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Vegetation change following catastrophic disturbance is a complex process which may include the invasion, interaction, replacement, and recovery of species. Permanent sample plots established prior to disturbance were used to examine the vegetation changes during 21 yr of succession in two clearcut and burned *Pseudotsuga* watersheds in the western Cascade Range of Oregon. The abundance of all vascular plant species was recorded in plots representing six initial forest communities exposed to a gradient in disturbance intensity. Patterns of floristic and physiognomic change, dynamics of species determining these patterns, and methods for portraying and interpreting alternate paths of succession and community response to disturbance, are presented in this study.

Logging and burning resulted in dramatic changes in vegetation structure and composition, although a majority of forest species persisted through disturbance. Invasion was rapid for 2-3 growing seasons following burning. Subsequent understory development was characterized by gradual shifts in the abundance of residual and invading vegetation groups. Three major trends were evident: vegetation stature increased with time, invaders showed greatest abundance and persistence on disturbed and burned sites, and residuals displayed greatest development on undisturbed sites. Contrasting patterns between watersheds were attributed to differences in history of logging and burning.

Many of the spatial and temporal trends in vegetation were explained by the life history traits of species in response to disturbance. Eleven population patterns were identified. Abundance patterns of invading species groups were correlated with propagule origin, life cycle phenology, spatial and temporal variation in disturbance, and potential for vegetative reproduction. Abundance patterns of residual species groups reflected initial species distributions, resistance to disturbance, reproductive mode, morphological characteristics, and spatial variation in disturbance.

Detrended correspondence analysis (DCA) ordination revealed alternate successional sequences arising from variation in initial composition and disturbance intensity. Measures of resistance and resilience, derived from Euclidean distances in ordination space, suggest that the maximum displacement and the long-term recovery of *Pseudotsuga* community composition are largely determined by the intensity of disturbance and by the life history traits of the dominant residual and invading species. However, both the immediate and long-term response of communities to disturbance may be modified by historical or stochastic phenomena.

Twenty-one Years of Secondary Succession in *Pseudotsuga* Forests of the Western Cascade Range, Oregon

by

Charles B. Halpern

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ERRATA

for

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Note the following corrections:

Page 29, paragraph 2, line 8--change ***Chimaphila umbellata*** to ***Chimaphila menziesii***.

Page 44, paragraph 2, line 4--change **39%** to **58%**.

Page 88, paragraph 1, line 11--change **1.6 yr** to **1.1 yr**.

Page 88, paragraph 1, line 12--change **3.2-3.3 yr** to **2.7-3.0 yr**.

Page 96, paragraph 2, line 6--change **82%** to **64%**.

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Chapter 1

INTRODUCTION

Catastrophic disturbance alters the structure and composition of vegetation in many terrestrial ecosystems (White 1979, Bazzaz 1983, Caine and Swanson 1983, Sousa 1984a). Where communities are comprised of resilient species, subsequent recovery may be rapid and complete. More often, however, the consequences of large-scale disturbance are dramatic, resulting in complex changes in community structure and composition. Succession initiated by fire has been widely studied in natural and managed systems (see reviews in Lutz 1956, Ahlgren and Ahlgren 1960, Wright and Heinselman 1973, Kozlowski and Ahlgren 1974, Conrad and Oechel 1977, Mooney and Conrad 1977, Mooney et al. 1980, Chandler et al. 1983). Yet, relatively few successional studies have used permanent plots to trace vegetation change. Instead, sites of varying ages are arranged chronologically to portray temporal sequences. In chronosequence studies, however, inferences with regard to successional age are confounded by possible differences among sites in initial vegetation, environment, disturbance history, and input of propagules.

Permanent sample plots provide an invaluable source of information on the dynamics of vegetation (Austin 1981, Franklin

1982). Long-term observations of permanent plots have been used to examine 1) the influence of herbivores in grasslands (Weaver and Bruner 1945, Albertson and Tomanek 1965, Smeins et al. 1976, Watt 1960, 1970, van der Maarel 1978, 1981, Anderson and Holte 1981, Austin et al. 1981); 2) the results of climatic or hydrologic fluctuations (e.g., in desert [Goldberg and Turner 1986], bog [Schwintzer and Williams 1974], dune grassland [van der Maarel 1978, 1981], salt marsh [Beeftink 1979, ter Borg 1979, Roozen and Westhoff 1985], and heath communities [Lippe et al. 1985]); and 3) the effects of fertilization (van den Bergh 1979, van der Maarel 1980). Permanent plots have also been used to study early secondary succession following volcanic eruption (Smathers and Mueller-Dombois 1974, Means et al. 1982, del Moral 1983, Halpern and Harmon 1983, Antos and Zobel 1985); abandonment of oldfields (Pickett 1982, Collins and Adams 1983); and harvest or burning of forests (Cremer and Mount 1965, Williams et al. 1969, Lyon 1971, 1984, Stickney 1980, 1981, 1985, 1986). Unfortunately, inferences from many permanent plot studies are also constrained by: 1) short periods of observation, 2) low sampling frequencies within relatively long-term studies, 3) absence of initial community data, and 4) a focus on trees in studies within forest ecosystems.

We have an incomplete understanding of early successional change in Pseudotsuga forests of the Pacific Northwest, despite previous studies tracing understory development in permanent plots (Ingram 1931, Isaac 1940, Yerkes 1958, Steen 1966, Gashwiler 1970, Morris 1970, Dyrness 1973, Kraemer 1977, Gholz et al. 1985). These authors have reached widely varying conclusions regarding the temporal patterns of abundance of major growth-forms and the response of residual and colonizing species to variation in disturbance. Comparisons of their results are hindered by differences in methods of sampling and analysis (e.g., differential assignment of species to vegetation groups or different measures of abundance). That successional patterns are heterogeneous is clear. However, the degree to which this heterogeneity reflects study design or natural variation (e.g., in initial conditions or disturbance history) is unclear.

In this thesis, I examine the physiognomic and compositional changes during 21 yr of secondary succession in Pseudotsuga forests. Permanent sample plots were observed within two clearcut and burned watersheds in the western Cascade Range of Oregon. Initiated in 1962 by C. T. Dyrness, the study represents one of the longest and most complete permanent plot records of secondary forest succession in North America. Plots classified by understory plant community were sampled prior to logging and were assigned to soil disturbance classes immediately after slash burning. This classification of plots facilitates study of the influence of initial composition and disturbance intensity in forest understory development.

Three chapters address different aspects of secondary succession. Chapter 2 is a detailed account of the floristic and physiognomic changes characterizing the two watersheds. I examine the influence of initial composition, intensity of disturbance, and timing of logging and burning on the origin and development of the principal vegetation strata.

Chapter 3 provides an analysis of the abundance patterns of species contributing to these strata. I interpret the temporal and spatial patterns of abundance of species in terms of the relationship between their life history characteristics and disturbance.

Long-term successional data are inherently complex, and the patterns of species replacement and community development are commonly diverse. Chapter 4 presents a multivariate method for characterizing alternate pathways of succession, and for assessing the relative resistance and resilience of communities.

In Chapter 5, I summarize the study.

Chapter 2

PATTERNS OF UNDERSTORY DEVELOPMENT DURING TWENTY-ONE YEARS OF SECONDARY SUCCESSION IN *PSEUDOTSUGA* FORESTS

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ABSTRACT

Permanent plots established prior to disturbance were used to examine vegetation patterns during 21 yr of secondary succession in two clearcut and burned *Pseudotsuga* watersheds in the western Cascade Range of Oregon. The origin and development of understory vegetation layers are described for six initial forest communities and for sites representing a gradient in disturbance intensity.

Logging and burning resulted in dramatic changes in vegetation structure and composition. Nevertheless, most forest species

persisted through disturbance or reemerged within 1-2 growing seasons following burning. Although species richness consistently increased with time, a majority of the dominant invading species established within 2-3 yr after burning. Long-term changes in composition were characterized by the differential growth and decline of dominant residual and invading species.

Physiognomic changes in seral understories were characterized by gradual shifts in dominance toward growth-forms of increasing stature. However, the relative importance of the five principal vegetation groups (i.e., invading herbs and low shrubs, residual herbs and low shrubs, invading tall shrubs, residual tall shrubs, and trees) varied with initial community composition and with intensity of disturbance.

The abundance of herbs and low shrubs peaked between 2 and 6 yr following burning, reflecting rapid invasion of wind-dispersed, winter annuals. Subsequent herb layer changes were characterized by gradual decline of invaders, transient or persistent release of initially subordinate residuals, and gradual vegetative recovery of original dominants. Invaders showed greatest development on disturbed and burned sites. Residuals dominated undisturbed sites, with recovery proportional to initial community abundance. Tall shrubs assumed co-dominance between 10 and 18 yr following burning. Invading tall shrubs, principally developing from buried seed, dominated disturbed and burned sites. Residual tall shrubs, sprouting from adventitious stem buds, recovered gradually, dominating undisturbed sites. Long-term recovery of residual shrubs

was proportional to initial community abundance. Tree development, partly attributed to artifical regeneration, was highly variable. Trends toward canopy closure were apparent only within the initially tree-dominated understory of the *Coptis* community.

Temporal and spatial differences in understory development between watersheds were attributed to history of logging and burning. In addition, historical and stochastic factors influenced the pre- and post-burning dynamics of dominant invading herb and tall shrub species and played an important role in early secondary succession.

INTRODUCTION

Large-scale disturbances are rarely uniform in their influence on vegetation. Thus, when fugitive colonizers and surviving individuals potentially contribute to a post-disturbance flora, heterogeneity in disturbance may initiate successional sequences that differ in both rate and direction of development. Historical or stochastic factors may further modify the response of vegetation to disturbance. Thus, variation in initial composition, availability of propagules, timing of disturbance, local climate, or herbivory, commonly result in alternate sequences of species replacement, in both terrestrial (Noble and Slatyer 1977, 1980, Cattelino et al. 1979, Glenn-Lewin 1980, Humphrey 1984, Abrams et al. 1985, Arno et al. 1985, Boerner 1985) and marine ecosystems (Lubchenco and Menge 1978, Turner 1983, Sousa 1979, 1984b, Olson 1985). In this paper we show that the seral understory strata in _Pseudotsuga_ forests similarly have diverse origins and paths of development following catastrophic disturbance.

We have an incomplete understanding of early structural and compositional change in _Pseudotsuga_ ecosystems, despite previous studies which have employed permanent plots (Ingram 1931, Isaac 1940, Yerkes 1958, Steen 1966, Gashwiler 1970, Morris 1970, Kraemer 1977, Gholz et al. 1985). Conclusions from these studies vary widely with regard to the abundance patterns of major growth-forms and to the relative importance of residual and invading floras. Comparisons are hindered by the absence of original understory data, incomplete descriptions of disturbance, and by differences in methods of sampling or analysis. Thus, whether the heterogeneity of successional trends reflects natural variation or study design is unclear.

In this paper, we examine 21 years of successional change in two clearcut and burned Pseudotsuga watersheds in the western Cascade Range of Oregon. The study represents one of the longest and most complete permanent plot records of forest succession in North America. Results from the first 5 yr of observation have been reported by Dyrness (1973).[1/] Plots were sampled prior to logging and were observed immediately after burning, permitting study of the influence of initial composition and disturbance intensity in understory development. Our objectives are two-fold: 1) to provide a detailed account of the floristic and physiognomic changes characterizing the period prior to canopy closure, and 2) to fit the observations into a more general framework recognizing the influences of initial community composition and intensity of disturbance in seral community development.

The differential growth and mortality of species following early establishment (initial floristics, [Egler 1954]), rather than their sequential recruitment and replacement (relay floristics), are considered the principal mechanisms of vegetation change following disturbance (Egler 1954, Drury and Nisbet 1973, Connell and Slatyer 1977, Peet and Christensen 1980). Originally developed for succession in old fields, the concept of initial floristics has been widely applied to forest succession following catastrophic disturbance (Cremer and Mount 1965, Johnson and Rowe 1977, Houssard et al. 1980, Trabaud and Lepart 1980, Uhl et al. 1981, Heinselman 1981, AuClair 1983, Felix et al. 1983, Foote 1983, Abrams and Dickmann 1984, Foster 1985, Stickney 1986). To examine the importance of initial floristics in this system, we assess both the persistence of the original flora and the temporal patterns of species invasion and loss following disturbance.

