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## EARLY SUCCESSIONAL PATTERNS OF FOREST SPECIES: INTERACTIONS OF LIFE HISTORY TRAITS AND DISTURBANCE<sup>1</sup>

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*Abstract.* Patterns of abundance were examined for vascular plant species during 21 yr of succession in two clear-cut and burned *Pseudotsuga* forests in the western Cascade Range of Oregon. A majority of forest understory species persisted through disturbance. Most colonizing species established within 2 yr after burning. Individualistic species responses were described by a series of broadly overlapping, unimodal curves of constancy and canopy cover, differing in time of initiation, duration, and magnitude. Thus, early successional change was characterized by gradual shifts in the abundance of generally persistent species.

Eleven population patterns (species groups) were identified. Interactions of life history traits and disturbance explain the temporal trends of the most common species. Within the groups of invading species, the timing of initial establishment, as well as the timing and magnitude of peak abundance were related to the origin of propagules, phenological traits, potential for vegetative expansion, and temporal and spatial variation in disturbance. Abundance patterns of invading species were also influenced by stochastic and historical factors. Contrasting responses of species between sites reflected differences in histories of logging and slash burning. Within the groups of residual species, temporal patterns of abundance reflected initial species distributions, resistance to logging and burning disturbance, mode of reproduction, morphological traits, and spatial variation in disturbance intensity.

These observations suggest that early secondary succession in *Pseudotsuga* forests has a deterministic component, founded in the life history traits of the available species, and a stochastic component reflecting site history and variation in disturbance.

*Key words:* abundance patterns; clear-cut logging; disturbance; individualistic species responses; invaders; life history traits; permanent plots; *Pseudotsuga menziesii*; residuals; slash burning; species dynamics; succession; western Cascade Range.

### INTRODUCTION

Succession, the directional change in vegetation over time, appears as varied as the ecosystems in which it occurs. Decades of observational and experimental study have revealed tremendous variation in the pattern and process by which species enter, develop, and depart from a community. Understandably, there have been numerous, often divergent approaches to a general, unifying theory of succession (cf. Clements 1916, Gleason 1917, Egler 1954, Margalef 1963, Odum 1969, Drury and Nisbet 1973, Whittaker 1975, Pickett 1976, Connell and Slatyer 1977, MacMahon 1980, Horn 1981, Finegan 1984, Pickett et al. 1987). Yet despite the variability inherent in this complex process, two patterns are commonly described for secondary seres: (1) most species either survive disturbance or colonize shortly thereafter, and (2) long-term changes in composition occur through gradual expansion and decline

of species, rather than through sequential recruitment and replacement. In this paper, I address two fundamental questions about early succession in *Pseudotsuga* forests: what are the patterns of species abundance and replacement following catastrophic disturbance, and what are the potential mechanisms responsible for these patterns?

In many terrestrial systems, models of successional change have been developed largely from studies that use stands of different ages arranged chronologically to portray temporal sequences. Interpretation of these chronosequences is necessarily based on the assumption that predisturbance vegetation, environment, and postdisturbance influences are uniform among sites. As a consequence, species patterns ostensibly associated with successional age may be confounded by historical or stochastic phenomena. To remove these confounding factors, studies based on the repeated observation of permanent plots have been employed. However, for permanent-plot studies to be useful in understanding the dynamics of short-lived species or of populations with episodic fluctuations, long-term, frequent sampling is necessary.

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TABLE 1. Characteristics of the six forest understory communities of Watersheds 1 and 3. Information derived from Rothacher et al. (1967), Dyrness (1973), and Halpern (1987). Communities are arranged in order of increasing available soil moisture.

Understory plant community	Topographic position and aspect	Dominant understory growth-form(s)	Dominant species
<i>Corylus cornuta-Gaultheria shallon</i>	ridgetops; south-facing upper-slopes	tall shrubs	<i>Corylus cornuta</i> , <i>Acer circinatum</i> , <i>Berberis nervosa</i>
<i>Rhododendron macrophyllum-Gaultheria shallon</i>	ridgetops; mid-slope benches	tall shrubs (herbs and low shrubs)	<i>Rhododendron macrophyllum</i> , <i>Gaultheria shallon</i>
<i>Acer circinatum-Gaultheria shallon</i>	mid- to upper-south-facing slopes	herbs and low shrubs, tall shrubs	<i>Gaultheria shallon</i> , <i>Acer circinatum</i>
<i>Acer circinatum-Berberis nervosa</i>	mid- to lower-slopes	tall shrubs	<i>Acer circinatum</i>
<i>Coptis laciniata</i>	mid- to lower-slopes	understory trees	<i>Tsuga heterophylla</i>
<i>Polystichum munitum</i>	bottom- and steep, north- to east-facing slopes, seeps	herbs and low shrubs (tall shrubs)	<i>Polystichum munitum</i> , <i>Acer circinatum</i>

In this paper, I use two long-term successional records to examine the abundance patterns of species following logging and burning of *Pseudotsuga* forests in the western Cascade Range of Oregon. Initiated by C. T. Dyrness in 1962, these studies have produced two of the longest and most complete permanent-plot records of forest understory development during secondary succession. In an earlier paper, Dyrness (1973) described successional patterns for 5 yr after burning in one of the sites discussed here. Permanent-plot studies have also been conducted in other western coniferous forests (e.g., Isaac 1940, Steen 1966, Morris 1970, Kraemer 1977, Stickney 1981, 1986, Lyon 1984). However, in many of these studies, an understanding of the origin and persistence of species is limited by the absence of predisturbance data, infrequent sampling, or short-term observation (but see Lyon 1984, Stickney 1986).

In this study, I examine the successional dynamics of an array of species using detailed records of their constancy, or frequency among sample plots, and of their mean canopy cover within plots. Constancy and cover data collected prior to disturbance form a baseline for assessing the survival, recovery, or expansion of original forest species and the invasion of others. In addition, characteristics of the disturbance response or tolerance of species are revealed through a plot-level classification of disturbance intensity. Further, estimates of the rates and magnitudes of population changes are enhanced by frequent, long-term remeasurements. I supplement the observations of this study with published accounts of species life history traits and responses to disturbance to attempt to explain their temporal dynamics during early secondary succession.

## STUDY AREA

### *Physical environment*

The study was conducted within two 100-ha watersheds of the H. J. Andrews Experimental Forest, which lies along the western slope of the central Cas-

cade Range, 80 km east of Eugene, Oregon. Watersheds 1 and 3 (WS1 and WS3) typify the mature, dissected topography of the region, with steep slopes and ridges separating small, tributary streams. Elevations range from 442 to 1082 m and slopes average >50%. Detailed information on the physical environment of the area is found in Rothacher et al. (1967). Colluvial soils are largely derived from pyroclastic tuffs and breccias, although basalts and andesites are also present. Profile development is poor; soils are loamy and moderately stony with high porosity and a large water storage capacity (Dyrness 1969).

The climate of the region is maritime with mild, wet winters and warm, dry summers. Annual precipitation averages 2302 mm, but only 6% falls between June and August. Average minimum temperatures range from -5.5° in January to 11.9°C in August, and average maxima range from 5.5° in January to 23.3° in July (Bierlmaier and McKee, *in press*). Although snowfall is common, snowpacks rarely persist for >1-2 wk.

### *Vegetation*

Vegetation of the study area is typical of the surrounding *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Prior to logging, forests were composed of dominant, old-growth *Pseudotsuga menziesii* (300- to 500-yr-old) and of *Tsuga heterophylla* in a range of size and age classes. Mature stands of *P. menziesii* (125-yr-old) were also present. Common subcanopy and understory tree species included the conifers, *Taxus brevifolia* and *Thuja plicata*, and the hardwoods, *Acer macrophyllum*, *Alnus rubra*, *Castanopsis chrysophylla*, and *Cornus nuttallii*. Nomenclature follows Hitchcock and Cronquist (1973).

The initial understory vegetation was classified into six plant communities arrayed along a gradient of available moisture (Rothacher et al. 1967, Dyrness 1973; Table 1). Detailed descriptions of community composition, structure, and distribution have been presented elsewhere (Rothacher et al. 1967, Dyrness 1973, Halpern 1987).

TABLE 2. The number of sample plots within each forest understory community and soil disturbance class on (A) Watershed 1 and (B) Watershed 3.

Understory plant community	Soil disturbance class				Total
	Undisturbed	Disturbed-unburned	Lightly burned	Heavily burned	
A. Watershed 1					
<i>Corylus-Gaultheria</i>	1	3	8	0	12
<i>Rhododendron-Gaultheria</i>	3	4	12	1	20
<i>Acer-Gaultheria</i>	0	1	4	2	7
<i>Acer-Berberis</i>	2	10	20	2	34
<i>Coptis</i>	3	9	8	3	23
<i>Polystichum</i>	2	11	17	2	32
Unclassified	0	2	1	0	3
Total	11	40	70	10	131
B. Watershed 3					
<i>Rhododendron-Gaultheria</i>	2	0	7	2	11
<i>Acer-Gaultheria</i>	1	5	3	2	11
<i>Acer-Berberis</i>	1	3	5	1	10
<i>Coptis</i>	1	6	4	1	12
<i>Polystichum</i>	4	4	2	1	11
Unclassified	2	3	1	0	6
Total	10	21	23	7	61

### History of disturbance

Although both watersheds were logged and broadcast burned, the timing and distribution of disturbance differed between sites. The entire 96 ha of WS1 was harvested over a 4-yr period, between fall 1962 and summer 1966. A skyline cable was used to transport logs to a single landing at the mouth of the watershed. Slash was broadcast burned in October 1966. On WS3, however, one-quarter of the watershed, consisting of stands of 5, 9, and 11 ha, was harvested during winter 1962–1963 using a high-lead cable to transfer logs to adjacent landings. Slash was broadcast burned in September 1963.

