0	0.34	0	0	0
Lupinus latifolius Agardh	0	0	1.45	0	0	0	0	0
Madia gracilis (J. E. Smith) Keck	0	0.44	0.02	0.006	0.001	0.06	0	0
Madia sp.	0	0.002	0	0	0	0	0	0
Montia sp.	0	0.01	0	0	0	0	0	0
Montia sibirica (L.) Howell	0	0.002	0.005	0.52	0.17	0	0.001	0.09
Penstemon cardwellii Howell	0	0.002	0	0.03	0.06	0	0	0
Pteridium aquilinum (L.) Kuhn.	0	0	0.007	0.45	0.3	3.14	0.15	1.44
Senecio sylvaticus L.	0	2.85	0.248	0.002	0.001	0	0	0
Tellima grandiflora (Pursh) Dougl.	0	0.02	0.05	0.006	0.002	0.003	0.3	0.001

absolute cover and relative cover among these structural classes were analyzed for each age class.

Diversity was calculated with two indices: richness, the total number of species (S) tallied per 300 m^2 transect, per 900 m^2 site, and per 2700 m^2 age class, and heterogeneity (H'), estimated by the Shannon-Wiener formula (Shannon and Weaver 1949),

$$H' = -\sum_{i=1}^{n} p_i \log_e p_i$$

where p_i is the relative percentage of cover of individual species on each transect (Figure 4) or in each age class (Figure 5). The latter index is applicable when a population is too large for all its members to be counted (Pielou 1966b). It considers both richness and evenness components of diversity; that is, the number of species and the evenness of their abundance. For example, ten species each occupying 10% of an area would have a higher H' than if one of the species occupied 91% and the other nine divided the remaining 9%. H' is also more sensitive to rare species than S (Peet 1974).

Many indices of diversity have been proposed (Peet 1974), yet these two remain among the most commonly used even though they have their drawbacks (Pielou 1966b, Peet 1974, Christensen and Peet 1984). Comparison with other studies is possible because of their wide use (e.g., Monk 1967, Loucks 1970, Auclair and Goff 1971, Bazzaz 1975, Zamora 1982, Hibbs 1983).

To compare the floristic similarity of seral stands to the undisturbed old-growth age class we calculated coefficients of community similarity using Sorenson's index (SI):

$$SI = \frac{2c}{A + B} \times 100$$

where c is the number of species in common between two age classes having A and B number of species respectively (Mueller-Dombois and Ellenberg 1974). SI values range from 100 for age classes having exactly the same species as the old-growth sites, to 0 for those having no species in common. SI values also reflect floristic changes between seral stages.

We also calculated species turnover (TO), a more direct measure of floristic change from one age class to the next:

$$TO = \frac{L + G}{A + B}$$

where L is the number of species lost and G is the number of species gained between age classes, and A and B are the same as in Sorenson's idex.

All variables were analyzed as a function of time since manipulation, and their patterns through time were examined for trends toward or away from original old-growth conditions.

RESULTS

A total of 132 plant species was found on the 23 sites, 55 in the 3 old-growth stands where late seral species account for 99% of total plant cover. Cover values of residual species during the first few growing seasons after clearcut