The structural development of vegetation during succession has been classically described as the successive replacement of growth-forms or vegetation layers of increasing stature (Clements 1916, 1928). The order and duration of growth-form phases may vary, however, with the life history characteristics of the available species. For example, in many ecosystems the progression of growth-forms is essentially absent, as species simply resprout following fire and communities rapidly resume initial stature (Hanes 1971, Black and Bliss 1978, Ohmann and Grigal 1979, Viereck and Dyrness 1979, Trabaud and Lepart 1980). In chaparral and coastal sage scrub vegetation, in contrast, ephemeral herbs originating from a buried seed bank are dominant for a period of 1-3 yr following fire and are succeeded by a persistent shrub phase (Horton and Kraebel 1955, Sweeney 1956, Christensen and Mueller 1975, Keeley and Keeley 1984, Keeley et al. 1985). An extended herb stage of 35 yr, in pinyon-juniper woodland, may reflect the slow regeneration of sagebrush from buried or off-site seed sources (Barney and Frischknecht 1974, Koniak 1985). An initial herb phase may be precluded, however, by rapid expansion of tall shrubs originating from a buried seed bank, as in eastern hardwood forests (Marks 1974), or by sprouting of residual shrubs, as in western coniferous forests (Stickney 1986). Rapid closure of the tree canopy may limit development of a transitional shrub stage in other coniferous systems (Corns and LaRoi 1975).

In this study, we examine the variation in physiognomic development of seral *Pseudotsuga* understories with respect to two factors: the initial composition and structure of communities and the intensity of initiating disturbance. In particular, we consider the transitions of dominance with time among major growth-forms (vegetation strata), and the origin and subsequent development of each stratum. To this end, we assess the influence of initial composition and structure, as well as of disturbance intensity, on the abundance patterns of the residual and invading flora comprising each stratum. We conclude by developing a general model of understory development in seral *Pseudotsuga* forests.

STUDY AREA

Physical Environment

The study sites, Watersheds 1 and 3 (WS1 and WS3), occur within the H. J. Andrews Experimental Forest, 80 km east of Eugene, Oregon, on the western slope of the Cascade Range (Fig. II-1). Their topography is typical of the mature, dissected terrain of the region, with small tributary streams incised between steep downward-trending ridges. Elevations range from 442-1082 m; moderately steep slopes average 50-60% and occasionally exceed 110% (Rothacher et al. 1967). The soils principally originate from pyroclastic tuffs and breccias, although basalts and andesites are also present. Soil profiles are generally poorly developed and colluvial deposits are often very deep (Dyrness 1969). Most of the soils are loam textured and moderately stony. A high porosity (60-70%) ensures rapid percolation and a large storage capacity.

Climate

The climate is maritime with mild, wet winters and warm, dry summers. Although annual precipitation is 2302 mm, only 6% falls during the months of June-August (Bierlmaier and McKee in press). Seventy-one percent occurs between November and March, during low intensity, long duration frontal storms. Although snowfall is

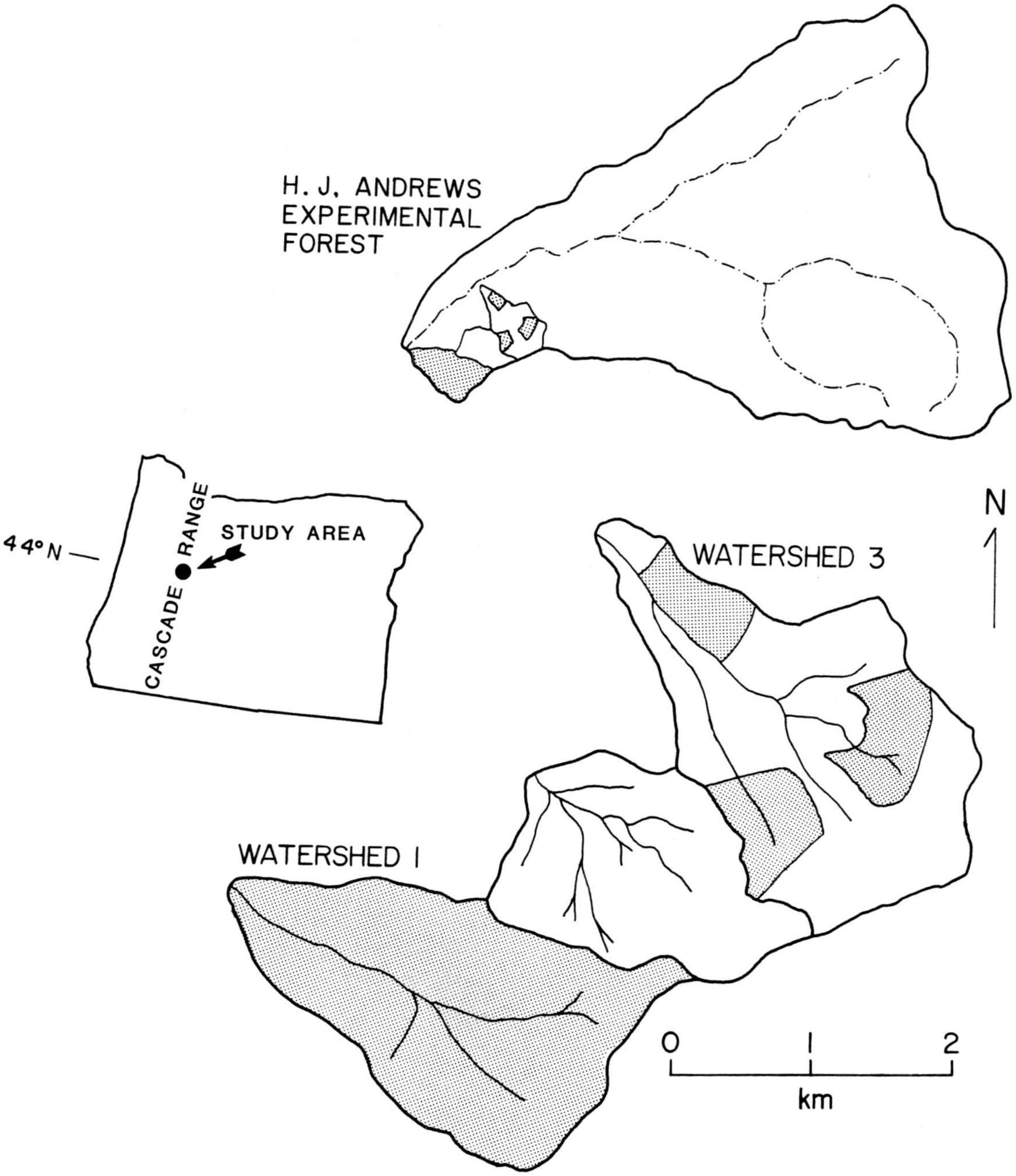


Figure II-1. The location of the study area.

common, snowpacks form only during prolonged periods of cold weather and rarely persist for longer than two weeks. Average minimum temperatures range from -5.5°C in January to 11.9°C in August, while average maxima range from 5.5°C in January to 23.3°C in July. The growing season (the frost-free period) averages 134 days, although it is extremely variable (Bierlmaier and McKee in press).

Vegetation

The vegetation is representative of the *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Prior to logging, forest canopies were largely dominated by old-growth *Pseudotsuga menziesii* (300-500 years-of-age), with *Tsuga heterophylla* in a variety of size and age classes. Mature stands of *P. menziesii*, primarily in the 125-year age class, were less common. Other widely distributed sub-canopy and understory tree species included *Taxus brevifolia*, *Cornus nuttallii*, and *Acer macrophyllum*. *Castanopsis chrysophylla* and *Pinus lambertiana* were restricted to upper slopes and ridgetops, whereas *Thuja plicata* was most common along lower slopes and drainages. *Alnus rubra* was found locally along streamside sites. Overstory canopy cover (> 8 m) averaged 62 and 58% and understory tree cover (< 8 m) averaged 59% and 42% on WS1 and WS3, respectively.

Six understory communities were described prior to disturbance (Rothacher et al. 1967, Dyrness 1973, Hawk and Dyrness 1973) (Tables

II-1 and II-2). Arrayed along a complex gradient of moisture and topographic position they were typical of sites of similar elevation and habitat throughout the Experimental Forest. The communities fall within the *Pseudotsuga menziesii* and *Tsuga heterophylla* series of Hemstrom et al. (1985). Although they were comprised of species with wide distribution, shifts in the relative abundance of the understory dominants reflected variations in physical environment, overstory canopy characteristics, and stand histories. Descriptions of the six communities follow, arranged in order of increasing available moisture. The names reflect the dominant herb and tall shrub species.

1. The *Corylus cornuta* - *Gaultheria shallon* community (COCO-GASH) was restricted to shallow soils on south-facing slopes of WS1--the driest site conditions. It is assignable to the *Pseudotsuga menziesii* / *Berberis nervosa* association of Hemstrom et al. (1985). Reproduction of *P. menziesii* was fairly common, attesting to the open tree canopy. *Taxus brevifolia*, the most common understory tree species, exhibited its greatest abundance in this community. A fairly open, tall shrub layer was dominated by *Corylus cornuta* and *Acer circinatum*, with lower abundance of *Vaccinium parvifolium*. *Berberis nervosa* dominated a species-rich, yet fairly open, herb and low shrub layer. *Gaultheria shallon*, *Linnaea borealis*, *Synthyris reniformis*, *Coptis laciniata*, and *Whipplea modesta* were common associated herbs.

2. The *Rhododendron macrophyllum* - *Gaultheria shallon* community (RHMA-GASH) was found on a variety of landforms typified by

Table II-1. Constancy and average cover for vascular plant species in the plant communities of Watershed 1 during 1962. Only species with constancy > 20% in at least one community are included. Total constancy for vegetation layers includes all species and total cover is additive. See Vegetation section for community abbreviations. Con = constancy (%); Cov = average cover (%); T = trace cover (<0.1%).

Plant community Number of plots	COCO-GASH 12		RHMA-GASH 20		ACCI-GASH 7		ACCI-BENE 34		COLA 23		POMU 32	
	Con	Cov	Con	Cov	Con	Cov	Con	Cov	Con	Cov	Con	Cov
Tree species												
Pseudotsuga menziesii	33	7.7	5	0.5	14	0.1	6	2.9	9	0.3	3	T
Taxus brevifolia	25	12.5	10	1.0	14	10.7	21	6.0	4	0.1	13	2.3
Thuja plicata	--	--	10	0.2	--	--	9	2.1	17	2.7	31	3.9
Tsuga heterophylla	17	7.1	50	9.1	29	0.3	53	18.2	52	14.6	38	11.8
Total tree:	67	29.2	70	18.9	43	11.1	79	31.1	74	18.5	63	18.7
Tall shrub species												
Acer circinatum	42	15.0	70	23.8	71	40.0	97	48.5	13	0.1	53	27.6
Corylus cornuta	83	19.3	10	1.3	14	3.6	--	--	--	--	3	1.1
Rhododendron macrophyllum	--	--	100	41.1	--	--	18	2.4	9	0.1	6	0.6
Rosa gymnocarpa	8	0.2	15	0.5	29	0.4	12	0.1	--	--	3	0.1
Vaccinium parvifolium	25	3.3	30	2.2	14	1.4	21	1.0	35	1.4	22	1.8
Total tall shrub:	83	37.8	100	68.8	86	45.7	100	52.1	47	1.8	59	32.6
Herb and low shrub species												
Achlys triphylla	42	0.1	10	0.2	14	0.2	6	T	--	--	9	T
Berberis nervosa	83	13.0	95	10.7	100	4.3	79	5.5	70	3.5	59	5.4
Chimaphila menziesii	--	--	5	0.1	29	0.1	9	T	9	T	9	T
Chimaphila umbellata	33	0.5	35	0.4	14	0.3	29	0.2	30	0.1	6	T
Coptis laciniata	42	2.5	35	1.7	--	--	29	1.2	74	2.4	59	3.3
Galium triflorum	25	T	--	--	--	--	12	0.2	4	T	47	0.3
Gaultheria shallon	42	1.2	85	15.1	100	30.9	15	0.4	17	0.2	13	0.3
Goodyera oblongifolia	8	T	20	0.1	43	1.1	21	0.1	4	T	6	T
Linnaea borealis	58	2.3	50	1.6	14	0.8	26	0.7	52	3.1	47	3.0
Polystichum munitum	58	0.8	15	1.3	43	1.1	18	0.2	17	T	100	32.8
Pteridium aquilinum	--	--	20	0.2	14	T	--	--	--	--	--	--
Pyrola picta	--	--	20	T	14	T	9	T	9	T	--	--
Rubus nivalis	--	--	15	0.1	--	--	--	--	22	0.3	--	--
Rubus ursinus	58	0.4	40	0.3	29	0.5	24	0.1	22	0.1	41	0.6
Synthyris reniformis	58	1.8	15	0.1	14	T	12	T	9	0.1	19	0.4
Tiarella unifoliata	--	--	5	T	--	--	--	--	22	0.2	19	T
Trientalis latifolia	33	0.5	15	0.2	14	0.1	18	0.1	--	--	19	0.4
Vancouveria hexandra	8	0.3	5	T	--	--	3	T	9	0.1	38	1.4
Viola sempervirens	17	0.6	40	0.5	43	1.2	17	T	48	0.1	41	1.0
Whipplea modesta	42	0.6	15	0.1	29	0.2	15	0.4	9	0.3	13	0.1
Total herb and low shrub:	100	26.3	100	33.0	100	40.9	91	9.8	100	11.6	100	53.1

Table II-2. Constancy and average cover for vascular plant species in the plant communities of Watershed 3 during 1962. Only species with constancy > 20% in at least one community are included. Total constancy for vegetation layers includes all species and total cover is additive. See Vegetation section for community abbreviations. Con = constancy (%); Cov = average cover (%); T = trace cover (<0.1%).