Artificial regeneration also differed between sites. *Pseudotsuga menziesii* was aeri ally seeded on WS1 during October 1967 and again, within a 10 ha area, during October 1968. Regeneration was poor, and in April and May 1969, 2-yr-old *P. menziesii* were planted. Again, in April 1971, 2- and 3-yr-old trees were planted on 40 ha of the south-facing slope. On WS3, all clear-cut units were planted with 3-yr-old *P. menziesii* between March and May 1964.

### METHODS

#### Field sampling

On both watersheds, permanently staked sample plots of 2 × 2 m were established along evenly spaced transects prior to clear-cut logging (summer 1962). WS1 was represented by 131 plots on a total of 6 transects, and WS3 by 61 plots on 10 transects. The position of the initial sample plot for each transect was determined randomly, and the remaining plots were placed at slope-corrected intervals of 30.5 m.

Within each plot, visual estimates of projected canopy cover were made for each vascular plant species

<6 m tall (to include herbs, tall shrubs, and regenerating trees). The sampling protocol is described in detail in Dyrness (1973) and Halpern (1987). Forest understories were initially sampled prior to disturbance, during summer 1962. After logging, plots were relocated or reestablished from field notes and resampled (1966 on WS1, 1963 on WS3). Both watersheds were broadcast-burned during the fall after logging; plots were relocated and resampled the following growing season. Postdisturbance remeasurements were conducted annually from 1967 through 1973 on WS1 and from 1964 through 1972 on WS3. Thereafter, through final sampling in 1983, remeasurements generally occurred biennially.

#### Data reduction and analysis

To assess the influence of initial community characteristics and intensity of disturbance on species patterns, sample plots were grouped by two criteria (Dyrness 1973; Table 2). First, each plot was assigned to one of the initial six understory plant communities (Rothacher et al. 1967, Dyrness 1973; Table 1). Second, immediately following slash burning, each plot was subjectively assigned to one of four soil disturbance classes (Dyrness 1973):

- 1) Undisturbed. The soil surface appeared similar to that prior to logging and burning, with minimal mixing of soil and litter and with no evidence of fire.
- 2) Disturbed-unburned. Disturbance from logging was evident. Litter was removed or mixed with mineral soil, but there was minimal evidence of fire.
- 3) Lightly burned. Surface litter was charred by fire but was not completely removed.

TABLE 3. Summary of abundance characteristics for the 11 seral species groups. Species groups: I = invaders, R = residuals. Growth-forms: H = herbs and low shrubs, S = tall shrubs, T = understory trees. Phase of peak abundance (period after burning): — = no peak in abundance, early = 0–4 yr, middle = 5–10 yr, late = >10 yr. Magnitude of peak abundance: major = >5% cover in any year, minor = consistently <5% cover. Duration of elevated abundance (number of years with >5% cover): — = 0 yr, short = 1–2 yr, moderate = 3–5 yr, long = >5 yr.

Species group	Growth-form(s)	Peak abundance		Duration of elevated abundance	Species
		Phase	Magnitude		
Invading species groups					
I1	H	early	major	short, moderate	<i>Senecio sylvaticus</i> , <i>Epilobium paniculatum</i> , <i>Coryza canadensis</i>
I2	H	early–middle	major	long	<i>Epilobium angustifolium</i>
I3	H	early–middle	minor	—	<i>Agoseris</i> spp., <i>Cirsium</i> spp., <i>Gnaphalium microcephalum</i> , <i>Lactuca serriola</i>
I4	H, S	middle	minor	—	<i>Anaphalis margaritacea</i> , <i>Rubus leucodermis</i> , <i>Collomia heterophylla</i> , <i>Vicia americana</i> , <i>Bromus</i> spp.
I5	S	middle	major	long	<i>Ceanothus velutinus</i> , <i>Ceanothus sanguineus</i>
I6	H, S, T	late	major, minor	—	<i>Pteridium aquilinum</i> , <i>Rubus parviflorus</i> , <i>Salix scouleriana</i> , <i>Prunus emarginata</i>
Residual species groups					
R1	H	early	major	long	<i>Rubus ursinus</i>
R2	H	middle	major	moderate–long	<i>Trientalis latifolia</i> , <i>Whipplea modesta</i> , <i>Hieracium albiflorum</i>
R3	H, S, T	middle–late, late	major	moderate, long	<i>Acer circinatum</i> , <i>Polystichum munitum</i> , <i>Gaultheria shallon</i> , <i>Rhododendron macrophyllum</i> , <i>Berberis nervosa</i> , <i>Corylus cornuta</i> , <i>Tsuga heterophylla</i>
R4	H, S, T	—	minor	—	<i>Coptis laciniata</i> , <i>Viola sempervirens</i> , <i>Vaccinium parvifolium</i> , <i>Castanopsis chrysophylla</i> , <i>Oxalis oregana</i> , <i>Rubus nivalis</i> , <i>Acer macrophyllum</i> , <i>Cornus nuttallii</i>
R5	H, T	—	minor	—	<i>Chimaphila umbellata</i> , <i>Thuja plicata</i> , <i>Goodyera oblongifolia</i> , <i>Synthyris reniformis</i> , <i>Taxus brevifolia</i>

- 4) Heavily burned. Surface litter was completely consumed by intense fire.

The computer programs CONDENSE and DATA-EDIT of the Cornell Ecology Program Series (Gauch 1973, Gauch and Singer 1982) and additional programs developed at Oregon State University (B. G. Smith, *personal communication*) were used to reduce and summarize species data. For all species, the constancy (frequency among sample plots) and the mean percent canopy cover ( $\pm 1$  SE) were calculated for each watershed for each sampling date. To aid in interpretation of species abundance patterns, constancy and mean cover were also calculated for each plant community and disturbance class, but these detailed statistics will not be presented here.

Although the abundance patterns of plant species through time formed a continuum, I subjectively grouped species according to four criteria (Table 3):

1) Seral origin. *Invaders* were defined as species either absent from the above-ground vegetation of undisturbed forest communities or restricted to locally disturbed microsites (Dyrness 1973). *Residuals* were defined as species characterizing the above-ground vegetation of undisturbed forest communities, regardless of their initial abundance or mode of recovery (i.e., from on- or off-site seed or from vegetative propa-

gules). The latter definition contrasts with that used to describe the potential flora of a community (sensu Major and Pyott 1966), because it excludes from the group of residuals, forest species that reside solely as buried viable seed.

2) Phase of peak abundance (period after disturbance but prior to canopy closure): no peak in abundance, early (0–4 yr), middle (5–10 yr), or late (>10 yr).

3) Magnitude of peak abundance. I defined major species as those exhibiting >5% canopy cover during any growing season and minor species as those with consistently <5% cover.

4) Duration of elevated abundance (period with canopy cover >5%): — (0 yr), short (1–2 yr), moderate (3–5 yr), or long (>5 yr).

The dynamics of each species group are illustrated by graphs of constancy and mean canopy cover for representative species, plotted as a function of time since disturbance (see Figs. 2–12). Although a total of 196 species made up the seral flora of Watersheds 1 and 3, for simplicity I consider only the 43 most common species, i.e., those with constancy >20% or canopy cover >1% for one or more growing seasons. Because the watersheds experienced chronologically different histories of logging and slash burning, a standardized time axis facilitates the comparison of species pattern between sites. Thus, predisturbance samples occur at