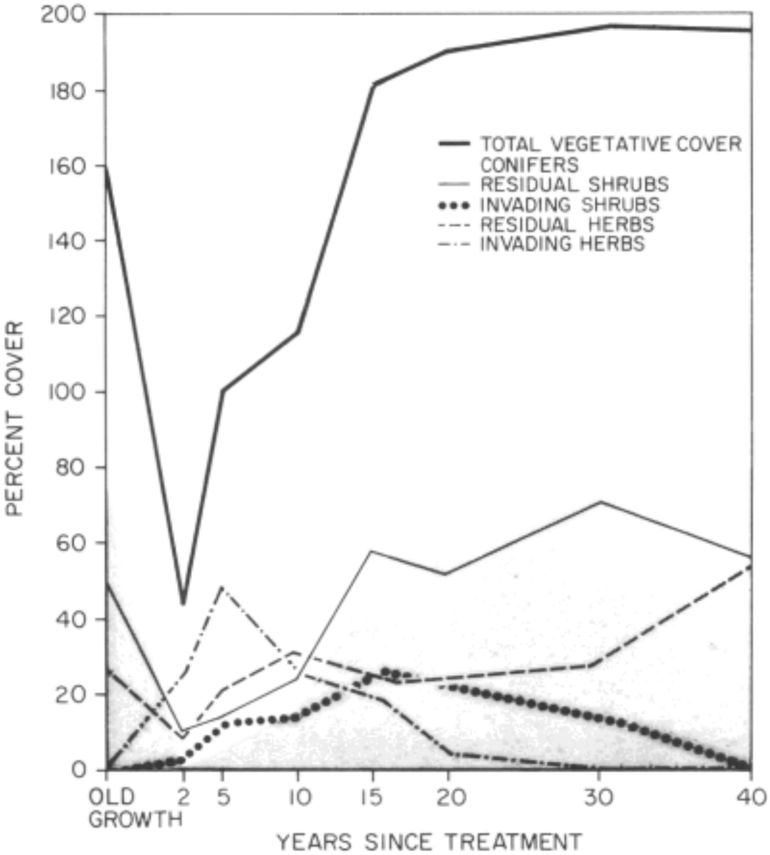

FIGURE 2. Percentage cover for growth-forms versus years since logging and burning. The values show early dominance by herbs, then by shrubs and finally by conifers. Total cover increases rapidly for 20 years; thereafter the rate of increase slows. Invading herbs and shrubs are nearly eliminated 40 years after treatment.

logging and broadcast burning are at first low but rapidly increase in importance. Residual species account for almost 40% of total cover at 5 years, 66% at 10 years, 73% at 15 years, 83% at 20 years, 90% at 30 years, and 97% at 40 years.

The general pattern of recovery on our sites during the first 40 years after logging (Figure 2) is similar to that observed elsewhere (Kienholtz 1929, Ingram 1931, Issac 1940, Zamora 1982):

1. Percentage cover of all growth-forms except invading herbs decreases sharply immediately after logging and burning.
2. Invading herbs, including some exotic species, increase rapidly, and such species as fireweed (*Epilobium angustifolium* L.), woodland groundsel (*Senecio sylvaticus* L.), common St. Johnswort (*Hypericum perforatum* L.) and common thistle (*Circium vulgare* [Savi] Airy-Shaw) dominate briefly. Total herb cover rises to almost 70% at 5 years.
3. An increase in residual herb cover lags slightly behind the dramatic rise of invading herbs.
4. Invading and residual shrubs increase concurrently with a decrease in invading and then residual herb cover.
5. Total percentage of cover increases rapidly up to 15 years; thereafter the rate of increase slackens.