Plant community	RHMA-GASH		ACCI-GASH		ACCI-BENE		COLA		POMU	
Number of plots	11		11		10		12		11	
	Con	Cov	Con	Cov	Con	Cov	Con	Cov	Con	Cov
Tree species										
Castanopsis chrysophylla	36	0.8	18	1.0	10	1.5	--	--	--	--
Pseudotsuga menziesii	--	--	9	0.1	--	--	25	0.3	9	0.1
Taxus brevifolia	18	1.3	18	10.5	10	0.5	25	1.0	--	--
Tsuga heterphylla	45	3.5	27	6.5	20	2.0	67	7.8	64	18.9
Total tree:	82	7.8	64	24.5	50	9.0	92	11.1	73	30.8
Tall shrub species										
Acer circinatum	45	18.2	64	22.7	100	35.5	8	0.4	45	9.3
Vaccinium parvifolium	45	2.6	36	1.0	10	5.0	25	1.4	27	3.7
Rhododendron macrophyllum	100	43.0	18	1.8	30	1.7	17	0.8	--	--
Total tall shrub:	100	63.8	64	25.5	100	42.2	42	2.7	64	14.7
Herb and low shrub species										
Achlys triphylla	27	0.3	18	T	--	--	8	T	9	T
Berberis nervosa	73	7.1	55	8.3	80	10.2	50	2.9	45	1.7
Chimaphila umbellata	36	0.5	18	0.6	20	T	25	T	--	--
Coptis laciniata	27	0.6	9	0.1	40	2.0	33	0.3	45	4.3
Galium triflorum	--	--	9	T	--	--	--	--	45	1.2
Gaultheria shallon	55	5.4	100	25.7	40	1.8	--	--	--	--
Linnaea borealis	64	1.3	64	3.1	10	0.3	25	2.2	36	1.8
Polystichum munitum	18	1.1	55	3.6	30	0.5	42	0.3	91	30.8
Pyrola asarifolia	27	0.5	--	--	10	0.1	--	--	--	--
Rubus nivalis	45	1.3	9	1.4	10	0.3	8	T	36	0.9
Rubus ursinus	9	0.1	55	1.4	10	T	8	0.1	45	0.7
Synthyris reniformis	--	--	27	0.3	--	--	8	0.1	--	--
Tiarella unifoliata	9	0.3	--	--	10	T	8	T	36	0.3
Trientalis latifolia	9	T	18	0.6	--	--	25	T	27	0.1
Trillium ovatum	--	--	18	0.1	10	0.1	8	T	27	0.2
Vancouveria hexandra	--	--	--	--	10	0.1	--	--	27	1.4
Xerophyllum tenax	--	--	27	1.8	--	--	--	--	--	--
Total herb and low shrub:	91	18.5	100	48.8	100	15.8	100	6.4	100	49.9

relatively dry growing conditions--along ridgetops, in other topographically exposed positions, and on mid-slope benches under fairly open tree canopies. It coincides with the *Tsuga heterophylla* / *Rhododendron macrophyllum* - *Gaultheria shallon* association of Hemstrom et al. (1985). The understory was characterized by a very dense, tall shrub layer of *Rhododendron macrophyllum* and *Acer circinatum*, with scattered individuals of *Vaccinium parvifolium*. *Castanopsis chrysophylla* exhibited its greatest abundance within this type and, together with *T. heterophylla*, comprised a major portion of the understory tree canopy. *Gaultheria shallon* and *Berberis nervosa* dominated a moderately dense herb and low shrub stratum. Additionally, *Linnaea borealis*, *Chimaphila umbellata*, and *Coptis laciniata* were occasional associates.

3. The *Acer circinatum* - *Gaultheria shallon* community (ACCI-GASH) was distributed primarily along mid- to upper-, south-facing slope positions under fairly open and young stands of *P. menziesii*. It can be equated with the *Tsuga heterophylla* / *Berberis nervosa* - *Gaultheria shallon* association of Hemstrom et al. (1985). *Acer circinatum* and *Gaultheria shallon* dominated dense tall shrub and herb layers, respectively. *Berberis nervosa* was a common associate while *Polystichum munitum* and *Linnaea borealis* were less important. The understory tree layer, although diverse, consisted of species with low constancy and canopy cover.

4. The *Acer circinatum* - *Berberis nervosa* community (ACCI-BENE) occupied moderately moist, fairly productive sites under forest stands of variable density. It belongs to the *Tsuga heterophylla* /

Berberis nervosa association of Hemstrom et al. (1985). Canopy cover of understory trees was fairly high and primarily composed of *Tsuga heterophylla* with minor amounts of *Taxus brevifolia*. *Acer circinatum* formed a dense, tall shrub layer over a rather depauperate herb stratum in which *Berberis nervosa* was the only species with > 50% constancy. Other rather infrequent herbs included *Coptis laciniata*, *Chimaphila umbellata*, *Linnaea borealis*, *Gaultheria shallon*, and *Polystichum munitum*.

5. The *Coptis laciniata* community (COLA) occupied site types similar to those of the *Acer circinatum* - *Berberis nervosa* community, but occurred under more shaded stands of *P. menziesii* and *T. heterophylla*. Thus, it probably represents a shade phase of the *Tsuga heterophylla* / *Berberis nervosa* association (Hemstrom et al. 1985). Cover of *T. heterophylla* was greater than in any other community, exceeding the combined cover of the poorly developed herb and tall shrub layers. Scattered *Vaccinium parvifolium* comprised a very sparse shrub layer and isolated individuals of *Berberis nervosa*, *Coptis laciniata*, and *Linnaea borealis* characterized a depauperate herb layer.

6. The *Polystichum munitum* community (POMU) was found on moist sites. It belongs to the *Tsuga heterophylla* / *Polystichum munitum* association of Hemstrom et al. (1985). It occupied the most productive sites--along bottom-slopes adjacent to drainages, on steep, north- and east-facing side-slopes, and in areas of seepage. Understory tree cover was abundant, primarily composed of *T. heterophylla* and *Thuja plicata*. Variable cover of *Acer circinatum*,

the only common shrub species, probably reflected differences in the density of the overstory tree canopy. *Polystichum munitum* dominated a lush, herb-rich understory. Other species diagnostic of these moist sites included *Vancouveria hexandra*, *Oxalis oregana*, *Galium* spp., and *Adiantum pedatum*. *Berberis nervosa*, *Coptis laciniata*, and *Linnaea borealis* were also common.

METHODS

Field Methods

Plot establishment

Permanently staked sample plots of 2 X 2 m were established along transects of both watersheds prior to logging (summer 1962). A total of 131 plots on 6 transects represented WS1 and 61 plots on 10 transects represented WS3. 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.

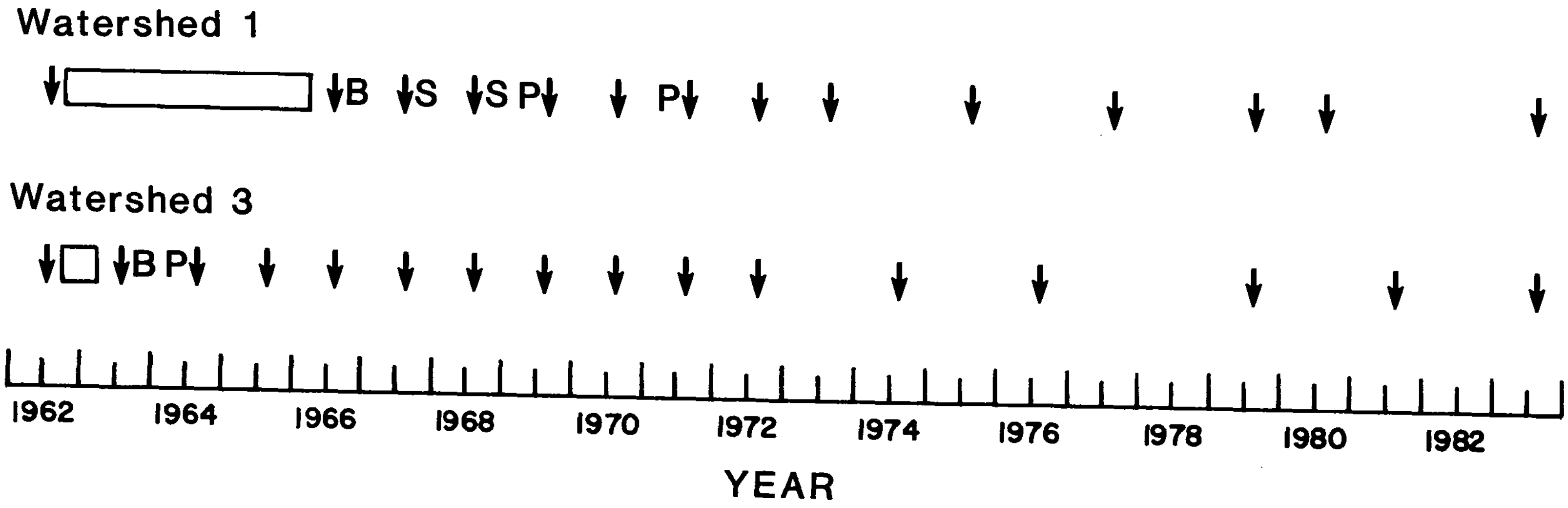
Plot classification and sampling schedule

To assess the influence of initial composition on vegetation development, each sample plot was assigned to one of the six understory plant communities within the initial classification (Tables II-1 and II-2). Nine plots that occurred in locally disturbed areas (e.g., slides or windthrow mounds) displayed rather unique species composition. These were not included in the community comparisons.

Spatial and temporal features of logging and burning disturbance, as well as methods of artificial regeneration, varied both between and within watersheds (Fig. II-2). The entire 96 ha of

Figure II-2. The history of disturbance and artificial regeneration on Watersheds 1 and 3. Arrows indicate sampling years. Open bars indicate periods of logging. B = slash burning. S = aerial seeding of *Pseudotsuga menziesii* (all of WS1 seeded in 1967, 10 ha in 1968). P = planting of *P. menziesii* (WS1: 1969 = entire watershed planted with 2 yr old trees; 1971 = 40 ha, 2 and 3 yr old trees. WS3: each clearcut unit, 3 yr old trees.)

Figure II-2.


Watershed 1
B
S
S
P
P
Watershed 3
B
P
1962
1964
1966
1968
1970
1972
1974
1976
1978
1980
1982
YEAR

WS1 was clearcut logged over a period of 4 yr (fall 1962 - summer 1966) using a skyline cable system. Slash was broadcast burned in October 1966. Pseudotsuga menziesii was aerially seeded at approximately 2.75 kg/ha in October 1967; an additional 5.5kg/ha was seeded on 10 ha in October 1968. Survival was poor, and in April and May 1969, 2 yr old P. menziesii were planted at a spacing of 3 X 3 m. Finally, in April 1971, 40 ha of the south-facing slope were replanted with 2 and 3 yr old P. menziesii spaced at 2.4 X 2.4 m. The specific areas encompassing the last three treatments are not known.

In contrast, on WS3, 3 stands of 5, 9, and 11 ha were clearcut logged during a single season (winter 1962 - 1963) using a high-lead cable system. Slash was burned in September 1963. All clearcut units were planted with 3 yr old P. menziesii between March and May 1964.

Plots were initially sampled during summer 1962, prior to logging. Following the completion of logging, plots were relocated or reestablished from field notes and resampled (WS1 in 1966 and WS3 in 1963). The watersheds were then broadcast burned and plots were relocated. To assess the influence of intensity of disturbance on vegetation development, each plot was subjectively assigned to one of four soil disturbance classes, based on the following classification (Tarrant 1956, Dyrness et al. 1957, Dyrness 1973):

1. Undisturbed. The soil surface appeared similar to that prior to disturbance, with minimal mixing of mineral soil and litter and with no evidence of fire.

2. Disturbed - Unburned. Disturbance from logging was evident. Although litter was removed or mixed with mineral soil, there was no evidence of fire.