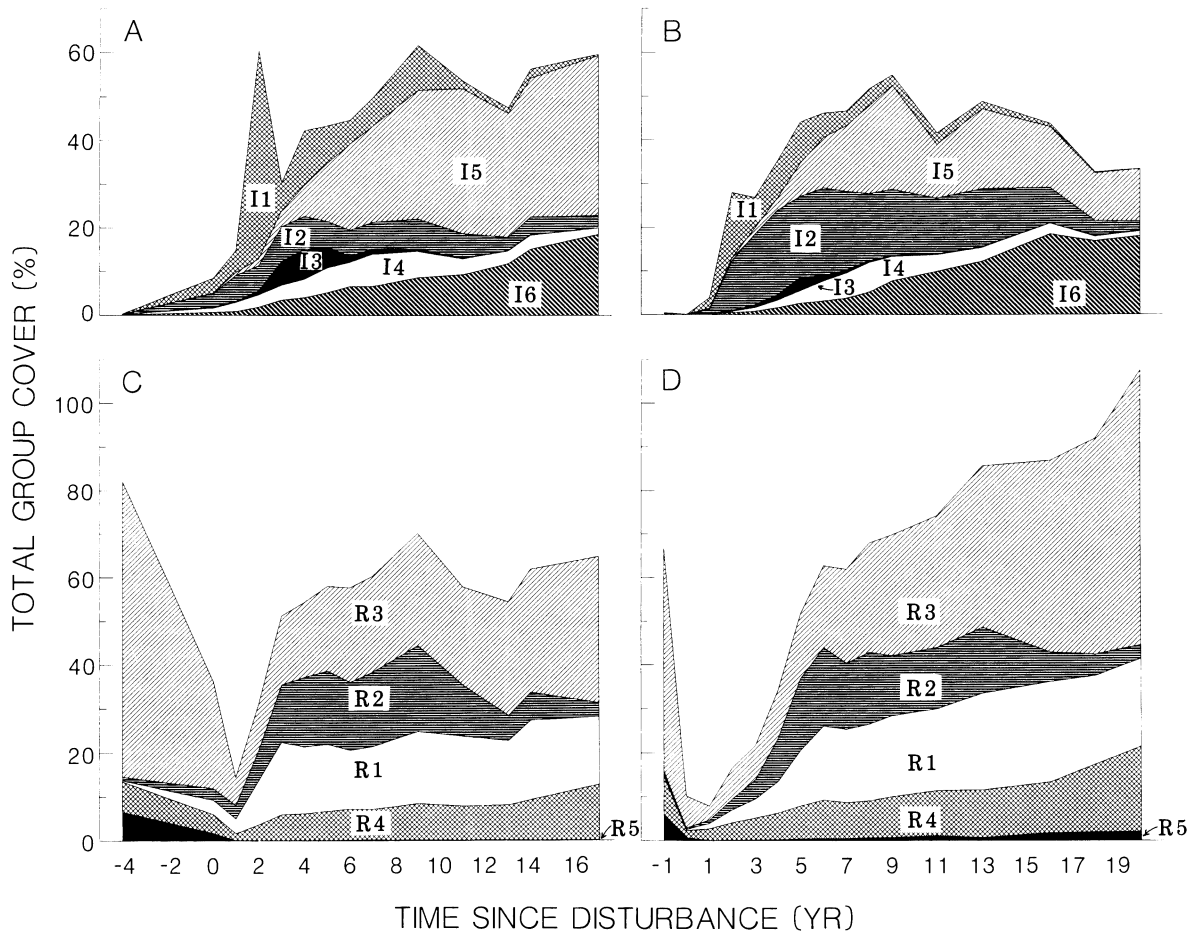


FIG. 1. Changes in total (additive) canopy cover with time for the 11 species groups. Invading and residual species groups are presented separately for clarity. (A) Groups of invading species on Watershed (WS) 1, (B) groups of invading species on WS3, (C) groups of residual species on WS1, (D) groups of residual species on WS3. See Table 3 for representative species in each group.

times “-4” and “-1” for WS1 and WS3, respectively; for both watersheds, time “0” represents the growing season following completion of logging and time “1,” that following slash burning.

## RESULTS AND DISCUSSION

### *General floristic and structural changes*

Forest understories on Watersheds 1 and 3 experienced major changes in composition and structure following disturbance. Species richness increased continuously on WS1, from 83 species in the predisturbance plots to 138 at final sampling. Similarly, on WS3, richness increased from 48 to 90, despite a temporary loss of 14 species after logging. Two major trends account for these patterns. First, most understory species persisted through disturbance. On WS1, 92% survived logging and 82%, slash burning; on WS3, 71% were present both after logging and burning. Second, species invasions were common (11–19 species/yr) for 2 yr after burning. Although new species continued to ar-

rive through final sampling (years 17 and 20 on WS1 and WS3, respectively), they remained rare.

Total canopy cover of herb and low shrub species peaked rapidly, at 93% in year 2 on WS1 and at 94% in year 6 on WS3. Canopy cover of tall shrub and regenerating tree species increased more slowly, but continuously with time. On both sites, tall shrub and tree cover peaked at final sampling, 76 and 44%, respectively, on WS1 and 60 and 63%, respectively, on WS3. Detailed information on floristic and physiognomic changes are presented in Halpern (1987).

### *General patterns of species groups*

Based on the abundance criteria defined earlier, 11 population patterns, or species groups, were identified (Table 3). The temporal relationships and the relative importance of these groups are illustrated by the patterns of total group cover through time (Fig. 1). Initial compositional changes in response to disturbance featured dramatic loss of canopy cover by initial understory dominants (group R3; Fig. 1C and D) and rapid

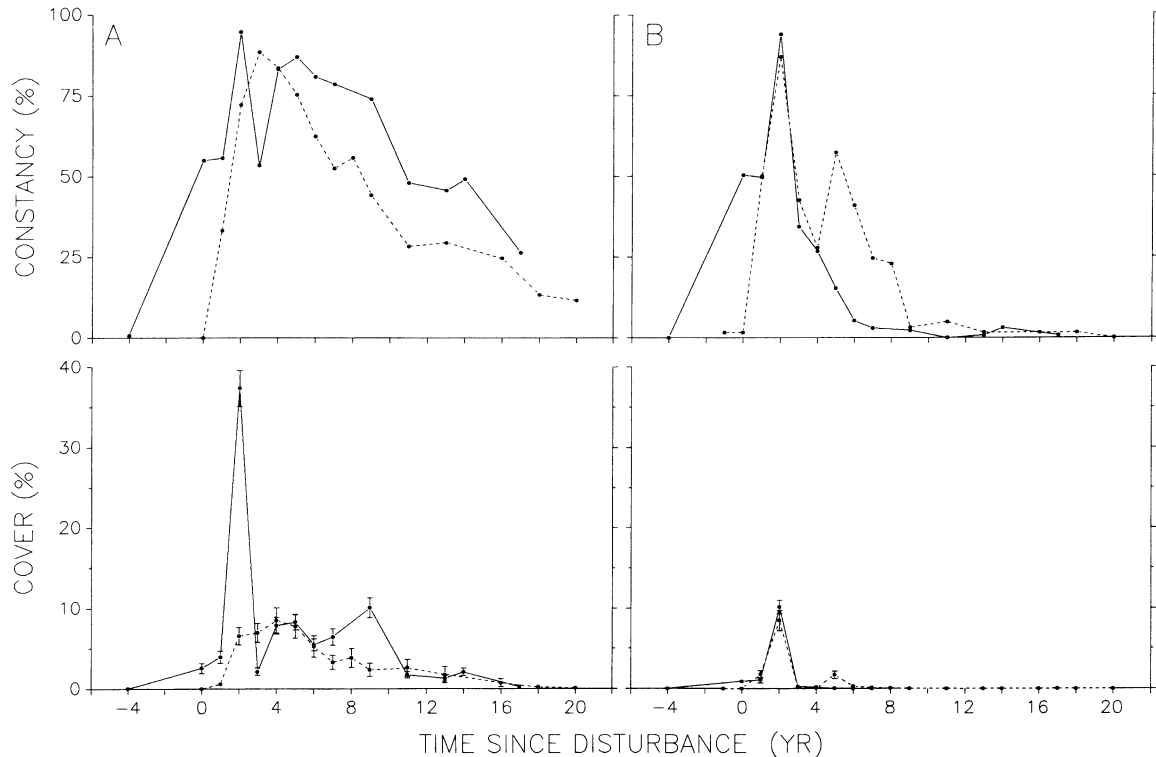


FIG. 2. Changes in constancy and mean canopy cover with time for species of group I1. (A) *Epilobium paniculatum*, (B) *Senecio sylvaticus*. — Watershed 1, --- Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

invasion of annual (I1) and perennial herb (I2) groups (Fig. 1A and B). However, long-term changes were typified by more gradual shifts in the importance of invading and residual species groups. Some of these major trends included varying rates of expansion and decline of invading species (groups I3–I6; Fig. 1A and B); temporary or persistent release of initially subordinate forest species (groups R2 and R1, respectively; Fig. 1C and D); and gradual recovery of other characteristic forest species (groups R3 and R4; Fig. 1C and D).

#### Population patterns of invading species

1. *Group I1 species.*—Species of group I1 were the first to peak in abundance, although their importance declined rapidly (Fig. 2). They include three classic fugitive annuals—the European alien *Senecio sylvaticus*, and two native species, *Epilobium paniculatum* and *Conyza canadensis*. The more widespread species, *E. paniculatum* (Fig. 2A) and *S. sylvaticus* (Fig. 2B), displayed a sharp spike in canopy cover 2 yr after slash burning on both watersheds. Although the constancy of each species increased as rapidly as its cover, constancy declined more slowly, particularly for the WS1 population of *E. paniculatum*. Thus, winter annuals continued to establish following peak abundance, but with greatly reduced densities.

The dynamics of *S. sylvaticus* and *E. paniculatum* reflected the interaction of a winter annual life cycle

with the timing of disturbance. West and Chilcote (1968) have described this relationship for *S. sylvaticus*. Copious, wind-borne seeds disperse between July and September. Germination occurs principally during the fall, and the small rosettes overwinter. Although secondary germination may occur the following spring, the life cycles of both types of germinants are completed by late summer.

Features of the disturbance regime greatly influenced both the initial establishment and the magnitude of abundance of winter annuals. On WS1, staggered harvesting provided germination sites for 1–3 yr prior to burning. On WS3, however, winter logging followed seed dispersal and thus precluded establishment prior to burning. Differences in the early (postlogging) establishment of annuals also influenced their postburning abundance. The markedly greater cover of *E. paniculatum* on WS1 than on WS3 (Fig. 2A) may have reflected a greater abundance of on-site seeds, i.e., those derived from individuals established prior to burning. Similar relationships between the timing of disturbance and the availability of propagules are important in the early successional dynamics of old fields (e.g., Keever 1950, 1979, Bazzaz 1968, Pickett 1982).