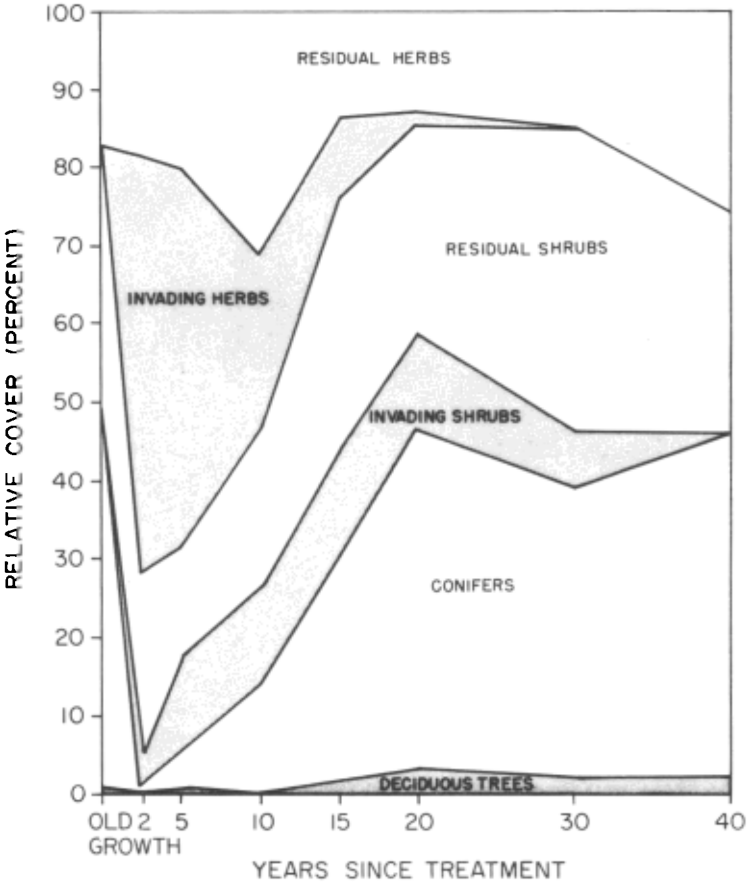

FIGURE 3. Relative cover values for growth-forms versus years since logging and burning. The patterns reveal early dominance by herbs after logging and burning of old-growth and subsequent dominance of shrubs and conifers. Deciduous trees account for little of the total cover in this habitat type.

6. Conifers and residual shrubs close the canopy at 20 to 30 years. Invading shrub and herb cover continues to decline.
7. Forty years after logging and burning, conifer cover is 82%, shrub cover is 57%, and herb cover is 53%. Cover by invading herbs and shrubs has become very small.

Residual herb cover is especially high on two of the 40-year sites. Much of this herb cover is Oregon oxalis (*Oxalis oregana* Nutt. ex T. & G.), indicating wetter conditions than typical for the *Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon* habitat type. If these two sites were excluded, herb cover at 30 and 40 years would be identical.

Relative percent cover reveals the pattern of dominance of various growth-forms in each age class (Figure 3). The old-growth forest is dominated by conifers (49% rel. cover) with lesser amounts of shrubs (33% rel. cover) and herbs (18% rel. cover). After logging and burning, we see first herb, then shrub, and finally conifer dominance with canopy closure at 20 to 30 years. At 2 years, 53% of relative cover is accounted for by invading herbs and 72% by invading and residual herbs combined. By 15 years, shrubs account for 46%, conifers for 28%, and herbs for 24% of relative

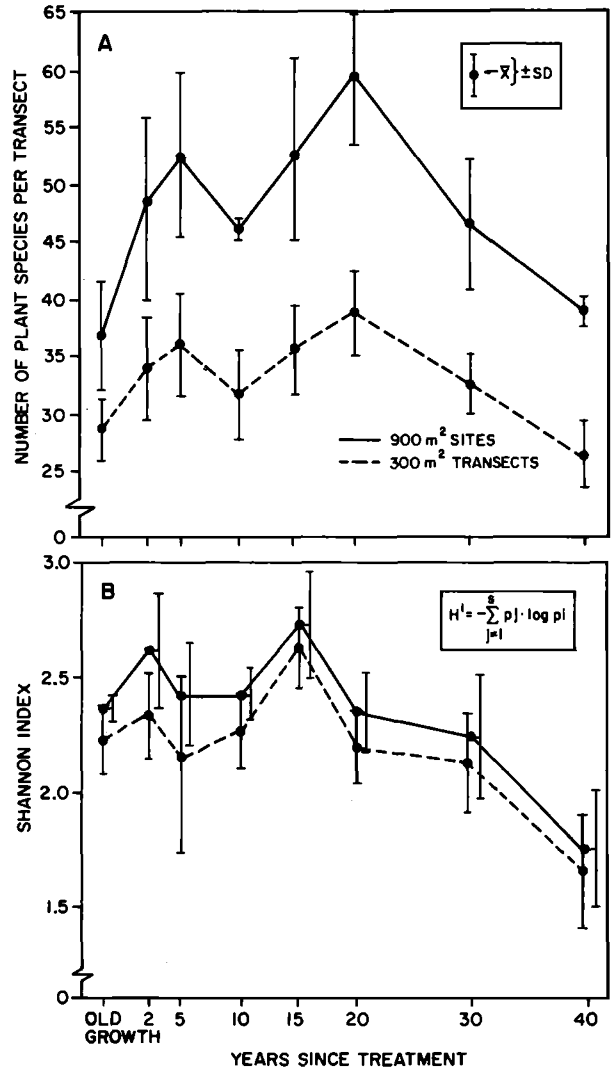

FIGURE 4. (a) Species richness (*S*) versus years since logging and burning. *S* is highest at 5 and 20 years and is relatively low for old-growth stands. (b) Heterogeneity (H') versus years since logging and burning. The peaks in H' (Shannon-Wiener index) at 2 and 15 years precede those for richness. Old-growth values for heterogeneity are moderately high. The trends in diversity remain the same when calculated by transect, site, and age class.

cover. At 20 years, conifers increase to 43%, shrubs decline to 38%, and herbs decline to 15%.