3. Lightly burned. Surface litter was charred by fire, but was not completely removed.

4. Heavily burned. Surface litter was completely consumed by intense fire, exposing a highly colored mineral soil.

Plots were resampled the first growing season following slash burning (WS1 in 1967 and WS3 in 1964). Post-disturbance remeasurements were continued annually through 1973 on WS1 and through 1972 on WS3. Thereafter, sampling generally occurred during alternate years (Fig. II-2).

Sampling methods

A modified, nested quadrat design was used to assess the abundance of vascular plant species. One quarter of each 2 X 2 m plot was divided into nine subplots (0.33 m on a side). Within each subplot visual estimates of projected canopy cover were made for herb and low shrub species (defined below) and for soil surface conditions (bare, stone, litter, and moss). An average cover value was then calculated for each species and soil surface condition within each plot. Herb and low shrub species absent from the subplots but present within the full plot were assigned trace canopy cover (0.1%). The sampling area was increased to that of the full plot in 1979 and 1980; subplots were sampled concurrently and the larger plots were deemed suitable for comparison.

Within the full plot, projected canopy cover was estimated for each species of tall shrub or tree (defined below) and for logs (> 0.1 m diameter) and stumps. Foliar cover at a height > 6 m was not estimated. For all species, cover values from 0-10% were estimated to the nearest integer, while cover > 10% was estimated to the nearest 5% class. Vascular plant taxonomy and nomenclature follow Hitchcock and Cronquist (1973).

Data Reduction and Analysis

To trace the structural development, as well as the origin of the seral vegetation, vascular plant species were assigned to understory strata (or growth-form classes) and to successional status groups (groups of residual or invading species).

Understory strata

Each vascular plant species was assigned to one of three understory strata--herb and low shrub, tall shrub, or tree--based on its growth-form and potential height at maturity (see Table II-3 in Results). All herbaceous species, ferns, and graminoids, as well as woody shrubs typically < 0.6 m at maturity (e.g., *Berberis nervosa* and *Gaultheria shallon*), were grouped in the herb and low shrub layer (which we herein refer to as the herb layer). Woody species > 0.6 m at maturity, but typically absent from the mature forest canopy, were grouped as tall shrubs. Woody species that characterized the original forest canopy were classed as trees. Although *Castanopsis chrysophylla* and *Cornus nuttallii* often exhibited a multiple-based, shrub-like morphology following disturbance, they potentially represent sub-canopy trees and thus, were assigned to the tree layer.

Successional status groups

To assess the origin of vegetation in each understory stratum, vascular plant species were assigned to one of two post-disturbance categories, invader or residual. Invaders were defined as species absent from undisturbed forest communities (although they may have persisted in seed banks) or occurring only on locally disturbed microsites such as windthrow mounds (e.g., *Epilobium angustifolium* and *Rubus parviflorus*). Residuals were defined as species that, regardless of their abundance, characteristically occurred in undisturbed forest communities.

For each plot during each sampling year we summed the canopy cover for all species 1) in each understory stratum and 2) in each successional status group within each stratum. The totals may exceed 100% as they represent the additive canopy cover of species.

We used this measure rather than an on-site estimate of total cover because it is more sensitive to the overlap of species canopies and more closely reflects changes in abundance.

The computer programs CONDENSE and DATAEDIT of the Cornell Ecology Program Series (Gauch 1973, Gauch and Singer 1982) and additional software developed at Oregon State University (B. G. Smith unpublished programs) were used for summarizing data. Because the timing of logging and slash burning differed between watersheds, we use a standardized time axis to compare temporal changes. Thus, in Figures II-3 to II-12 the abscissa expresses the time since disturbance. Times "-4" and "-1" represent the pre-disturbance samples for WS1 and WS3, respectively; for both sites, times "0" and "1" represent the growing seasons following completion of logging and slash burning, respectively. Changes in abundance are expressed as absolute percent cover.

RESULTS

Overall Watershed Patterns

Floristic changes

A diverse vascular flora characterized Watersheds 1 and 3 during the period from 1962 to 1983 (Table II-3). A total of 188 species represented 52 families and 141 genera on WS1; 130 species represented 43 families and 99 genera on WS3. On both sites the five families with the greatest number of genera and species were, in decreasing order, the Compositae, Gramineae, Rosaceae, Ericaceae, and Polypodiaceae. However, the diversity of a family had little relation to its overall abundance during the sere, as dominance was concentrated within relatively few species representing families relatively poor in taxa.

A majority of forest species persisted through disturbance. Of an initial 83 species on WS1, 92% were present following logging and 82% following burning. Thereafter, with the exception of year 11 (in which 82% were present), the proportion of original species ranged from 87 to 92%. Six species were comletely lost from the sample plots on WS1--2 each during the initial post-logging and burning years and 1 each in years 2 and 4. These included *Pyrola asarifolia*, *P. picta*, *Chimaphila umbellata*, *Corallorhiza menziesii*, *Listera cordata*, and *Pinus lambertiana*.

On WS3, of an initial 48 species, 71% were present following

Table II-3. Characteristics of the vascular plant species on Watersheds 1 and 3. Species with two or more occurrences are included. Successional status: I = invader, R = residual. Stratum: H = herb and low shrub, S = tall shrub, T = tree. Life history (herbs only): ann = annual, bien = biennial, per = perennial. (Parentheses indicate less common life history.) Description: Growth form (herbs only): herb = herbaceous, sub = sub-shrub, low = low shrub. Habit: caesp = caespitose, decumb = decumbent, stolon = stoloniferous, suffr = suffrutescent, trail = trailing. Root morphology (where known): bulb = bulbous, caud = caudex, fibr = fibrous-rooted, rhiz = rhizomatous, rstock = rootstock, tap = taproot, tub = tuberous. (Other terms describing habit and root morphology are not abbreviated.) Phenology: ever = evergreen or persistent. (Assumed deciduous unless given.) Life history and descriptive information from Hitchcock et al. (1969).

FAMILY Species	Succ. Status	Stratum	Life History	Description
ACERACEAE				
Acer circinatum	R	S		layering
A. macrophyllum	R	T		
A. glabrum	I	S		
ANACARDIACEAE				
Rhus diversiloba	R	S		
APOCYNACEAE				
Apocynum androsaemifolium	I	H	per	herb, rhiz
ARALIACEAE				
Aralia californica	I	H	per	herb
ARISTOLOCHIACEAE				
Asarum caudatum	R	H	per	herb, extensive rstock, ever
BERBERIDACEAE				
Achlys triphylla	R	H	per	herb, rhiz
Berberis nervosa	R	H	per	low, rhiz
Vancouveria hexandra	R	H	per	herb, rhiz
BETULACEAE				
Alnus rubra	R	T		
Corylus cornuta	R	S		
CAMPANULACEAE				
Campanula scouleri	H	I	per	herb, tap (caud)
CAPRIFOLIACEAE				
Linnaea borealis	R	H	per	sub, trail, ever
Lonicera ciliosa	I	H	per	low, twining
Sambucus cerulea	I	S		
Symphoricarpos mollis	I	H	per	sub, trail
CARYOPHYLLACEAE				
Arenaria macrophylla	I	H	per	herb, slender rhiz
Cerastium arvense	I	H	per	herb, trail, caesp
C. viscosum	I	H	ann	herb, decumb
C. vulgatum	I	H	bien, per	herb, decumb

Table II-3. (Continued).

FAMILY Species	Succ. Status	Stratum	Life History	Description
CELASTRACEAE				
Pachistima myrsinites	I	H	per	lov, ever
COMPOSITAE				
Adenocaulon bicolor	R	H	per	herb, fibr
Agoseris aurantiaca	I	H	per	herb, tap
A. grandiflora	I	H	per	herb, tap
A. heterophylla	I	H	ann	herb
Anaphalis margaritacea	I	H	per	herb, rhiz
Arnica discoidea	R	H	per	herb, rhiz
Chrysanthemum leucanthemum	I	H	per	herb, rhiz
Cirsium arvense	I	H	per	herb; deep-seated, creeping roots
C. brevistylum	I	H	per	herb, tap
C. vulgare	I	H	bien	herb
Conyza canadensis	I	H	ann	herb
Crepis capillaris	I	H	ann (bien)	herb
Gnaphalium microcephalum	I	H	per	herb, tap
Hieracium albiflorum	R	H	per	herb, caud, fibr
Hypochaeris radicata	I	H	per	herb, caud, fibr
Lactuca biennis	I	H	ann (bien)	herb
L. muralis	I	H	ann, bien	herb
L. serriola	I	H	bien (ann)	herb
Madia gracilis	I	H	ann	herb
M. madioides	I	H	bien (per)	herb, rhiz
Petasites frigidus	I	H	per	herb, rhiz
Senecio jacobea	I	H	bien (per)	herb, tap
S. sylvaticus	I	H	ann	herb, tap
Sonchus asper	I	H	ann	herb, tap
Tragopogon dubius	I	H	bien (ann)	herb
CONVOLVULACEAE				
Convolvulus nyctagineus	I	H	per	herb, slender rstock
CORNACEAE				
Cornus nuttallii	R	T		
CRASSULACEAE				
Sedum oreganum	I	H	per	herb, rhiz
CRUCIFERAE				
Cardamine oligosperma	I	H	ann, bien	herb, tap
C. pulcherrima	I	H	per	herb, short slender rhiz
CUPRESSACEAE				
Thuja plicata	R	T		ever
CYPERACEAE				
Carex deweyana	I	H	per	herb, fibr
C. rossii	I	H	per	herb, fibr

Table II-3. (Continued).

FAMILY Species	Succ. Status	Stratum	Life History	Description
ERICACEAE				
Arbutus menziesii	I	T		ever
Arctostaphylos columbiana	I	S		ever
Chimaphila menziesii	R	H	per	sub, ever
C. umbellata	R	H	per	sub, ever
Gaultheria shallon	R	H	per	low, ever
Pyrola asarifolia	R	H	per	herb, rhiz, ever
P. secunda	R	H	per	herb, rhiz, ever
P. picta	R	H	per	herb, rhiz, ever
Rhododendron macrophyllum	R	S		ever
Vaccinium membranaceum	R	S		
V. parvifolium	R	S		
EQUISETACEAE				
Equisetum arvense	I	H	per	herb, rhiz
E. telmateia	I	H	per	herb, rhiz
FAGACEAE				
Castanopsis chrysophylla	R	T		ever
FUMARIACEAE				
Dicentra formosa	I	H	per	herb, slender rhiz
GRAMINEAE				
Agrostis alba	I	H	per	herb, rhiz
A. diegoensis	I	H	per	herb, tufted, rhiz
A. exarata	I	H	per	herb, tufted, rhiz
Aira caryophyllea	I	H	ann	herb
Bromus ciliatus	I	H	per	herb, fibr
B. sitchensis	I	H	per	herb, fibr
B. vulgaris	R	H	per	herb, fibr
Deschampsia elongata	I	H	per	herb, caesp
Elymus glaucus	I	H	per	herb, caesp
Festuca myuros	I	H	ann	herb
F. occidentalis	R	H	per	herb, caesp
F. subulata	I	H	per	herb, caesp
Holcus lanatus	I	H	per	herb, caesp
Lolium perenne	I	H	per	herb, tufted, fibr
Melica harfordii	I	H	per	herb, caesp
M. subulata	I	H	per	herb, caesp
Stipa occidentalis	I	H	per	herb, tufted, fibr
Trisetum canescens	I	H	per	herb, caesp
GROSSULARIACEAE				
Ribes sanguineum	I	S		
R. lacustre	I	S		
R. lobbii	I	S		
HYDRANGEACEAE				
Whipplea modesta	R	H	per	sub, trail, ever (dec)
HYDROPHYLLACEAE				
Nemophila parviflora	I	H	ann	herb, tap
Phacelia heterophylla	I	H	bien, per	herb, tap

Table II-3. (Continued).