The most striking characteristics of I1 populations were their short-lived dominance and their prominence on burned microsites, phenomena widely observed after fire in other western coniferous forests (e.g., Yerkes 1958, Dyrness 1973, Kraemer 1977, Stickney

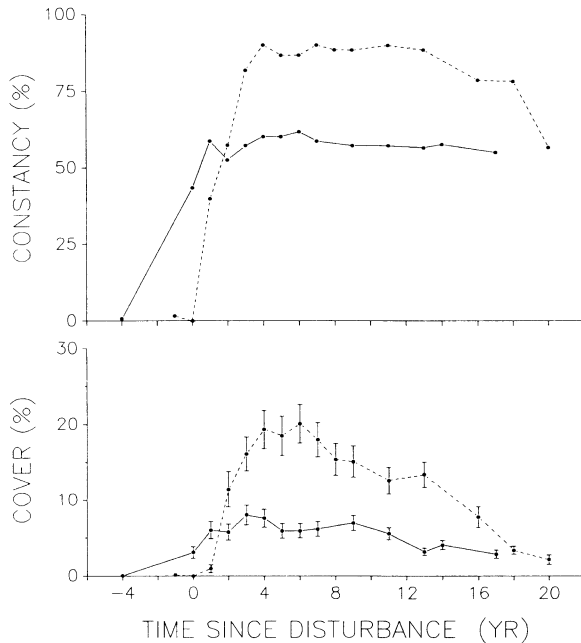


FIG. 3. Changes in constancy and mean canopy cover with time for *Epilobium angustifolium* (group I2). — Watershed 1, - - - Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

1981). Peak abundances typically occur during the second growing season due to the timing of seed availability and the tendency for slash burning or wildfire to occur in the fall. The affinity for burned soils and the transient nature of *S. sylvaticus* have been attributed to: (1) a requirement for high soil fertility associated with recent burns (West and Chilcote 1968) and (2) poor competitive ability compared with perennials such as *E. angustifolium* which, once established, are more efficient in nutrient uptake (van Andel and Vera 1977). *Epilobium paniculatum* had a protracted period of recruitment (Fig. 2A), suggesting that it may be less limited by nutrients and by competition from associated species than *S. sylvaticus*.

2. *Group I2 species*.—A single, perennial colonizer, *Epilobium angustifolium*, characterizes this species group. Its establishment and expansion were relatively rapid and widespread on both watersheds (Fig. 3). Constancy reached a plateau in year 1 on WS1 and in year 4 on WS3, 5 yr after the initiation of logging on each site. Mean canopy cover increased similarly, but peaked 2 yr later. Thereafter, constancy remained high, whereas cover declined slowly. Thus, *E. angustifolium* persisted as a major herb species through most of the study period.

The long-term dynamics of *E. angustifolium* suggest a complex reproductive and competitive response following disturbance. Its prominence likely derived from multiple mechanisms of invasion and expansion. Initial establishment was primarily from off-site wind-dispersed seed. Subsequent increases in cover reflected

lateral spread because vegetative propagation, rather than continued recruitment, commonly follows initial seedling establishment (van Andel and Rozema 1974, van Andel 1975). However, additional recruitment of seed from off-site and local sources probably occurred in adjacent, open microsites.

Patterns of early expansion of *E. angustifolium* were temporally displaced between watersheds due to differences in logging history (Fig. 3). On WS1, individuals which developed during the period of staggered harvesting sprouted vigorously from rhizomes following burning, a response which reflects the depth of their perennating buds (Moss 1936). On WS3, in contrast, establishment of *E. angustifolium* was insignificant prior to burning (year 0, Fig. 3) because harvesting occurred after fall seed dissemination. Although the early dynamics of *E. angustifolium* on Watersheds 1 and 3 reflected differing histories of disturbance, subsequent trends in abundance were similar, including its long-term persistence in both open and shaded communities.

3. *Group I3 species*.—The species representing this group comprise a suite of minor, invading herbs which achieved greatest abundance between years 3 and 5 (Fig. 4). All were wind-dispersed members of the Compositae, including the annual *Agoseris heterophylla*; the biennials *Cirsium vulgare* and *Lactuca serriola*; and the short-lived perennials *Agoseris grandiflora*, *C. arvense*, *C. brevistylum*, and *Gnaphalium microcephalum*. *Agoseris* (Fig. 4A) and *Cirsium* species (Fig. 4B) are each treated as a single taxon due to the difficulty in identifying 1st-yr rosettes to species. Trajectories of constancy for all taxa in group I3 were typically bell-shaped curves with long tails during their decline, reflecting enhanced establishment during the early-to-middle portion of the study period followed by gradual extinction. Changes in cover were similar, but reduced in magnitude; maximum constancy (20–70%) coincided with peak canopy cover (1–3%; Fig. 4). The species as a group were most abundant within the lightly and heavily burned soil classes and within the *Acer-Gaultheria* community.

Compared with I1 and I2 species, the slower development and minor peak in abundance of I3 species may be explained by several phenological and morphological traits. Because the developmental cycles of biennial and short-lived perennial species are typically slower than those of winter annuals, I3 species increased in cover more slowly than did I1 species. Additionally, for biennials, the transition from basal rosettes to upright and flowering individuals may be highly dependent on resource availability (Peterson and Bazaz 1978, Kelly 1985). Consequently, following fall disturbance, biennial populations recruited from late-summer, windborne seed would not reach maximum abundance until at least 3 yr after slash burning. Finally, the root and shoot morphologies of I3 species may limit their potential for lateral spread, compared



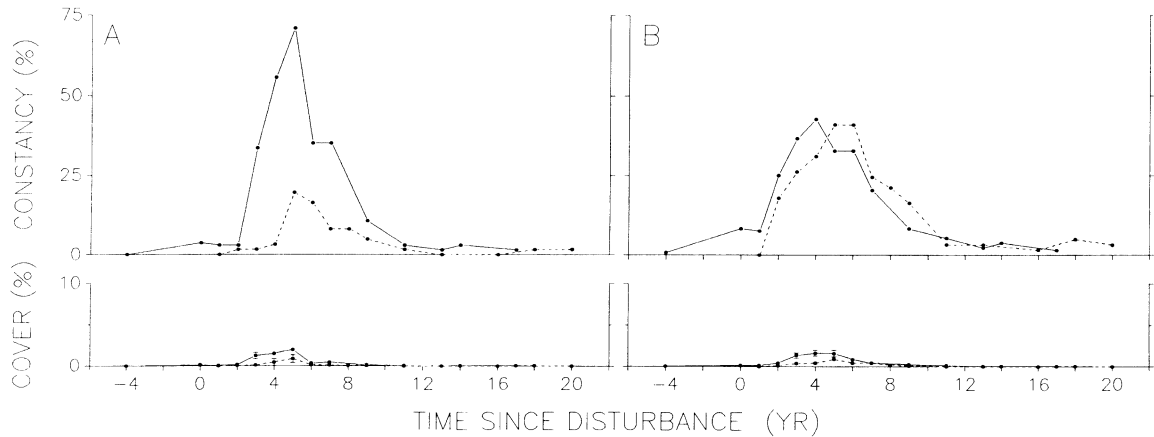


FIG. 4. Changes in constancy and mean canopy cover with time for species of group I3. (A) *Agoseris* spp., (B) *Cirsium* spp. — Watershed 1, - - - Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

to long-lived rhizomatous herbs such as *Epilobium angustifolium* (group I2). As a result, annual increases in mean canopy cover of I3 species may be as dependent on continuous recruitment as on expansion of established individuals.

That a majority of the biennial and short-lived perennial species of Watersheds 1 and 3 were most abundant during the early-to-middle portion of the study period is consistent with the observation that biennial species are typically found in a transitional vegetation stage between an initial, open, disturbed phase and a subsequent, closed, competitive phase (Fenner 1985).

4. *Group I4 species.*—This group is composed of minor, invading herbs and shrubs that reached greatest abundance between years 3 and 9 (Fig. 5). Two principal trends in constancy were evident: a moderate increase to a plateau for species such as *Anaphalis margaritacea* (Fig. 5A) and *Collomia heterophylla*, and a broad, shallow, bell-shaped curve for taxa such as *Rubus leucodermis* (Fig. 5B), *Vicia americana*, and *Bromus* spp. Trajectories of canopy cover for all taxa were flattened, bell-shaped curves with maxima <5% and

with long persistent tails. Thus, species of group I4 were distinguished from those of group I3 by slower rates of invasion or expansion and by later peak abundance. As a group, I4 species showed little consistent relationship with site characteristics, although the most common species, *A. margaritacea* and *R. leucodermis*, were most abundant in the mesic and moist communities.

The changes in constancy for these perennials suggest slow continuous entrance into sample plots and greater persistence than species of group I3. Although *A. margaritacea* and *R. leucodermis* are rhizomatous perennials, both produce prolific seed. Thus, gradual increases in their constancy may have represented continuous recruitment of seedlings into the plots or lateral growth of adjacent individuals. Initial establishment of *A. margaritacea* was most likely by wind-dispersed seed, although buried viable seeds (of indeterminate age) have also been found within old-growth and seral forest communities (Kellman 1974). *Rubus leucodermis* may have originated from buried seeds or from fleshy fruits dispersed by animals. Although the

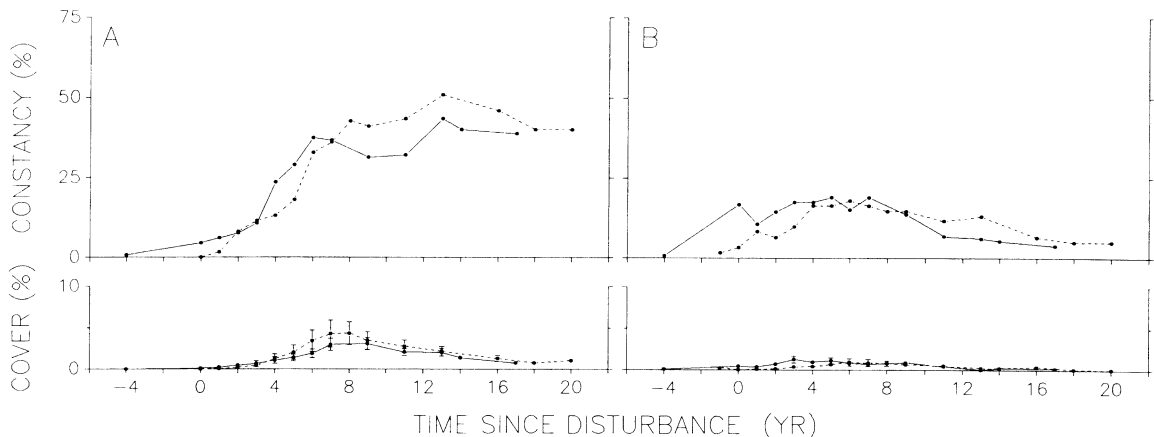


FIG. 5. Changes in constancy and mean canopy cover with time for species of group I4. (A) *Anaphalis margaritacea*, (B) *Rubus leucodermis*. — Watershed 1, - - - Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