Heterogeneity and species richness increase slightly to peak at 15 and 20 years respectively after logging and burning. Then they decline to low values at 40 years (Figure 4). In comparison with early-successional stands, old-growth forests have relatively high heterogeneity but low species richness. Only the 40-year age class has fewer species. After logging and burning, species richness rises irregularly (with a dip at 10 years) to a high of 39 species per 300 m^2 at 20 years, then declines to a low of 28 species per 300 m^2 at 40 years (Figure 4a). Heterogeneity shows a similar trend with some notable exceptions: the peak is at 15 instead of 20 years; the dip is at 5 years; and the old-growth value is higher than that of four other seral age classes (Figure 4b). The pattern of high diversity at shrub and herb stages, lower diversity in old-growth, and lowest diversity in young conifer stands occurs regardless of the area for which it is calculated (i.e., 300 m^2 transects, 900 m^2 sites, or 3 sites combined for 2700 m^2 age classes). An analysis of variance shows that there is no significant variation between transects (Table 3), and that variation between ages is significant. Variation due to age is substantially greater ($F_S = 16.51$, $F_{H'} = 22.59$) than among site variation ($F_S = 5.33$, $F_{H'} = 5.01$). If a quadratic term is added to the analysis, it accounts for a significant ($P < 0.001$) amount of the variation due to age, indicating that the rise and fall of both indicies around 15 to 20 years is a real trend. Least significant differences between age classes for S and H' are 2.87 and 0.16 ($P < 0.05$) and 3.73 and 0.21 ($P < 0.01$).

Species richness and heterogeneity for various growth-forms follow similar but more variable trajectories than the composite pattern for all species (Figure 5). The number of tree species remains essentially the same throughout the chronosequence whereas heterogeneity declines, reflecting the increased dominance of Douglas-fir. Heterogeneity and richness of shrubs and herbs peaks at 2 to 5 years and again at 15 to 20 years, and thereafter declines. Variation between age classes is much higher for invading shrubs and herbs than for residual species in these growth forms.

Coefficient of community values (relative to old-growth conditions) decrease from 2 to 15 years, then increase from 20 to 40 years as the canopy closes (Figure 6a). The downward trend in similarity to the old-growth community is due to an abundance of invading species more than to a loss of residual species. The subsequent increase in similarity is due to a decline in invading species (especially herbs) and a slight increase in residual species.

Species turnover declines from 2 through 30 years with a slight increase at 20 years (Figure 6b) before beginning to climb again after canopy closure. Again, the initial high values are due more to invading species gained than to a loss of residuals. From 5 through 40 years, number of species lost is about equal to number of species gained.

DISCUSSION

The pattern of rapid change from herb, to shrub, and finally conifer dominance upon canopy closure at 20–30 years was expected. The high species turnover (Figure 6b) immediately after treatment followed by a leveling off at 30–40 years indicates sudden change and partial recovery. The steep drop and subsequent increase in coefficient of community values (Figure 6a) also indicate rapid initial compositional change, which appears to slacken with canopy closure. Higher community coefficients at 30 and 40 years suggest

TABLE 3. Analysis of variance for transect, site, and age (general linear model procedure).