FAMILY Species	Succ. Status	Stratum	Life History	Description
HYPERICACEAE				
Hypericum perforatum	I	H	per	
IRIDACEAE				
Iris chrysophylla	I	H	per	herb, slender rhiz
I. tenax	I	H	per	herb, slender rhiz
JUNCACEAE				
Juncus spp.	I	H	-	-
Luzula campestris	I	H	per	herb, caesp
L. parviflora	I	H	per	herb, caesp
LABIATAE				
Stachys cooleyae	I	H	per	herb, rhiz
LEGUMINOSAE				
Lathyrus polyphyllus	I	H	per	herb, rhiz
Lotus crassifolius	I	H	per	herb, rhiz
L. micranthus	I	H	ann	herb
L. purshianus	I	H	ann	herb
Lupinus latifolius	I	H	per	herb
Trifolium microcephalum	I	H	ann	herb
Vicia americana	I	H	per	herb, trail
LILIACEAE				
Brodiaea congesta	I	H	per	herb, corm
Clintonia uniflora	R	H	per	herb, rhiz
Disporum hookeri	R	H	per	herb, rhiz
D. smithii	R	H	per	herb, rhiz
Lilium washingtonianum	R	H	per	herb, bulb, semi-rhiz
Smilacina racemosa	R	H	per	herb, rhiz
S. stellata	R	H	per	herb, rhiz
Trillium ovatum	R	H	per	herb, short rhiz
Xerophyllum tenax	R	H	per	herb, short rhiz
ONAGRACEAE				
Circaea alpina	R	H	per	herb, slender rstock
Epilobium angustifolium	I	H	per	herb, rhiz
E. minutum	I	H	ann	herb
E. paniculatum	I	H	ann	herb
E. watsonii	I	H	per	herb, short rstock
ORCHIDACEAE				
Corallorhiza mertensiana	R	H	per	herb, rhiz
Goodyera oblongifolia	R	H	per	herb, short rhiz
Habenaria unalascensis	I	H	per	herb, tuber
Listera cordata	R	H	per	herb, rhiz
OXALIDACEAE				
Oxalis oregana	R	H	per	herb, rhiz

Table II-3. (Continued).

FAMILY Species	Succ. Status	Stratum	Life History	Description
PINACEAE				
Pinus lambertiana	R	T		ever
Pseudotsuga menziesii	R	T		ever
Tsuga heterophylla	R	T		ever
POLEMONIACEAE				
Collomia heterophylla	I	H	ann	herb
Gilia capitata	I	H	ann	herb
Phlox adsurgens	I	H	per	herb, tap
POLYPODIACEAE				
Adiantum pedatum	R	H	per	herb, rhiz
Athyrium filix-femina	R	H	per	herb, short rhiz
Blechnum spicant	R	H	per	herb, short rhiz, ever
Cystopteris fragilis	I	H	per	herb, short rhiz
Polystichum munitum	R	H	per	herb, short rhiz, ever
Pteridium aquilinum	I	H	per	herb; deep-seated, elongate rhiz
PORTULACACEAE				
Montia parvifolia	I	H	per	herb, slender rstock
M. perfoliata	I	H	ann	herb, tap
M. sibirica	I	H	ann	herb, tap
PRIMULACEAE				
Trientalis latifolia	R	H	per	herb, short tub
RANUNCULACEAE				
Actaea rubra	R	H	per	herb; short, branching rstock
Anemone deltoidea	R	H	per	herb, slender rhiz
A. lyallii	R	H	per	herb, slender rhiz
Coptis laciniata	R	H	per	herb, slender rhiz, ever
Ranunculus uncinatus	I	H	ann, per	herb, fibr
RHAMNACEAE				
Ceanothus integerrimus	I	S		
C. sanguineus	I	S		
C. velutinus	I	S		ever
Rhamnus purshiana	R	T		
ROSACEAE				
Amelanchier alnifolia	I	S		
Aruncus sylvester	I	H	per	herb, rhiz
Fragaria vesca	I	H	per	herb, stolon
Holodiscus discolor	R	S		
Oemleria cerasiformis	I	S		
Potentilla glandulosa	I	H	per	herb, rstock
Prunus emarginata	I	T		
Rosa gymnocarpa	R	S		
Rubus leucodermis	I	S		
R. nivalis	R	H	per	sub, trail, ever
R. parviflorus	I	S		
R. ursinus	R	H	per	sub, trail

Table II-3. (Continued).

FAMILY Species	Succ. Status	Stratum	Life History	Description
RUBIACEAE				
Galium aparine	I	H	ann	herb
G. oreganum	R	H	per	herb, creeping rhiz
G. triflorum	R	H	per	herb, creeping rhiz
SALICACEAE				
Populus trichocarpa	I	T		
Salix sitchensis	I	S		
S. scouleriana	I	S		
SAXIFRAGACEAE				
Boykinia elata	I	H	per	herb, rstock
Heuchera micrantha	I	H	per	herb, rstock
Mitella ovalis	I	H	per	herb, rhiz
Saxifraga occidentalis	I	H	per	herb, short rhiz
Tiarella unifoliata	R	H	per	herb, rhiz
Tellima grandiflorum	I	H	per	herb, rstock
SCROPHULARIACEAE				
Castilleja hispida	I	H	per	herb, suffr
Mimulus alsinoides	I	H	ann	herb
M. guttatus	I	H	per	herb, stolon
Synthyris reniformis	R	H	per	herb, rhiz, caud
SELAGINELLACEAE				
Selaginella wallacei	I	H	per	herb, matted, ever
TAXACEAE				
Taxus brevifolia	R	T		ever
UMBELLIFERAE				
Osmorhiza chilensis	I	H	per	herb, tap (caud)
VALERIANACEAE				
Valeriana scouleri	I	H	per	herb, rhiz (caud), fibr
VIOLACEAE				
Viola glabella	I	H	per	herb, rstock
V. sempervirens	R	H	per	herb, rhiz, stolon

logging and burning. Thereafter, the proportion increased continuously to 90%. Two species were completely lost from the sample plots on WS3--Clintonia uniflora disappeared following logging and Disporum smithii, following burning.

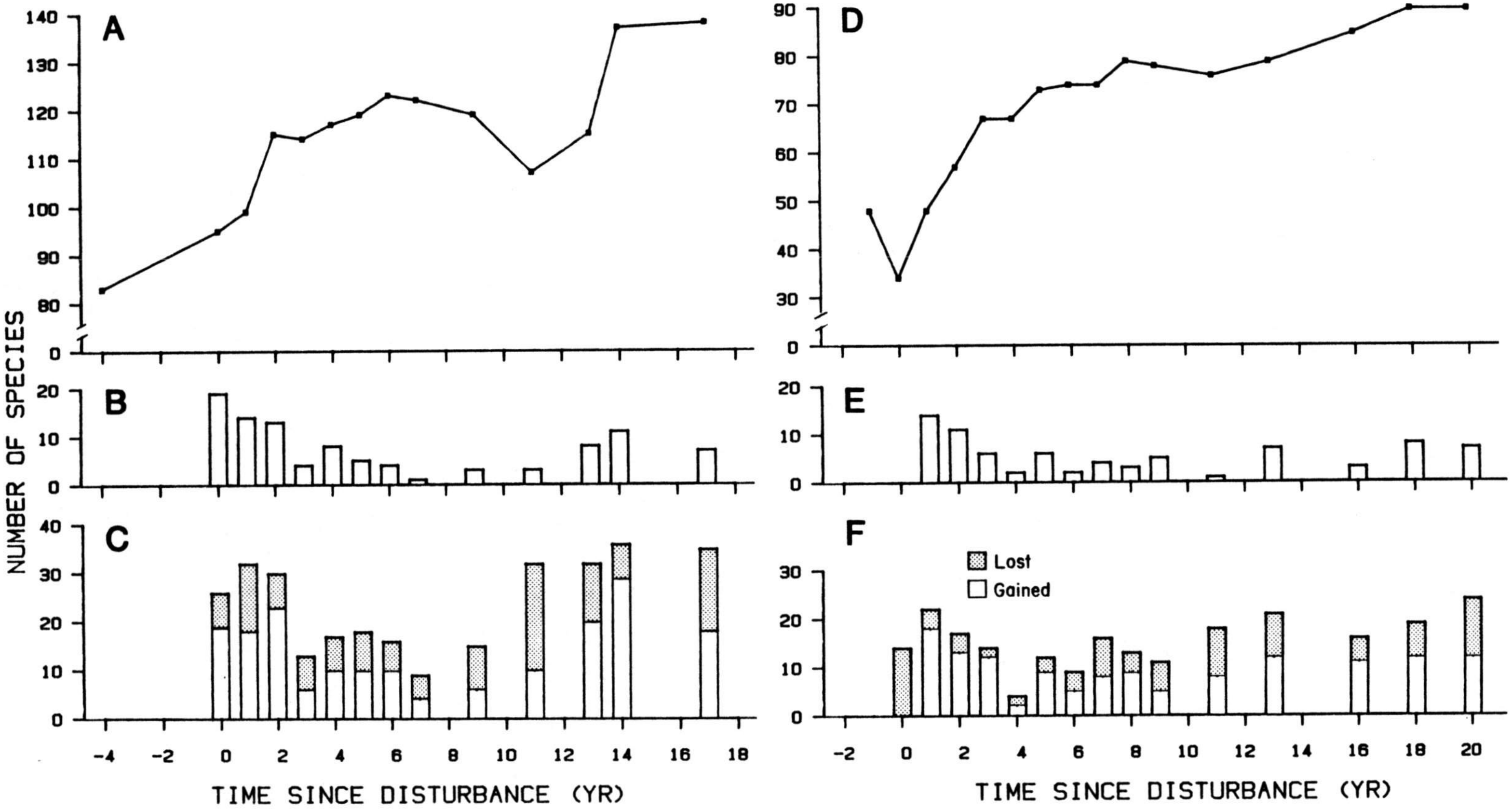
The total number of species increased with time in both seres (Figs. II-3A and D). From year to year, however, species were gained or lost. (In this analysis, the loss of a species in one growing season does not imply its absence in subsequent years.) On WS1, species richness increased from 83 in the initial forest to 138 at final sampling (Fig. II-3A). Species present for the first time (11-20% of the flora) were particularly common following logging and for 2 growing seasons following slash burning (Fig. II-3B). The greatest annual loss of species on WS1 (15-16% of the flora) occurred in years 1 (following burning) and 11 (Fig. II-3C).

On WS3, species richness increased from 48 in the initial forest to 90 at final sampling (Fig. II-3D). Despite a loss of 14 species following logging, richness subsequently increased rapidly to 67 in year 3, then more gradually through year 20. Species present for the first time (19-29% of the flora) were most common for 2 yr following burning (Fig. II-3E). Annual loss of species on WS3 was greatest following logging (29% of the flora) and was moderately high during years 1, 11, 13, and 20 (12-13% of the flora) (Fig. II-3F). Although the number of new species establishing after year 2 on both watersheds represented from 1-9% of the flora (Fig. II-3B and E), they were rare.

We estimated annual species turnover (Figs. II-3C and F) as the

Figure II-3. Floristic changes with time on Watersheds 1 and 3. **A)** Species richness on WS1. **B)** Number of species present for the first time on WS1. **C)** Annual species turnover on WS1, comprised of the number of species gained and lost between growing seasons. **D)** Species richness on WS3. **E)** Number of species present for the first time on WS3. **F)** Annual species turnover on WS3, comprised of the number of species gained and lost between growing seasons.

Figure II-3.


A
B
C
D
E
F
NUMBER OF SPECIES
140
130
120
110
100
90
80
0
20
10
0
40
30
20
10
0
90
80
70
60
50
40
30
0
20
10
0
30
20
10
0
▨ Lost
☐ Gained
-4
-2
0
2
4
6
8
10
12
14
16
18
-2
0
2
4
6
8
10
12
14
16
18
20
TIME SINCE DISTURBANCE (YR)
TIME SINCE DISTURBANCE (YR)

sum of the number of species lost and gained between growing seasons. Annual turnover was greatest during years 0-2, representing 19-34% and 29-65% of the flora on WS1 (Fig. II-3C) and WS3 (Fig. II-3F), respectively. Although annual turnover ranged from 5-28% during the remainder of the seres it was attributed principally to uncommon species.