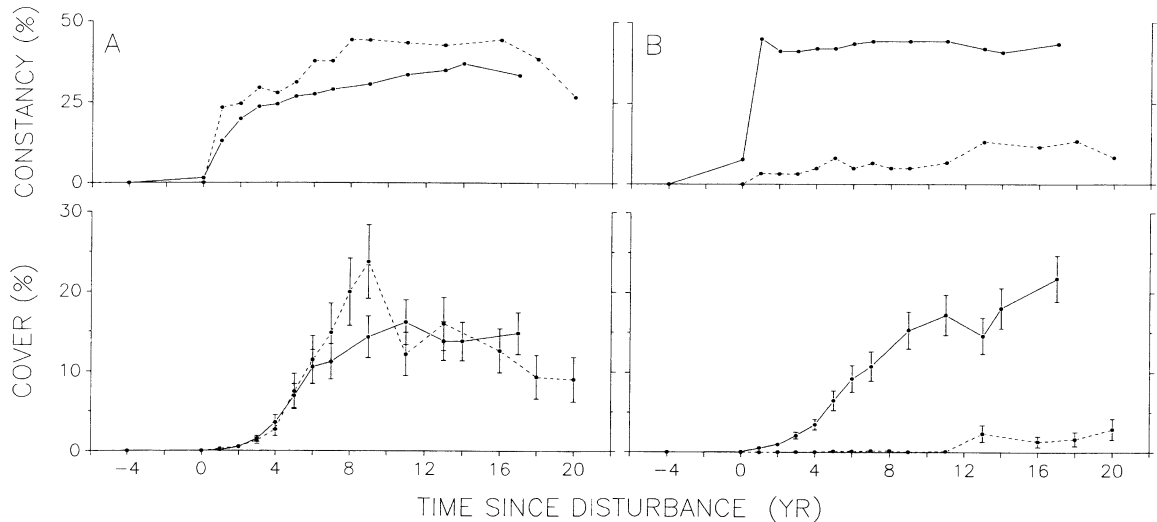


FIG. 6. Changes in constancy and mean canopy cover with time for species of group I5. (A) *Ceanothus velutinus*, (B) *Ceanothus sanguineus*. — Watershed 1, --- Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

longevity of its buried seeds is unknown, other species in the genus *Rubus* typically form a persistent seed bank (e.g., Olmsted and Curtis 1947, Livingston and Allesio 1968, Kellman 1970, Marks 1974). Thus, both seed and vegetative traits may contribute to the pattern of gradual increase in abundance of species of group I4.

**5. Group I5 species.**—Represented by the tall shrubs, *Ceanothus velutinus* and *C. sanguineus*, this invading group dominated during the middle-to-late portion of the study period (Fig. 6). Recruitment from buried seed was most rapid following slash burning, although scattered individuals appeared after logging on WS1 (year 0). Thus, constancy increased rapidly between years 0 and 2, then either increased more slowly or reached a plateau. On WS1, both *C. velutinus* and *C. sanguineus* exhibited a smooth, sigmoid increase in cover to peak levels between years 11 and 17. On WS3, however, cover of *C. velutinus* (Fig. 6A) peaked sharply, declining rapidly between years 9 and 11, and more slowly thereafter. The importance of both species increased with intensity of disturbance. Peak cover on heavily burned sites was 3–5 times as great as that on undisturbed sites.

The temporal and spatial dynamics of *Ceanothus* populations on Watersheds 1 and 3 reflect life histories which are dependent on fire, but they also suggest the influence of historical and stochastic factors. Seed banks containing as many as  $2.5 \times 10^5$ – $6 \times 10^5$  viable seeds/ha (Gratkowski 1962, Hickey and Legee 1970, Lyon 1971) may persist in the soil for centuries. Burning stimulates germination by cracking the hilar fissure (Gratkowski 1962). Germination may also be stimulated by mechanical scarification or by elevated soil temperatures associated with insolation, although subsequent establishment is usually much poorer (e.g., Hickey and Legee 1970, Orme and Legee 1976). As observed on WS1

and WS3, *Ceanothus* typically establishes during the first growing season after burning and stratification, with subsequent emergence decreasing rapidly with time (Cronemiller 1959, Orme and Legee 1976).

The development of *C. velutinus* on the heavily burned sites of WS3 was no greater than that on lightly burned sites. This contrasts sharply with its pattern on WS1, where its abundance was correlated with burn intensity (see also Biswell 1961, Orme and Legee 1976). As dispersal from off-site sources is highly unlikely (Conard et al. 1985, Morgan and Neuenschwander 1985) this pattern may indicate local differences in the historical distribution of the species. However, it may also reflect competitive interactions with co-occurring shrub species such as *Salix scouleriana*. The relative scarcity of *C. sanguineus* on WS3 (Fig. 6B) may similarly suggest variation in its historical distribution, although at a coarser scale.

On WS3, the precipitous decline in cover of *C. velutinus* between years 9 and 11 (Fig. 6A) may be consequence of severe winter frost during 1972–1973 (see also Kraemer 1977). The apparent absence of dieback on WS1 is puzzling; it may reflect the greater vigor of younger individuals on that site or differences in local weather conditions. In the Oregon Cascade Range, the functional life span of *C. velutinus* is estimated as 20–40 yr (Conard et al. 1985). However, early senescence of *Ceanothus* may be promoted by environmental and biotic influences, including injury to root crowns from snow loading (Zavitkovski and Newton 1968), stem dieback after severe frost (Legee and Hickey 1975, Kraemer 1977), herbivory by ungulates and insects (Hickey and Legee 1970, Wittinger et al. 1977), and fungal infection (Tarry 1968, Zavitkovski and Newton 1968).

Differences in the dynamics of *Ceanothus* on Watersheds 1 and 3 emphasize the complex nature of its

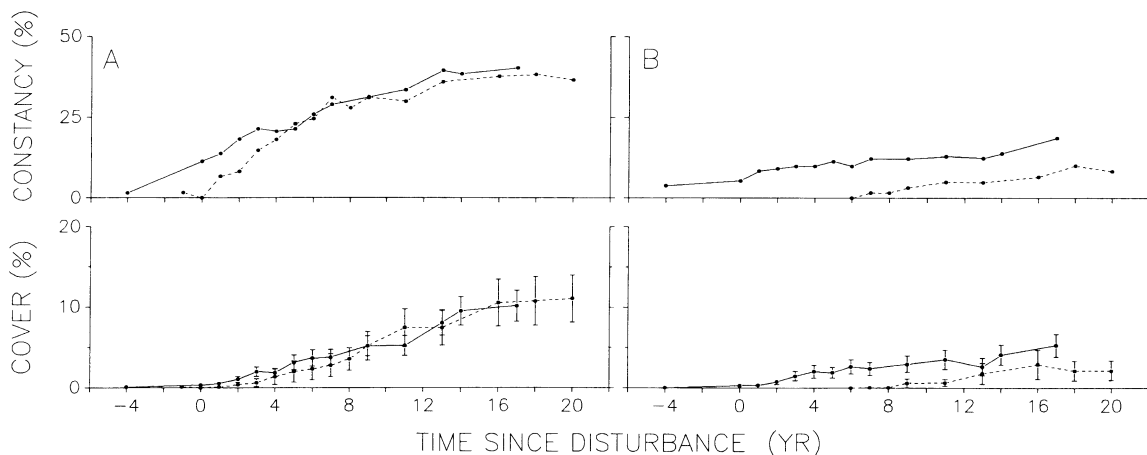


FIG. 7. Changes in constancy and mean canopy cover with time for species of group I6. (A) *Rubus parviflorus*, (B) *Pteridium aquilinum*. — Watershed 1, --- Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

distribution and persistence following catastrophic disturbance. Its site preferences vary locally and regionally (Conard et al. 1985), but may be masked by variation in the intensity of disturbance or by local historical or stochastic factors.

6. *Group I6 species*.—These species are invading perennials of various growth-forms which achieved dominance late in the study period. The most abundant species include the shrub *Rubus parviflorus* (Fig. 7A) and the fern *Pteridium aquilinum* (Fig. 7B), although *Salix scouleriana* and *Prunus emarginata* were locally common. Trajectories of constancy and canopy cover were parallel, increasing slowly and continuously with time. Maximum frequency of occurrence ranged from 15 to 40%, while peak cover averaged between 3 and 11%. Species of group I6 had the greatest longevity of any colonizers observed.

Similar postdisturbance patterns of abundance for *Rubus parviflorus* and *Pteridium aquilinum* have been described for other seral forests in the Cascade Range (Isaac 1940, Kraemer 1977) and in the northern Rocky Mountains (Zamora 1975, Irwin and Peek 1979, Stickney 1986). However, these populations may have derived from surviving understory individuals, unlike the colonizers on Watersheds 1 and 3. Although both *R. parviflorus* and *P. aquilinum* were observed in initial forest plots on WS1 and WS3, they were rare, restricted to disturbed microsites (Dyrness 1973). Thus, the contribution of surviving individuals to the postdisturbance vegetation was probably small.