Source of variation	DF	F_S	P	$F_{H'}$	P
Transect	2	0.82	n.s.	0.30	n.s.
Age	7	16.51	0.001	22.59	0.001
Site (age)	15	5.33	0.001	5.01	0.001
Error	44				
Total	68				

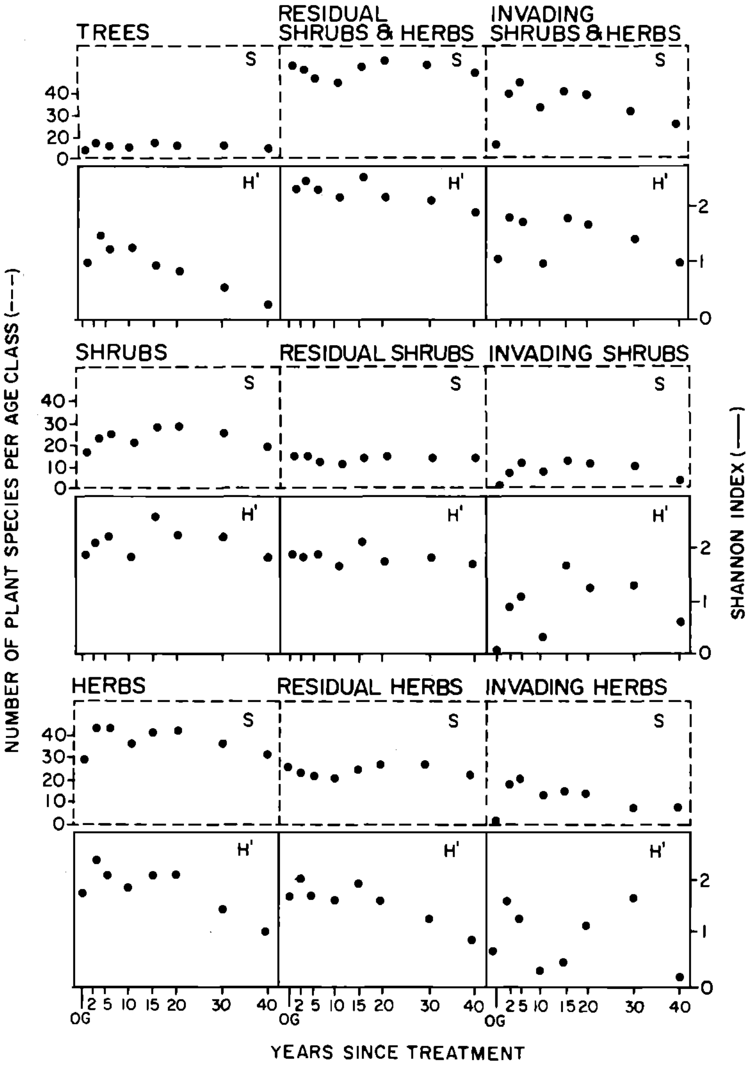

FIGURE 5. Species richness (S) and heterogeneity (H') values for selected growth-forms versus years since logging and burning. Invading herbs and shrubs contribute most to overall diversity patterns from 2 to 5 years and shrubs contribute most from 15 to 20 years.

that species composition is most dynamic during the first 30 years of succession, approaching but by no means reaching that of an old-growth forest; further changes under more uniform conditions are due to slower processes of mortality and species replacement, which may take hundreds of years in the Pacific Northwest.

After clearcutting and burning, species diversity is initially low, peaks at 15 to 20 years, then declines after canopy closure. The high diversity up to 20 years is brief, lasting less than one-third of the rotation period in intensively managed forests in this region, and is boosted slightly by exotic species. An initial increase in species diversity followed by a decrease during secondary forest succession has been documented for areas other than the Pacific Northwest by many authors (Loucks 1970, Auclair and Goff