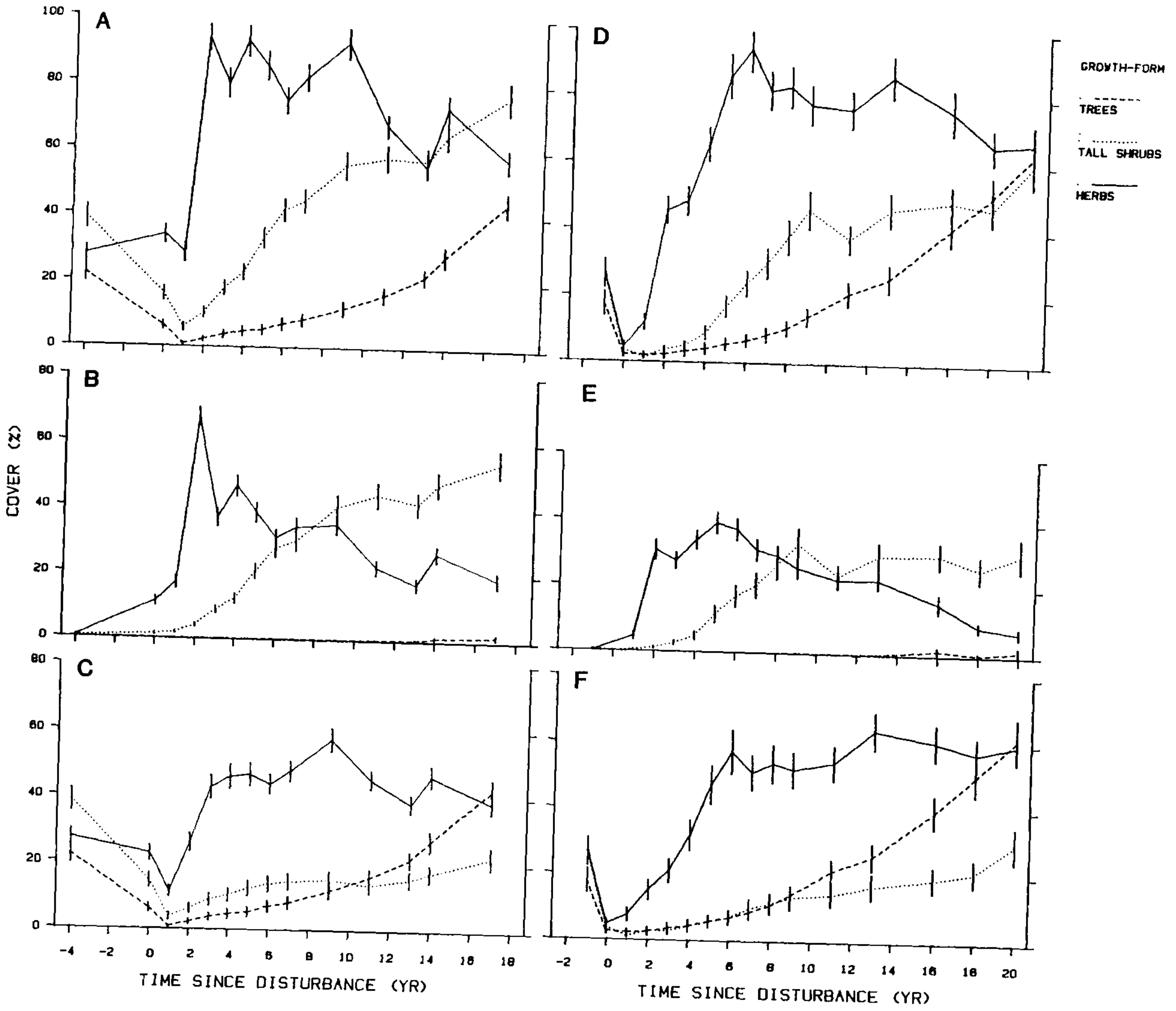
Physiognomic changes

Gradual shifts in structure characterized vegetation changes on Watersheds 1 and 3. On WS1, herbs and low shrubs were the dominant growth-form for 9 yr following logging (Fig. II-4A). Thereafter, tall shrubs were co-dominant. Although consistently sub-dominant, trees displayed increasing abundance with time. On WS3, herbs and low shrubs dominated through the entire sere (Fig. II-4D). Tall shrubs and trees attained co-dominance within 18-20 yr.

Herb and low shrub stratum. The immediate effects of logging and slash burning on the herb and low shrub layer differed between watersheds. On WS1, total herb and low shrub cover (Fig. II-4A) remained unchanged following staggered logging, due to an increase of invading herbs (Fig. II-4B) with a concomitant decrease in residuals (Fig. II-4C). During this period the principal colonizing herb was the perennial, _Epilobium angustifolium_. Although the cover of initial dominants (e.g., _Berberis nervosa_, _Gaultheria shallon_, and _Polystichum munitum_) declined, the cover of subordinate sub-

Figure II-4. Changes in additive canopy cover with time for the three principal vegetation strata of Watersheds 1 and 3. **A)** Total cover on WS1. **B)** Invading species groups on WS1. **C)** Residual species groups on WS1. **D)** Total cover on WS3. **E)** Invading species groups on WS3. **F)** Residual species groups on WS3. Herbs includes herbs and low shrubs. Vertical bars represent ± 1 SE.

Figure II-4.


A
B
C
D
E
F
100
80
60
40
20
0
COVER (%)
-4 -2 0 2 4 6 8 10 12 14 16 18
TIME SINCE DISTURBANCE (YR)
-2 0 2 4 6 8 10 12 14 16 18 20
TIME SINCE DISTURBANCE (YR)
GROWTH-FORM
TREES
TALL SHRUBS
HERBS

shrubs (e.g., *Rubus ursinus*) increased. In contrast, on WS3, single season logging greatly reduced total herb and low shrub cover (Fig. II-4D). Invasion was minimal (Fig. II-4E) and residuals were greatly reduced (Fig. II-4F).

Post-burning total herb cover dramatically increased on both watersheds. Within two growing seasons after burning, total cover peaked at 93% on WS1 (Fig. II-4A). The greater than three-fold increase in the abundance of invading herbs (Fig. II-4B), reflected rapid, widespread establishment of winter annuals, (e.g., *Epilobium paniculatum* and *Senecio sylvaticus*). Residual herb abundance was low by comparison, although it equaled that of the pre-disturbance watershed average (Fig. II-4C). On WS3, total herb and low shrub cover increased more slowly, peaking at 94% in year 6 (Fig. II-4D). During this period invading herbs peaked in year 4 (Fig. II-4E) and residuals in year 6 (Fig. II-4F). Principal colonizers included annuals, (e.g., *Senecio sylvaticus* and *Epilobium paniculatum*), although the perennial, *E. angustifolium*, was equally abundant. *Rubus ursinus* was the dominant residual; other trailing sub-shrubs (e.g., *Linnaea borealis* and *Whipplea modesta*) and tuberous herbs (e.g., *Trientalis latifolia*) also increased.

Subsequent to peak cover on WS1, herb layer changes were characterized by two dynamic stages, 2-9 and 9-17 yr after burning. Total cover fluctuated between 75 and 93% during the first stage, but declined to 39% in the latter (Fig. II-4A). The abundance of invading herbs declined through both periods (Fig. II-4B), initiated by a precipitous loss of annuals between years 2 and 3. The abundance of residual herbs increased during the first period, reflecting the release of *Rubus ursinus*, *Trientalis latifolia*, and *Whipplea modesta* (Fig. II-4C). During the second period residuals also declined, as the loss in cover of *Trientalis latifolia* and *Whipplea modesta* exceeded the gain in initial community dominants.

On WS3, patterns of total herb abundance similar to those on WS1, characterized the period following peak cover (Fig. II-4D). Invading herbs gradually declined (Fig. II-4E); annual colonizers were largely eliminated, and although *E. angustifolium* persisted, its cover was greatly reduced. Residuals slightly increased with time (Fig. II-4F). *Rubus ursinus* was persistent, and while *Whipplea modesta* and *Trientalis latifolia* gradually declined, initial dominants (e.g., *Berberis nervosa*, *Gaultheria shallon*, and *Polystichum munitum*) slowly recovered to their initial abundance.

Tall shrub stratum. The effect of disturbance on the tall shrub layer greatly altered understory structure on both watersheds. On WS1, total tall shrub cover declined from 39 to 16% following logging and to 6% following slash burning (Fig. II-4A). Similarly, on WS3, cover declined from 27 to 4% following logging and to 1% following burning (Fig. II-4D). *Acer circinatum* and *Rhododendron macrophyllum* were greatly reduced on both sites.

Subsequent post-disturbance recovery of the tall shrub stratum differed between sites. On WS1, development was rapid, as total cover increased to 42% by year 6 and to 77% by year 17. Invading shrubs (e.g., *Ceanothus sanguineus* and *C. velutinus*) established early and expanded rapidly (Fig. II-4B), whereas residuals recovered slowly (Fig. II-4C). Although the cover of both groups was similar through year 4, invaders were subsequently 2-3 times as abundant as residuals. In contrast, on WS3, two phases of development character the post-disturbance period (Fig. II-4D). During an initial period of 9 yr, cover increased rapidly, reflecting the expansion of the principal invader, Ceanothus velutinus (Fig. II-4E). During the period between years 10 and 20 the cover of invading shrubs remained fairly constant, while that of residuals slowly increased to pre-disturbance levels (Fig. II-4F). Although C. velutinus declined during this period, other invaders (e.g., Rubus parviflorus and Salix scouleriana) increased. The canopies of residual forest shrubs (Acer circinatum and Rhododendron macrophyllum) completely recovered.

Tree stratum. The understory tree layer, like the tall shrub layer (< 6m tall) was severely reduced by disturbance on both sites. On WS1, total tree cover declined from 22 to 6% following logging and to 1% following slash burning (Fig. II-4A). On WS3, cover declined from 18 to 2% following logging, with no additional change following burning (Fig. II-4D). Following disturbance, a parallel accelerating rate of increase in tree cover occurred on both sites. Total understory tree cover surpassed initial cover 10-13 yr following burning, reaching 43% on WS1 and 63% on WS3 at final sampling (years 17 and 20, respectively). This increase was entirely due to the residual tree group (Figs. II-4C and F), primarily Pseudotsuga menziesii and Tsuga heterophylla. An unknown portion of tree regeneration, however, represented planted individuals or those established from artificial seeding. In contrast, cover of invading trees (e.g., Populus trichocarpa and Prunus emarginata) was insignificant (Figs. II-4B and E).

Patterns Among Plant Communities

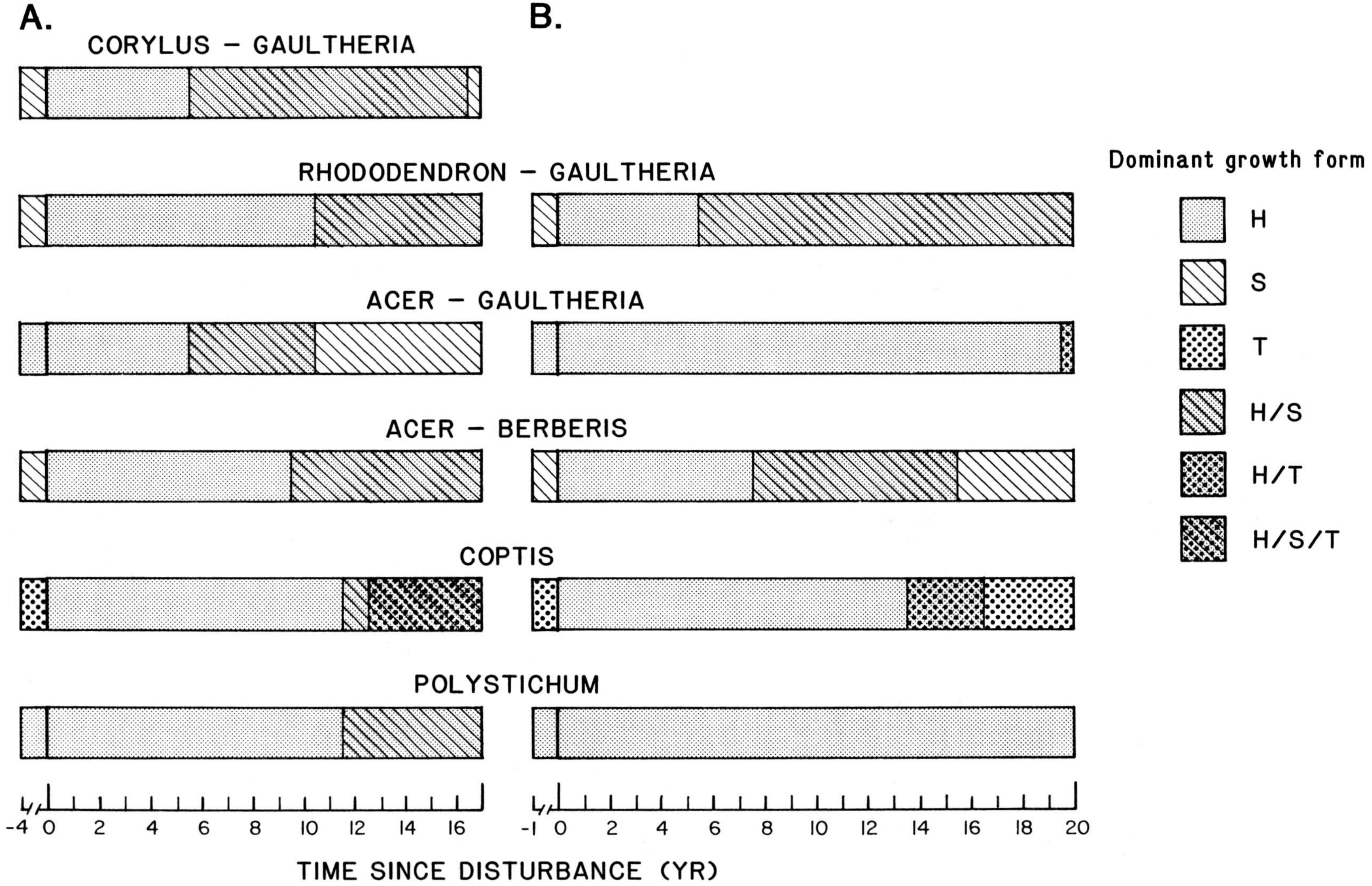
Structural changes in vegetation varied among the understory community types on Watersheds 1 and 3. To illustrate this variation we compare 1) the patterns of transition among the growth-form dominants and 2) the origin and development of each understory stratum, based mainly on the principal species determining the community patterns. A growth-form was considered co-dominant if its cover was 75% that of the dominant growth-form. In the following descriptions we commonly refer to herbs and low shrubs simply as herbs, to tall shrubs as shrubs.