Species of group I6 possess numerous modes of origin: (1) buried viable seeds (e.g., *Rubus parviflorus* and *Prunus emarginata*), (2) animal-dispersed seeds (e.g., *Rubus parviflorus* and *Prunus emarginata*), and (3) wind-dispersed seeds and spores (e.g., *Salix scouleriana* and *Pteridium aquilinum*). Although the longevity of *R. parviflorus* seeds is unknown, they may be abundant within forest soils of the *Tsuga heterophylla* zone and may be stimulated to germinate by soil distur-

bance, canopy removal, or fire. Estimates of buried viable seed from forests in coastal British Columbia (Kellman 1970) and in the Oregon Coast Range (Stewart 1978) average  $6.2 \times 10^4$  to  $2.4 \times 10^5$  individuals/ha. Reproduction of *Pteridium aquilinum* from spores has been demonstrated on a diversity of natural and man-made substrates, including burned soils (Fletcher and Kirkwood 1979, and references therein). However, germination appears poor within established colonies or under closed vegetation (Haeussler and Coates 1986).

Persistent increases in the constancy and canopy cover of *Rubus parviflorus* and *Pteridium aquilinum* may be explained by extensive lateral spread of deeply buried rhizomes. This method of expansion has been widely observed in other systems (e.g., Fletcher and Kirkwood 1979, Volland and Dell 1981, Hobbs et al. 1984, Haeussler and Coates 1986, Stickney 1986). Although the abundance patterns of *R. parviflorus* (Fig. 7A) somewhat resemble the patterns of *Ceanothus* species (group I5, Fig. 6), slower increases in its constancy and canopy cover suggest an inherently slower rate of growth. However, these differences may also indicate that while *Ceanothus* species emerge from a seed bank immediately after disturbance, seeds of *R. parviflorus* may be largely introduced by animals. Haeussler and Coates (1986) suggest that germination of newly deposited seed is one of the principal means by which *R. parviflorus* establishes. Within old-field seres, similar patterns of delayed invasion have been documented for species of shrubs and trees with large fruits requiring animal dispersal (e.g., Bazzaz 1968, McDonnell and Stiles 1983). The establishment of these species appears to be temporally related to the availability of suitable animal habitat, vertical structure (e.g., perches), or sources of food.

#### *Population patterns of residual species*

1. *Group R1 species*.—*Rubus ursinus*, a native trailing blackberry and an inconspicuous member of the

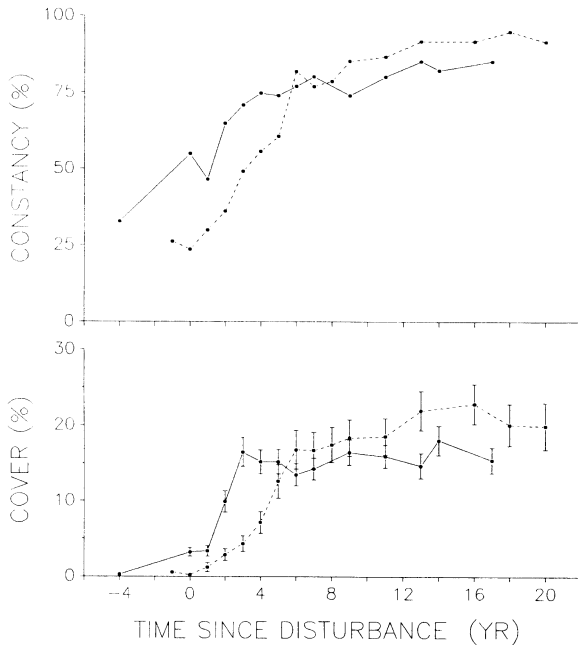


FIG. 8. Changes in constancy and mean canopy cover with time for *Rubus ursinus* (group R1). — Watershed 1, --- Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

predisturbance forest understory, is the only species in this group. Populations expanded dramatically following disturbance and remained prominent throughout the 20-yr study period (Fig. 8). Constancy increased rapidly to 75 and 82% by years 4 and 6 on WS1 and WS3, respectively, and continued to rise, although more slowly, through final sampling. Mean canopy cover increased rapidly to 16% after 3 yr on WS1 and to 17%

after 6 yr on WS3. Subsequent changes in cover differed between sites, increasing slowly to >20% on WS3 and fluctuating between 13 and 18% on WS1. Patterns of abundance showed little consistent relationship with community type or disturbance intensity. Together with the annual and perennial colonizers of groups I1 and I2, *R. ursinus* dominated the herb stratum as early as 2–5 yr after burning, exhibiting the most rapid expansion of any forest residual.

Release of *R. ursinus* has been widely observed following catastrophic disturbance in *Pseudotsuga* forests of the Pacific Northwest (Isaac 1940, Yerkes 1958, Steen 1966, Dyrness 1973, Kraemer 1977). Rapid increases in constancy and cover on Watersheds 1 and 3 resulted from the vigorous spread of trailing and climbing stems over logs, stones, and stumps; among associated herb and low shrub species; and vertically into the crowns of tall shrubs and trees. The released sub-shrub appeared both highly competitive following canopy removal and rather tolerant of fire, although its expansion was delayed on heavily burned sites. Current trends in constancy and cover suggest that *R. ursinus* may persist as a dominant component of the herb stratum until it is suppressed by canopy closure.

2. *Group R2 species.*—This group is made up of three initially subordinate forest herbs and sub-shrubs that were temporarily released by disturbance, *Trientalis latifolia*, *Whipplea modesta*, and *Hieracium albiflorum* (Fig. 9). Changes in their frequency of occurrence resembled those of *Rubus ursinus*, increasing rapidly for 4–6 yr after disturbance and fluctuating near peak levels thereafter. However, the canopy cover of R2 species (Fig. 9) gradually increased, then decreased, differing from that of *R. ursinus* (Fig. 8), which in-

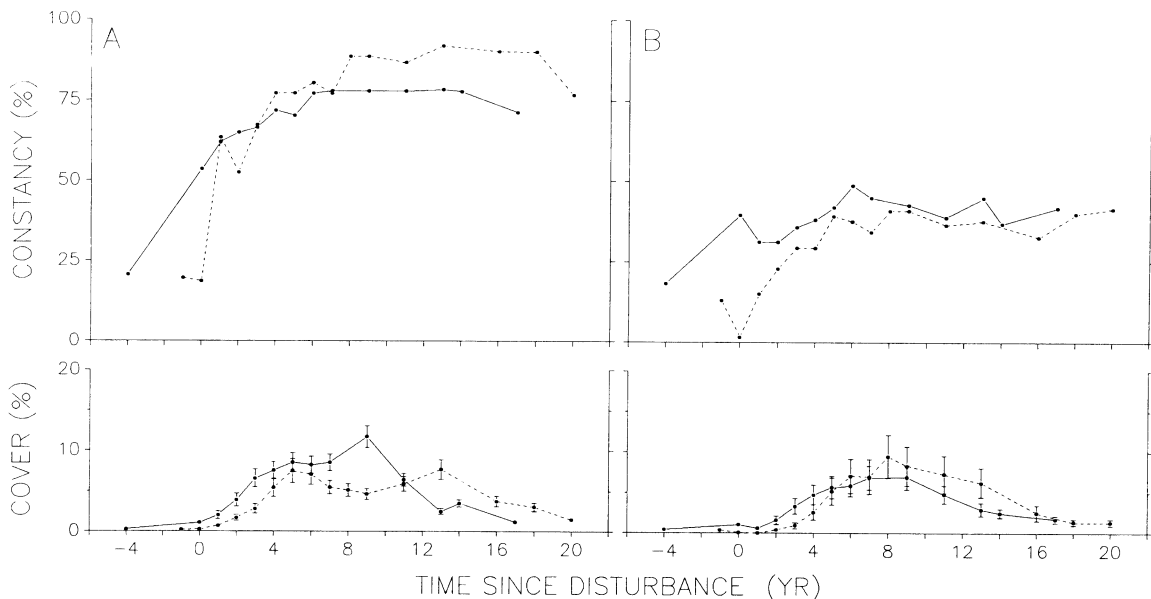


FIG. 9. Changes in constancy and mean canopy cover with time for species of group R2. (A) *Trientalis latifolia*, (B) *Whipplea modesta*, (C) *Hieracium albiflorum*. — Watershed 1, --- Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

creased rapidly and remained high. Peak cover of R2 species ranged from 4 to 12% between years 4 and 9. Thus, trends in cover of R2 species were similar to those of I4 species (Fig. 5), although the latter were generally less abundant.

Differences in the regenerative strategies of species of group R2 were reflected in their response to disturbance. *Trientalis latifolia* (Fig. 9A) has short, thickened tubers that are deeply buried and thus should be relatively insensitive to fire. It expanded within all soil disturbance classes, but progressively later with increased disturbance. In contrast, *Whipplea modesta* (Fig. 9B), a trailing sub-shrub that freely roots at the nodes (Hitchcock and Cronquist 1973), was most abundant within the two unburned soil classes and was uncommon within the heavily burned class. Its susceptibility to fire probably reflects the aboveground position of its perennating structures. On the other hand, the principal means of reproduction of *Hieracium albiflorum* (Fig. 9C) is through recruitment by copious, wind-borne seed (McLean 1968). Thus, although shallow burial of its short, caudex-like rhizome confers rather poor resistance to fire, seed germination and establishment were promoted on heavily burned plots, where regeneration sites were abundant. However, the duration of recruitment and expansion of *H. albiflorum* was limited, resulting in an earlier and shorter period of elevated abundance than that of the other R2 species. Despite these distinct regenerative strategies, the initially subordinate forest species of group R2 displayed a similar temporary release in response to disturbance.