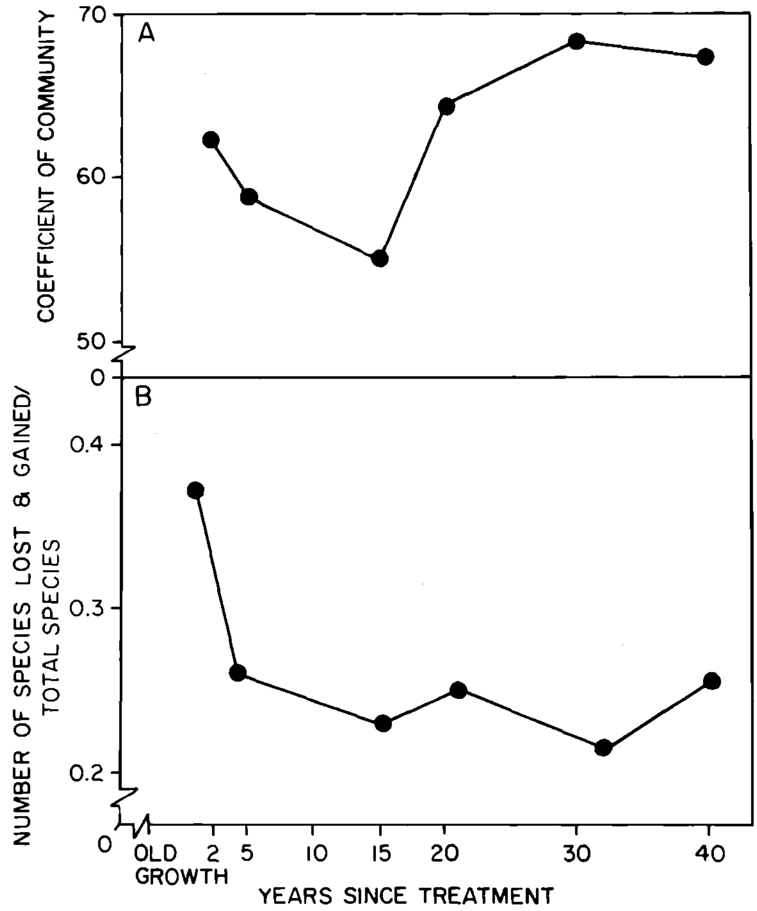

Figure 6. (a) Coefficient of community versus years since logging and burning. The coefficient declines through 15 years after treatment, then rises as residual species increase and invaders are lost. (b) Species turnover versus years since logging and burning. The high value at 2 years in species turnover is due to initial invaders. Values decline from 2 to 30 years.

1971, Shafi and Yarranton 1973, Bormann and Likens 1979, and Hibbs 1983).

The trends for the two indices of diversity are weak, with relatively large variances that tend to be minimal in old-growth sites. The weak trends and high variation indicate the uncertainty of predicting species diversity through these and subsequent stages of secondary succession.

An unexpected observation is that high values for heterogeneity immediately precede peaks for species richness (Figure 4). A possible explanation is that periods of peak heterogeneity in secondary succession coincide with periods of unresolved competition in both early herb-dominated and later shrub-dominated stages. As a few species become more successful, many more decline in abundance without being eliminated. This results in a decline in heterogeneity but an increase in species richness because new species are continually being added. Another view is that high diversity occurs during transition from one assemblage to another and may reflect an overlap of assemblages.

A review of the first 20 years of the chronosequence clarifies this pattern. An early peak in heterogeneity 2 years after clearcutting and burning is due to high numbers of all growth-forms, invading herbs being dominant. At 5 years after treatment, species richness has been increased by invading herbs and shrubs, and heterogeneity has been decreased by preemption by a few dominant invading species without elimination of many species. *Epilobium* species account for only 23% of cover at 2 years, but at 5 years they account for 39% of cover, and the five most dominant species account for 63% of cover. Invading species, herbs and invading herbs are the only vegetation classes in which heterogeneity precedes richness at 2 to 5 years (Figure 5), and thus they may be largely responsible for the composite pattern at this early stage.

The second peak for heterogeneity at 15 years precedes the high value for species richness at 20 years, possibly because 20-year-old sites, like 5-year-old sites, have several dominant species as well as holdover species that are rapidly declining. The five most dominant species account for 56% of total cover in the 20-year age class compared to only 44% in the 15-year age class. High heterogeneity values at 15 years precede peak richness at 20 years for residual shrubs and residual herbs (Figure 5), suggesting that these vegetation classes are responsible for the composite pattern at the shrub stage.

Old-growth forests in the study area are species-poor relative to early seral communities, but they have moderately high heterogeneity because of the equitability of species. Whittaker (1965) noted the low species richness of coniferous forests in the Pacific Northwest; however, the evenness of abundance that produces moderately high heterogeneity has not been previously shown. That late-successional ecosystems might have lower species diversity than earlier successional stages has been predicted by Margalef (1958, 1968), Whittaker (1975) and Horn (1974), and is confirmed here for this forest type.