Growth-form phases

A gradual transition between dominant growth-forms occurred in most communities (Fig. II-5). On WS1, most communities exhibited a 5-11 yr period of herb dominance followed by a period of herb and tall shrub co-dominance through final sampling (Fig. II-5A). In two communities, however, phase changes were more rapid. First, in the Acer - Gaultheria community, tall shrubs dominated within 10 yr,

Figure II-5. Changes in the dominant growth-form with time for the plant communities of Watersheds 1 and 3. **A)** WS1, **B)** WS3. A growth-form was considered co-dominant if its cover was 75% that of the dominant growth-form. Dominant growth-form codes: H = herbs and low shrubs, S = tall shrubs, T = trees.

Figure II-5.


A.
B.
CORYLUS – GAULTHERIA
RHODODENDRON – GAULTHERIA
ACER – GAULTHERIA
ACER – BERBERIS
COPTIS
POLYSTICHUM
Dominant growth form
H
S
T
H/S
H/T
H/S/T
-4
0
2
4
6
8
10
12
14
16
-1
0
2
4
6
8
10
12
14
16
18
20
TIME SINCE DISTURBANCE (YR)

corresponding with the rapid expansion of invading species (e.g., *Ceanothus sanguineus* and *C. velutinus*). Second, in the *Coptis* community, a brief transitional herb-shrub stage was followed by co-dominance of herbs, shrubs, and trees (year 12). This reflected poor recovery of residual shrubs and rapid growth of trees (e.g., *Pseudotsuga menziesii* and *Tsuga heterophylla*).

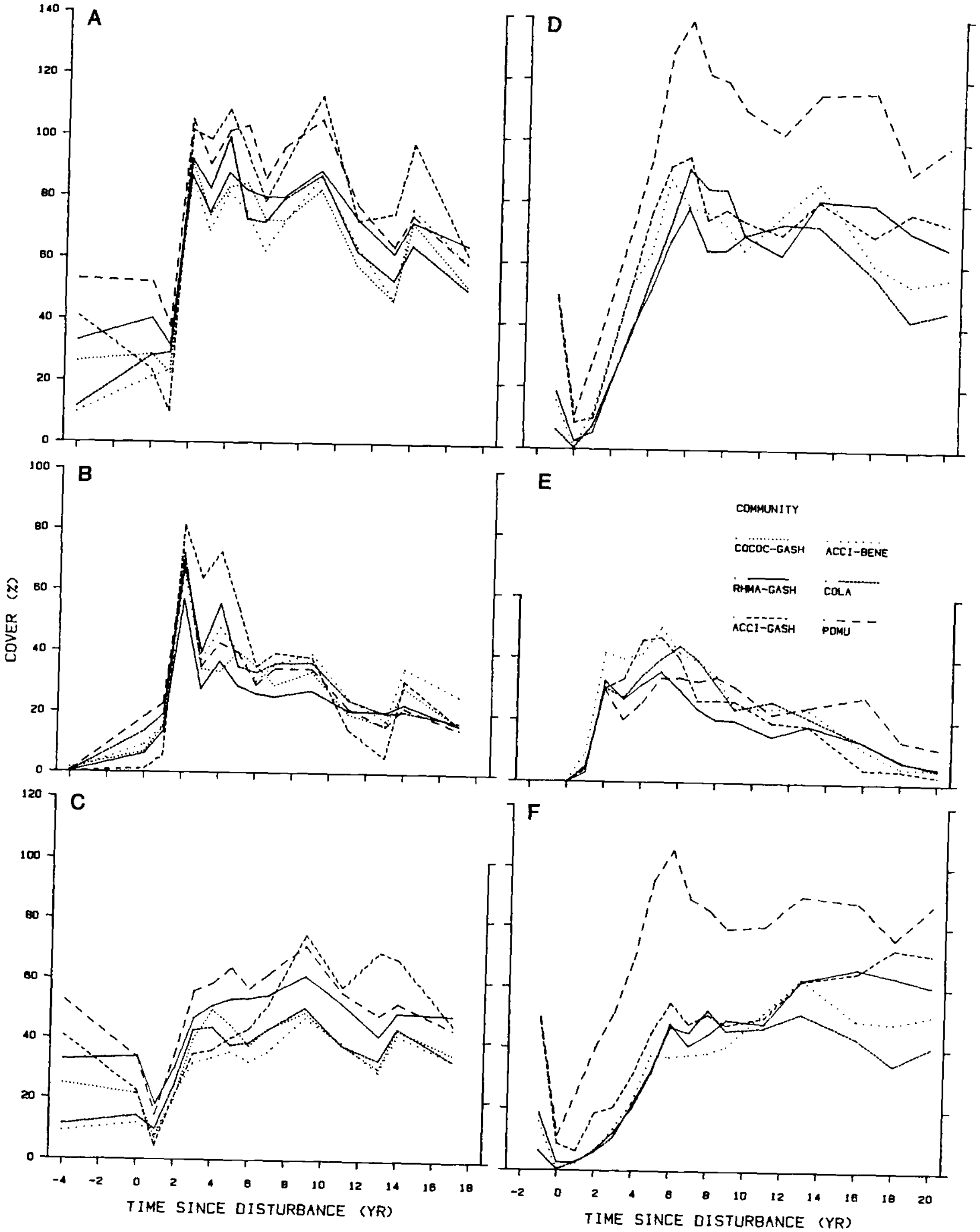
On WS3, three patterns of transition among growth-forms were evident, corresponding with initial community structure (Fig. II-5B). First, in initially herb-dominated communities (*Acer* - *Gaultheria* and *Polystichum*), the herb layer was dominant for the entire sere. Second, in tall shrub-dominated communities (*Rhododendron* - *Gaultheria* and *Acer* - *Berberis*), an herb phase of 6-7 yr was succeeded by a period of herb and tall shrub co-dominance. Additionally, within the *Acer* - *Berberis* community, tall shrubs dominated after 16 yr. Finally, in the depauperate *Coptis* community, an herb phase of 13 yr was replaced by a rapidly developing tree stratum.

Herb and low shrub stratum

The initial response of the herb layer to disturbance differed among the communities of WS1. Three types of response to logging were evident. First, in four communities--*Corylus* - *Gaultheria*, *Rhododendron* - *Gaultheria*, *Acer* - *Berberis*, and *Coptis*--total herb cover increased following logging (Fig. II-6A). Cover of invaders

Figure II-6. Changes in additive canopy cover with time in the herb stratum for the plant communities of Watersheds 1 and 3. **A)** Total herbs and low shrubs on WS1. **B)** Invading herbs and low shrubs on WS1. **C)** Residual herbs and low shrubs on WS1. **D)** Total herbs and low shrubs on WS3. **E)** Invading herbs and low shrubs on WS3. **F)** Residual herbs and low shrubs on WS3. Community abbreviations: COCO-GASH = *Corylus-Gaultheria*, RHMA-GASH = *Rhododendron-Gaultheria*, ACCI-GASH = *Acer-Gaultheria*, ACCI-BENE = *Acer-Berberis*, COLA = *Coptis*, POMU = *Polystichum*.

Figure II-6.


A
B
C
D
E
F
COVER (%)
TIME SINCE DISTURBANCE (YR)
TIME SINCE DISTURBANCE (YR)
140
120
100
80
60
40
20
0
100
80
60
40
20
0
120
100
80
60
40
20
0
-4
-2
0
2
4
6
8
10
12
14
16
18
-2
0
2
4
6
8
10
12
14
16
18
20
COMMUNITY
COCOC-GASH
ACCI-BENE
RHMA-GASH
COLA
ACCI-GASH
POMU

increased by 5-13% (Fig. II-6B), but net changes in the abundance of residual herbs were small (Fig. II-6C). Two native species of *Epilobium* were the principal colonizers, the perennial *E. angustifolium* and the annual *E. paniculatum*. Second, in the mesic *Acer* - *Gaultheria* community, total herb cover declined following logging, reflecting loss of residual cover of 20% (primarily of the dominant low shrub, *Gaultheria shallon*) (Fig. II-6C). Third, in the moist *Polystichum* community, total herb cover remained unchanged. Cover of residual herbs (primarily the dominant evergreen fern, *Polystichum munitum*) declined by 20% (Fig. II-6C), but invaders (e.g., *Epilobium paniculatum* and *E. angustifolium*) increased by a similar amount.

In the first year following slash burning on WS1, total herb cover declined in communities with initially well-developed herb strata (*Rhododendron* - *Gaultheria*, *Acer* - *Gaultheria*, and *Polystichum*) (Fig. II-6A). Losses of residuals (Fig. II-6C) were not offset by gains of invaders (Fig. II-6B). The low shrubs, *Gaultheria shallon* and *Berberis nervosa*, the sub-shrub, *Linnaea borealis*, and the fern, *Polystichum munitum*, were largely reduced in cover (3-10%) and frequency of occurrence. However, in communities with poorly developed pre-disturbance herb strata (*Coptis* and *Corylus* - *Gaultheria*), total herb cover increased, because increases in invading herbs (Fig. II-6B) exceeded losses of residuals (Fig. II-6C). *Epilobium angustifolium*, *E. paniculatum*, and *Senecio sylvaticus* were the most abundant invaders.

Following disturbance, herbs dramatically increased in all communities on WS1. Within 2 growing seasons following burning, total herb cover had reached a maximum (Fig. II-6A), exceeding 80% within all communities and ranging to 105% in the initially lush *Polystichum* type. This widespread peak corresponded to rapid establishment of invading herbs (Fig. II-6B). *Epilobium paniculatum* and *Senecio sylvaticus* were ubiquitous, occurring in 80-100% of plots in all communities. Other abundant invaders with greater community fidelity included *Montia sibirica* (in the *Polystichum* type) and *Epilobium angustifolium* (in *Acer* - *Berberis*, *Coptis* and *Polystichum* communities). The greater magnitude and persistence of invading herbs in the *Acer* - *Gaultheria* community was due to the sequential prominence of *Epilobium paniculatum*, *Conyza canadensis*, and *Vicia americana*.

Among the residuals associated with peak herb cover on WS1, only *Rubus ursinus* was widespread, with 11-18% cover. Other residuals with greater community fidelity included 1) uncommon forest herbs such as *Galium triflorum* in the *Corylus* - *Gaultheria* type, *Hieracium albiflorum* in the *Coptis* type, and *Trientalis latifolia* in the *Acer* - *Berberis*, *Coptis*, and *Polystichum* types; and 2) original community dominants such as *Gaultheria shallon* in the *Rhododendron* - *Gaultheria* and *Acer* - *Gaultheria* types, *Berberis nervosa* in the *Acer* - *Gaultheria* type, and *Polystichum munitum* in the *Polystichum* type.

Following the peak in total herb and low shrub cover on WS1, abundance fluctuated rather widely among communities (Fig. II-6A). Cover of invading herbs at first dropped sharply with the loss of annuals, then declined more gradually (Fig. II-6B). This pattern was delayed in the Acer - Gaultheria community, however, due to successive peaks in additional perennial invaders (e.g., Vicia americana and Pteridium aquilinum). On the other hand, cover of residual herbs and low shrubs increased slowly, peaking 9 yr following burning (Fig. II-6C). Maxima ranged from 47% in the Acer - Berberis type to 75% in the Acer - Gaultheria type. Rubus ursinus was ubiquitous, contributing 10-25% cover. The remaining residuals displayed various trends. Following peak residual herb cover, species that were initially released by disturbance (e.g., Trientalis latifolia, Whipplea modesta, and Hieracium albiflorum) returned toward pre-disturbance levels. Initial community dominants, however, slowly regained original cover.

On WS3, in all but the Polystichum community, patterns of herb and low shrub abundance were strikingly similar (Fig. II-6D). Reductions in cover following logging were proportional to initial abundance, reflecting the decline of Berberis nervosa and Gaultheria shallon on dry and mesic sites and of Polystichum munitum on moist sites. Total herb cover peaked between years 5 and 6, ranging from 79-91%, except in the Polystichum community, which reached 139% cover. These peaks coincided with the maximum abundance of invading herbs (Fig. II-6E). Epilobium angustifolium was ubiquitous; other colonizing species had greater community fidelity. Annuals such as E. paniculatum and Senecio sylvaticus characterized dry to mesic communities (Rhododendron - Gaultheria, Acer - Gaultheria, and Acer - Berberis), whereas the perennial, Anaphalis margaritacea, typified moist communities (Coptis and Polystichum).