3. *Group R3 species.*—This group contains the initial understory dominants on Watersheds 1 and 3. Popu-

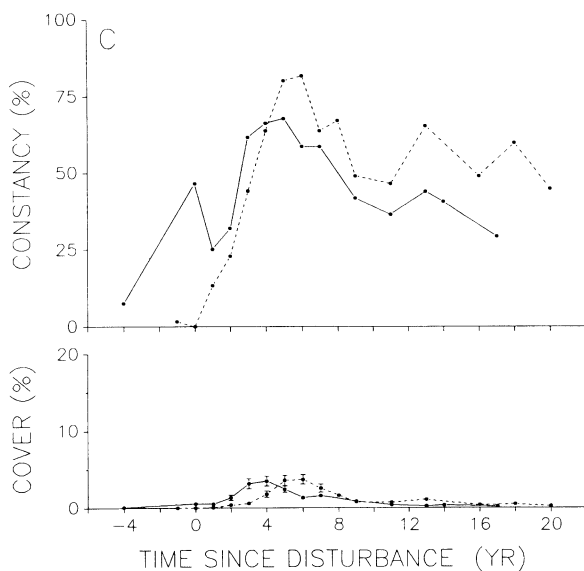


FIG. 9. Continued.

lation patterns were typified by dramatic reductions in response to logging and slash burning, followed by parallel recovery in constancy and cover (Fig. 10). All growth-forms are represented: herbs and low shrubs (*Gautheria shallon*, *Polystichum munitum*, and *Berberis nervosa*); tall shrubs (*Acer circinatum*, *Rhododendron macrophyllum*, and *Corylus cornuta*); and regenerating trees (*Tsuga heterophylla*). Recovery was continuous, but varied among species. Late in the study period, species of group R3 were dominant within portions of both watersheds.

Three patterns suggest that vegetative recovery rather than reproduction from seed was the principal means of regeneration among R3 species. First, species constancy and cover through time were generally proportional to initial community values. Second, long-term recovery was inversely proportional to the intensity of disturbance. Finally, multiple-stemmed, sprouting individuals were common. Sprouting from the bases of stems and along rhizomes may afford R3 species moderate resistance to fire (Sabhasri 1961, McLean 1968, Volland and Dell 1981, Haeussler and Coates 1986). Observational studies in similar ecosystems suggest that these understory dominants recover better on unburned than on burned sites, although responses vary (cf. Steen 1966, Anderson 1969, Kraemer 1977). The role of sexual reproduction in initiating postdisturbance populations is unknown for most forest understory species. However, seed reproduction has been reported as poor in *A. circinatum* (Anderson 1967, Russel 1974, USDA 1974) and *G. shallon* (Sabhasri 1961, Haeussler and Coates 1986). Thus, it is likely that vegetative reproduction dominated postdisturbance recovery for both herb and shrub species of group R3.

4. *Group R4 species.*—This is a diverse group of initially subordinate forest species that showed relatively minor long-term changes in abundance following disturbance (Fig. 11). The species represent an array of growth-forms, including herbs (*Viola sempervirens*, *Coptis laciniata*, *Oxalis oregana*, and *Rubus nivalis*); deciduous shrubs (*Vaccinium parvifolium*); sclerophyllous trees (*Castanopsis chrysophylla*); and deciduous hardwoods (*Acer macrophyllum* and *Cornus nuttallii*). Logging and burning initially reduced both the constancy and cover of each species. However, subsequent patterns of abundance varied. On WS1, constancy remained relatively stable for all species. On WS3, constancy varied little for *Coptis laciniata* (Fig. 11A) but increased for *Vaccinium parvifolium* (Fig. 11B), *Viola sempervirens* (Fig. 11C), and *Castanopsis chrysophylla* (Fig. 11D). Change in canopy cover were generally less pronounced. Among the clearest trends were gradual, continuous increases in the cover of *Vaccinium parvifolium* on WS3 and of *Castanopsis chrysophylla* on both watersheds. Nevertheless, unlike the initial understory dominants of group R3, R4 species never achieved 50% constancy or 5% canopy cover.

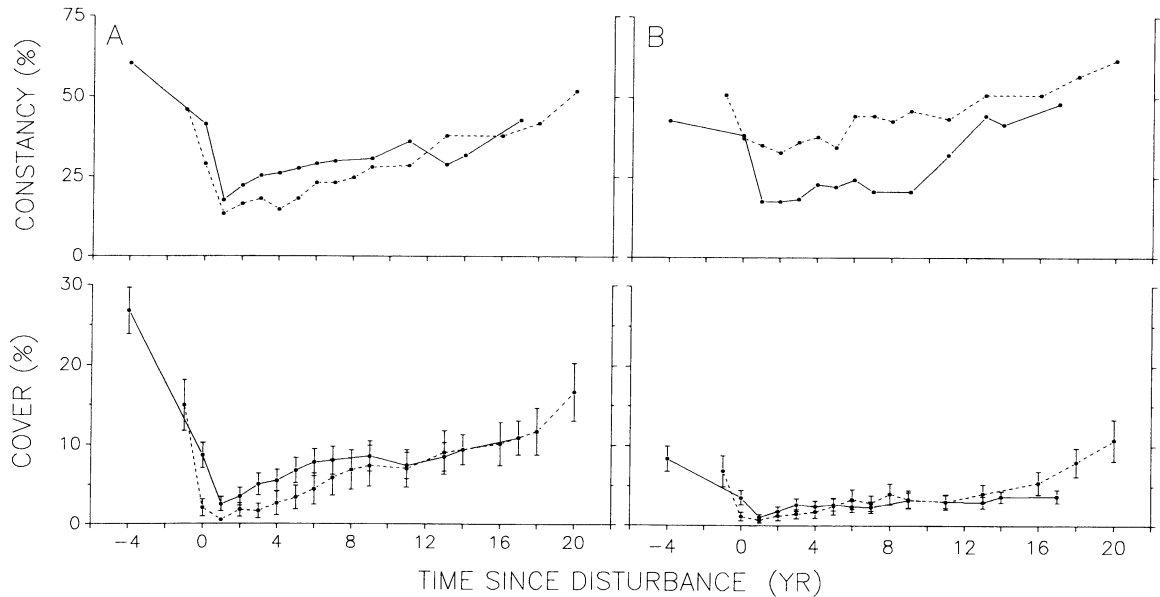


FIG. 10. Changes in constancy and mean canopy cover with time for species of group R3. (A) *Acer circinatum*, (B) *Polystichum munitum*. — Watershed 1, --- Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

Stem sprouting of both *Vaccinium parvifolium* and *Castanopsis chrysophylla* confers moderate resistance to fire. Thus, with the exception of heavily burned sites, postdisturbance distributions generally remained similar to those of the initial forest understory. In contrast, the postdisturbance dynamics of the herb populations were more correlated with differences in disturbance intensity than with initial distributions. *Coptis laciniata* was briefly released on undisturbed sites but was greatly reduced on burned sites. Although *Viola sempervirens* was not reduced by burning, it expanded only on undisturbed sites.

The relatively minor changes in postdisturbance abundance of R4 species may be related to both their growth form and predisturbance distribution. *Vaccinium parvifolium* and *Castanopsis chrysophylla* possess a limited potential for lateral growth relative to the trailing and strongly rhizomatous species of the pre-

vious residual groups. Compounded with their initially sparse distributions, this morphological constraint may have restricted their seral abundance on Watersheds 1 and 3. On the other hand, the postdisturbance abundance of herb species such as *Viola sempervirens* and *Coptis laciniata* may be limited by two factors. First, although they appear to expand vegetatively through stolons and slender rhizomes, the location of perennating buds on or near the soil surface affords them little resistance to fire. Second, the abundance of R4 herbs may be limited simply by their small stature in an herb layer dominated by taller herbs and sub-shrubs.

5. *Group R5 species*.—This group encompasses a variety of uncommon, but characteristic, forest species that, unlike those of the previous residual groups, had minimal postdisturbance recovery (Fig. 12). Among the most frequent species are the sub-shrub *Chimaphila umbellata*; the herbs *Goodyera oblongifolia* and

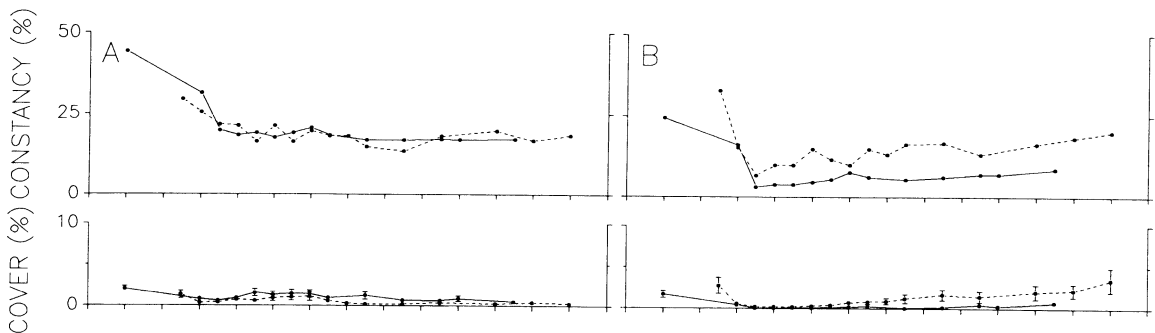


FIG. 11. Changes in constancy and mean canopy cover with time for species of group R4. (A) *Coptis laciniata*, (B) *Vaccinium parvifolium*, (C) *Viola sempervirens*, (D) *Castanopsis chrysophylla*. — Watershed 1, --- Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

*Synthyris reniformis*; and the coniferous trees *Thuja plicata* and *Taxus brevifolia* (both occurring as suppressed understory individuals).