Old-growth stands were slightly higher in richness than 40-year stands and higher in heterogeneity than 30- and 40-year stands. These young forests may be less diverse because the dense closed canopy of a 30- to 40-year Douglas-fir stand creates a relatively uniform low-light environment which fewer understory species can tolerate. The growth of shade-tolerant species into the canopy and eventual fragmentation of the canopy, creating a more heterogeneous light regime, permits establishment and growth of a wider variety of species.

The overall pattern of diversity during secondary succession on our sites follows that proposed by Norse et al.(1986) with a few exceptions. Instead of one peak, two periods of peak diversity corresponding to herb-dominated and shrub-dominated stages, occur in early succession. In addition, old-growth forests appear to have lower species diversity values than some early-successional stages whereas Norse et al. (1986) depict old-growth forests as the most diverse.

While some early-successional stages are more diverse than old-growth stages, clearcutting does not necessarily generate the highest species diversity on a larger landscape scale. Brown and Curtis (1985) suggest that small- to moderate-sized clearcuts followed by planting and even-aged management increases between-stand diversity while decreasing within-stand diversity. This may be true in many cases, especially with respect to wildlife habitat, but in regard to plant species diversity it is an oversimplification. Our results show that changes in plant species diversity during secondary succession are complex and difficult to predict. Diversity within a clearcut fluctuates between high and low values several times during the course of succession. The richness and evenness components of diversity may peak at different times, and diversity values for different growth-forms and suites of species (early- vs. late-successional) may be different yet interdependent.

The implications for managers are manifold. If diversity changes throughout a sere, especially in early stages, how is plant species diversity estimated for a forest of many even-aged patches? One method might entail using data such as ours to determine the relative amount of each successional stage that produces a given species diversity over the landscape. The manager should bear in mind, however, that there are many indices of diversity, each sensitive to different components of diversity (Christensen and Peet 1984). Species diversity should be evaluated with carefully selected indices in conjunction with other information, and in light of site specific factors and the spatial scale under consideration.

At the stand level, postlogging treatment may be especially influential on subsequent changes in diversity. A hard burn may eliminate, at least temporarily, some residual species that would otherwise return quickly via sprouting. Timing of treatment may also be important. For example, the effet of herbicides on species diversity may depend on when (both during a growing season and during a rotation) the chemicals are applied. Given that the goal of herbicide use is to release crop species and thus hasten the successional sequence, the period of highest plant species diversity (from 15–20 years) may be greatly reduced or bypassed altogether. In addition, dense stocking with Douglas-fir preempts space from other species and results in early canopy closure, further reducing species-rich herb and shrub stages.

Yet maximizing species diversity may not be an appropriate goal under certain circumstances. Many plants in the most diverse herb and shrub stages are common weedy species unlikely to become threatened or endangered, especially as more forests are converted to younger age classes. Rather, maintaining species diversity of particular ecosystems or habitats may be paramount where the total area of the habitat in question has been reduced to the point where species could become locally extinct.

Few old-growth species were eradicated during the first 40 years after logging and burning. Only two disappeared, Merten's coralroot (*Corallorhiza mertensiana* Bong.) and pinedrops (*Pterospora andromedea* Nutt.). The loss of these species should be cause for concern for land managers who are charged with maintaining species diversity because both are mycotrophs, indicator species for an organic-rich forest floor. Once eradicated, their return may depend in part on recolonization of the site by mycorrhizal fungi dispersed by animals (Maser et al. 1978). Thus these plant species may not readily return or be easily reintroduced, especially under conditions of intensive management where most stems are removed and remaining debris burned in 60- to 90-year rotations.

Plant species diversity should be documented beyond 40 years after clearcutting. Studies currently underway at the H. J. Andrews Experimental Forest are gathering such data and are being carried out on permanent study sites in a variety of habitats and geographic locations. More studies are needed, however, with larger samples including rarer species that may be more sensititve to clearcutting and prone to eradication.

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