R5 species showed broad susceptibility to the disturbance of logging and burning, in contrast to R3 and R4 species. Constancy declined from 10–24% before logging to 0–3% after slash burning (Fig. 12). Reappearance of *Thuja plicata* (Fig. 12A) was delayed for 8–9 yr within the moist *Coptis* and *Polystichum* communities of WS3. Although scattered individuals probably survived disturbance in protected microsites, long-term recovery of *T. plicata* will largely depend on regeneration by seed. Its greater postdisturbance abundance on WS3 likely reflected the more pronounced edge effect and the greater seed availability associated with smaller cutting units. The long-term patterns on both watersheds suggest that, relative to the vegetative recovery of other residual species, establishment from seed is slow.

*Chimaphila umbellata* (Fig. 12B) was severely reduced on the burned sites of both watersheds and was completely eliminated from the sample plots of all but one community on WS1. Others report the absence of fire resistance in herbs belonging to group R5 (McLean 1968, Volland and Dell 1981, Crane et al. 1983). Although *C. umbellata* has deep, fibrous roots and rhizomes, new shoots are apparently initiated only from rootstalks near the soil surface (McLean 1968). Loss of the long-lived evergreen leaves may also reduce survival following fire (J. A. Antos, *personal communication*). Vegetative recovery will depend primarily on the scattered individuals surviving within undisturbed microsites. Thus, poor initial survival combined with limited postdisturbance recovery contribute to the minor role of R5 species during early secondary succession.

#### CONCLUSIONS

Early secondary succession in these coniferous forests proceeds through gradual changes in the abundance of a diversity of invading and residual species. Patterns of species cover generally described broadly

overlapping, unimodal curves differing in time of initiation, duration, and magnitude. Temporal displacement of populations suggests that species respond individually (sensu Gleason 1917) to changes in resource availability and stress through time, as well as along environmental gradients (see also Drury and Nisbet 1973, Gomez-Pompa and Vazquez-Yanes 1974, Whittaker 1975, Pickett 1976, 1982). Further, these patterns of species abundance support Egler's (1954) initial floristics model of succession, although aspects of relay floristics were also apparent in the subsequent invasion of additional, but uncommon, species. Initial floristics, a concept originally developed to describe succession in old fields, has been widely observed in forest systems where residual species and rapidly establishing invaders are major contributors to secondary seres (e.g., Cremer and Mount 1965, Trabaud and Lepart 1980, Abrams and Dickmann 1984, Stickney 1986). In this study, a majority of the dominant or subordinate species either survived disturbance or established within 2 yr after burning. In addition, initial understory dominants and perennial colonizers did not sequentially recruit, but gradually recovered or expanded. Furthermore, nearly all major invading species that eventually decreased in abundance did not become extinct, but exhibited slow rates of decline. Thus, early succession was characterized by a gradual shift in the abundance of generally persistent species, rather than by a series of replacements.

Species were subjectively placed within groups to emphasize similarities in their patterns of abundance. These similarities commonly derived from characteristics of parallel life cycles or from similar disturbance responses or tolerances. For example, among the invading groups, I1 species were winter annuals, I3 species were biennials or short-lived perennials, and I6 species were long-lived perennials. Consequently, the period of elevated abundance occurred progressively later in each group, corresponding with the rate of development and the longevity of the representative species. Similarly, the relationship between the timing of disturbance and the dispersal of seeds of I1 annuals, the

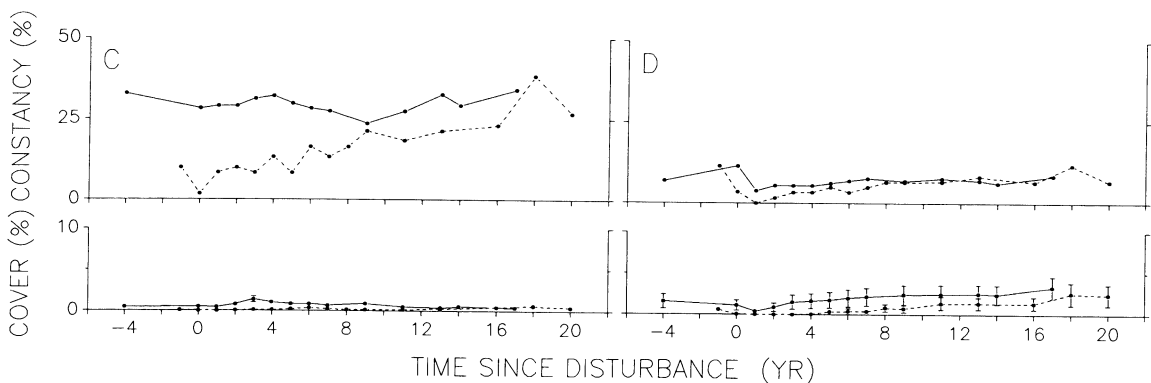


FIG. 11. Continued.

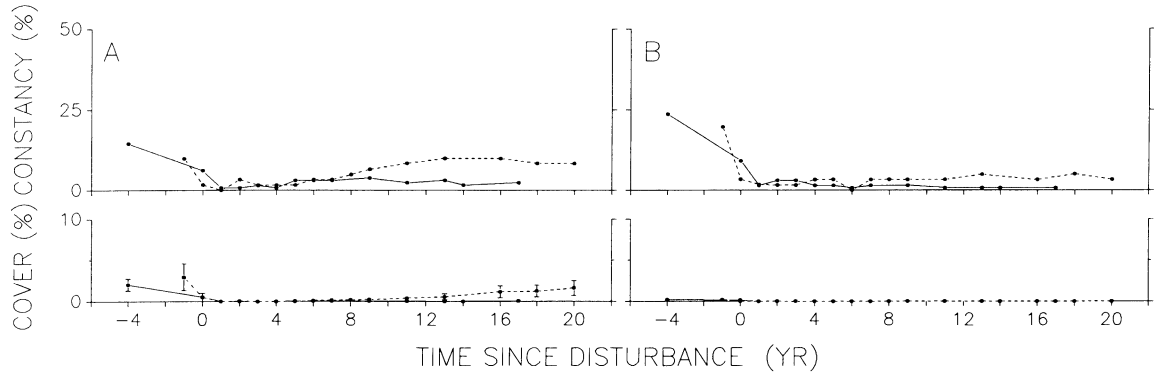


FIG. 12. Changes in constancy and mean canopy cover with time for species of group R5. (A) *Thuja plicata*, (B) *Chimaphila umbellata*. — Watershed 1, --- Watershed 3. Vertical bars in cover graphs represent  $\pm 1$  SE.

stimulating response of fire on buried seeds of I5 species, and the gradual regeneration by sprouting of disturbance-tolerant R3 perennials, were evident in their respective abundance patterns.

Alternate mechanisms of dispersal, establishment, or expansion may complicate the interpretation of species dynamics. In fact, for many species on Watersheds 1 and 3, multiple modes of regeneration occurred simultaneously. For example, establishment of *Epilobium angustifolium* from seed probably continued in open microsites throughout the study period, whereas expansion in closed communities was probably limited to spread via rhizomes. Similarly, resprouting of initially dominant forest residuals may have been common on undisturbed and moderately disturbed sites, whereas reproduction on heavily burned sites, although limited, may have been largely by seed. Features of the long-term abundance of many invading and residual species varied correspondingly among these sites (Halpern 1987, 1988).

Life history traits and responses to disturbance may also explain the dynamics of some common species that were not easily assigned to 1 of the 11 population patterns. For example, the trailing sub-shrub, *Linnaea borealis*, exhibited a bell-shaped pattern of cover resembling that of group R2 and a gradual increase in constancy, similar to that of group R3. The potential for this subordinate, forest residual to spread vegetatively following canopy removal may exceed that of *Whipplea modesta*. However, the aboveground location of its perennating buds makes *L. borealis* particularly sensitive to burning (McLean 1968, Crane et al. 1983, Rowe 1983, Bradley 1984). Thus, its unique pattern of abundance reflected dramatic expansion of surviving individuals on undisturbed sites, but widespread elimination on disturbed and burned sites.

The patterns of abundance of many understory species were similar between watersheds, suggesting that succession in these forests has a deterministic component founded in life history traits and responses to disturbance of the available species. However, for some species (e.g., *Epilobium* spp. and *Ceanothus* spp.), there

were dramatic differences in abundance patterns between watersheds correlated with variation in: (1) timing and intensity of disturbance, (2) predisturbance distributions of understory species and seed banks, (3) postdisturbance dispersal of propagules, and (4) local weather conditions. Long-term successional records such as these reveal the potential importance of unpredictable phenomena in the dynamics of individual populations and entire communities.

The use of life history characteristics to explain abundance patterns is a common approach to successional analysis (e.g., Cattalino et al. 1979, Noble and Slatyer 1980, Pickett 1982, Hobbs et al. 1984, Walker et al. 1986, Halpern 1988). However, in *Pseudotsuga* forests, this is rendered difficult by the paucity of information on the life histories of common understory species. Uncertainty about the causes of changing abundance in populations clearly points to the need for further research on the autecology of these species. Our understanding of early successional dynamics in this system would be enhanced by additional observational and experimental study on the roles and mechanisms of sexual and vegetative reproduction, on the longevity and distribution of buried seeds, and on the competitive relationships among invading and residual species following disturbance.

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