In most communities on WS3, invaders (Fig. II-6E) and residuals (Fig. II-6F) contributed equally to the peak in total herb and low shrub cover (year 6). In the Polystichum community, however, dramatic expansion of residuals accounted for the distinct peak (Fig. II-6F). These included initially uncommon herbs and subshrubs (e.g., Rubus ursinus, Linnaea borealis, Galium triflorum, and Oxalis oregana). The initial dominant, Polystichum munitum, was also important. Within the herb-poor communities (Acer - Berberis and Coptis) where development of residual herbs was comparatively slower, initially subordinate species (e.g., Whipplea modesta, Hieracium albiflorum, and Trientalis latifolia) were also released. In the remaining communities (Rhododendron - Gaultheria and Acer - Gaultheria), recovery of initial dominants, (e.g., Berberis nervosa and Gaultheria shallon) accounted for most of the peak in residual herb cover.

Following the peak in total herb and low shrub cover, invaders declined in all communities (Fig. II-6E). Patterns among residual herbs were more complex, but typically included 1) the persistence of Rubus ursinus, 2) the decline of other sub-dominant herbs that had experienced early release, and 3) the complete recovery of initial community dominants. As a consequence, the abundance of residual herbs during the second decade of succession largely reflected abundances in the corresponding pre-disturbance community (Fig. II-6E).

Tall shrub stratum

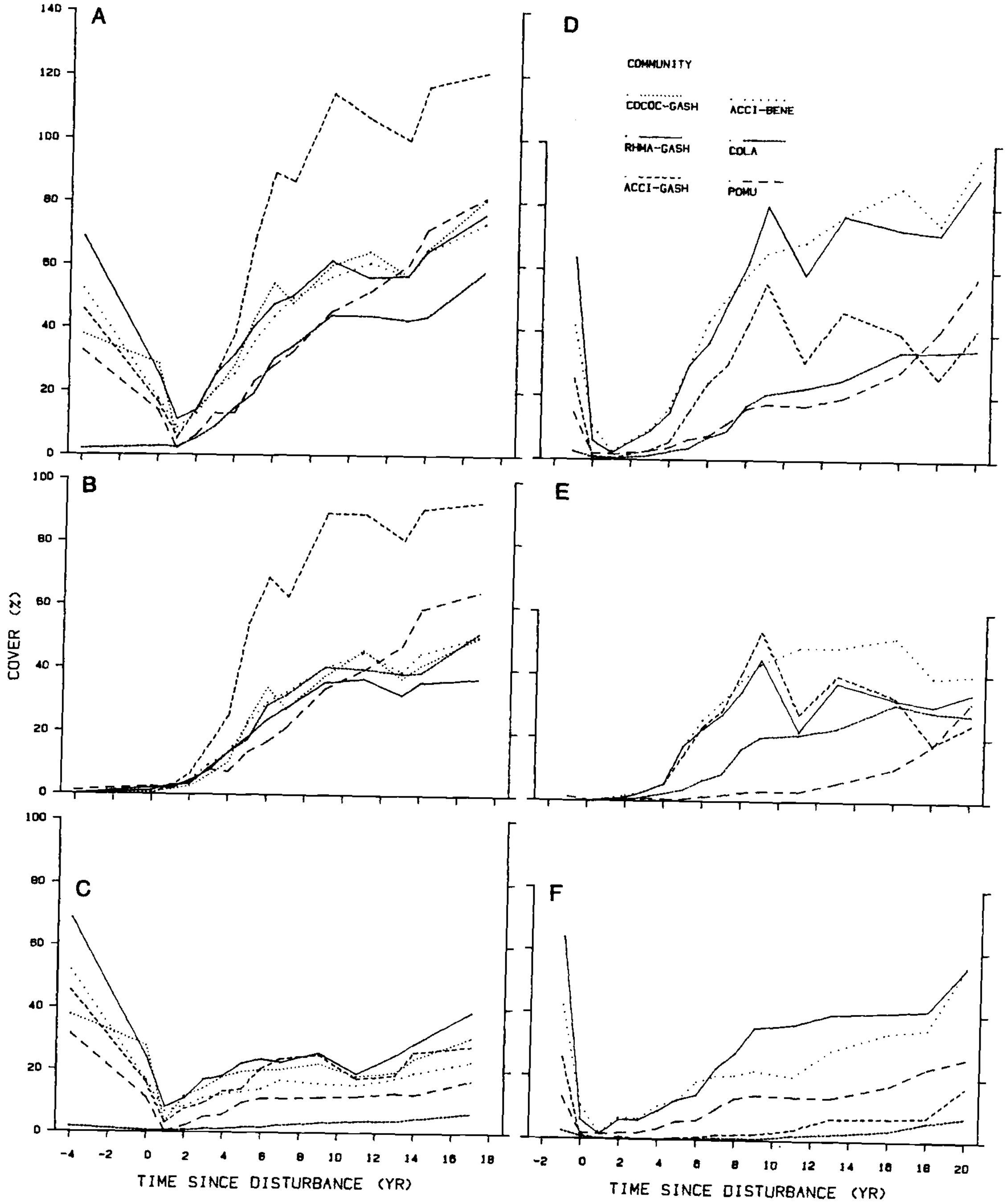
Cover of tall shrubs was initially reduced in response to disturbance in all communities (Figs. II-7A and D). Species showing the greatest reductions included *Corylus cornuta* in the *Corylus - Gaultheria* community (and to a lesser extent in the *Acer - Gaultheria* type), *Rhododendron macrophyllum* in the *Rhododendron - Gaultheria* community, and *Acer circinatum* in all but the *Coptis* community.

Subsequent to disturbance, on WS1, tall shrubs generally showed parallel patterns of development in all communities (Fig. II-7A). Invaders rapidly expanded and persisted (Fig. II-7B); residuals recovered relatively slowly (Fig. II-7C). Invading shrubs were particularly prominent in the *Acer - Gaultheria* community beginning 5 yr after burning; cover was > 60% after 6 yr and > 90% at final sampling (Fig. II-7B). In the remaining communities cover of invading shrubs generally remained < 60%. *Ceanothus sanguineus* and *C. velutinus* were co-dominant in all types, although *Rubus parviflorus* was fairly abundant in *Coptis* and *Polystichum* communities late in the sere.

Post-disturbance abundance of residual shrubs on WS1 paralleled that of the initial community (Fig. II-7C). Unlike residual herbs, however, residual shrubs did not recover to pre-disturbance levels. *Acer circinatum* and *Rhododendron macrophyllum* regained 25-50% of their initial abundance; only *Corylus cornuta* showed complete recovery.

Figure II-7. Changes in additive canopy cover with time in the tall shrub stratum for the plant communities of Watersheds 1 and 3. **A)** Total tall shrubs on WS1. **B)** Invading tall shrubs on WS1. **C)** Residual tall shrubs on WS1. **D)** Total tall shrubs on WS3. **E)** Invading tall shrubs on WS3. **F)** Residual tall shrubs on WS3. Community abbreviations: COCO-GASH = *Corylus*-*Gaultheria*, RHMA-GASH = *Rhododendron*-*Gaultheria*, ACCI-GASH = *Acer*-*Gaultheria*, ACCI-BENE = *Acer*-*Berberis*, COLA = *Coptis*, POMU = *Polystichum*.

Figure II-7.


A
B
C
D
E
F
140
120
100
80
60
40
20
0
COVER (%)
COMMUNITY
COCOC-GASH
ACCI-BENE
RHMA-GASH
COLA
ACCI-GASH
POMU
-4
-2
0
2
4
6
8
10
12
14
16
18
20
TIME SINCE DISTURBANCE (YR)

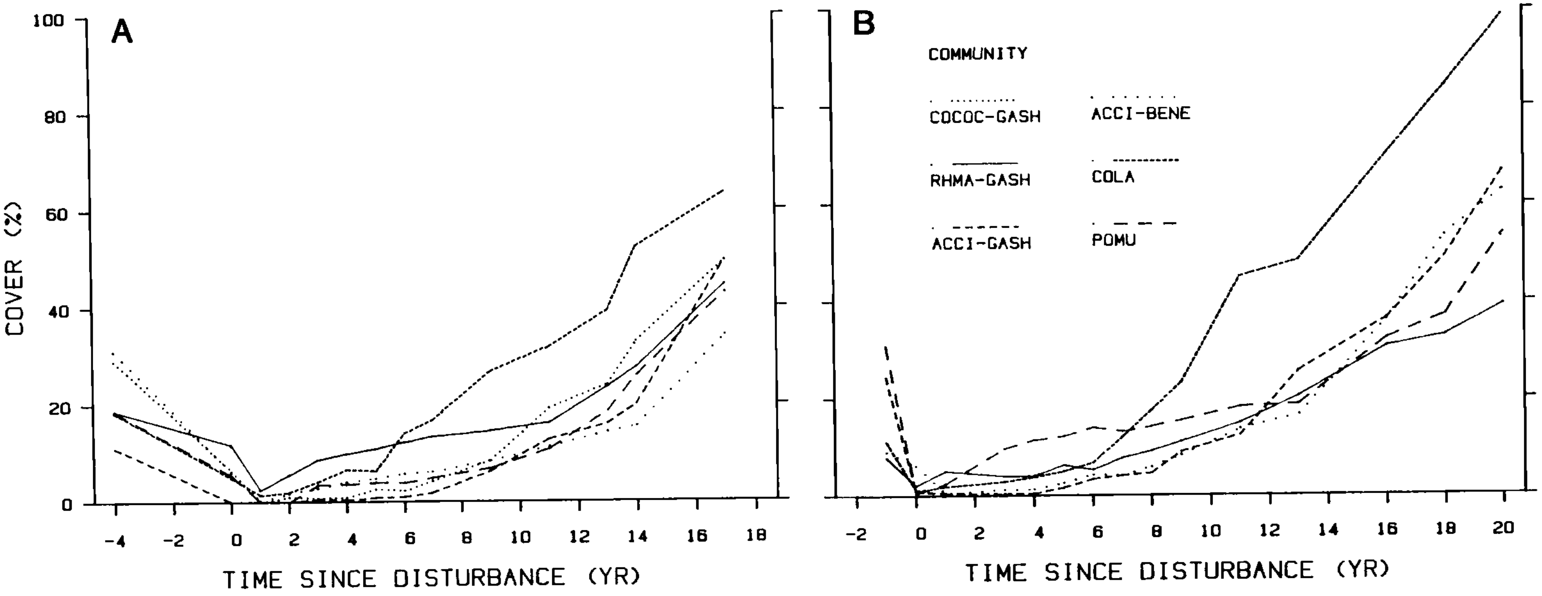
On WS3, development of the tall shrub stratum (Fig. II-7D) varied among communities more than on WS1. Invading shrubs (principally *Ceanothus velutinus*) expanded rapidly among the mesic to dry communities and subsequently declined in the *Rhododendron* - *Gaultheria* and *Acer* - *Gaultheria* types in year 11 (Fig. II-7E). However, gradual expansion of *Rubus parviflorus* maintained high cover of invading shrubs in the *Acer* - *Berberis* community. *Rubus parviflorus* also dominated the relatively slow development of invaders in the *Coptis* and *Polystichum* communities (Fig. II-7E). The post-disturbance abundance of residual shrubs on WS3 largely reflected initial community levels; additionally, recovery was complete (Fig. II-7F).

Tree stratum

Understory tree cover was widely reduced by logging and burning on both watersheds (Fig. II-8). Post-disturbance development was attributed to accelerating rates of increase in the residual tree group among all communities. In the *Coptis* community, however, trees showed distinctly greater development. For example, on WS1, rapid growth of *Pseudotsuga menziesii* and *Tsuga heterophylla* resulted in 63% tree cover at final sampling (year 17) (Fig. II-8A). In the *Coptis* community on WS3, canopy closure (100% cover) occurred in year 20 (Fig. II-8B). Maximum tree cover in the remaining communities was significantly lower on both watersheds.

Figure II-8. Changes in additive canopy cover with time in the tree stratum for the plant communities of Watersheds 1 and 3. **A)** Total trees on WS1. **B)** Total trees on WS3. Community abbreviations: COCO-GASH = *Corylus-Gaultheria*, RHMA-GASH = *Rhododendron-Gaultheria*, ACCI-GASH = *Acer-Gaultheria*, ACCI-BENE = *Acer-Berberis*, COLA = *Coptis*, POMU = *Polystichum*.

Figure II-8.


A
B
COVER (%)
100
80
60
40
20
0
-4
-2
0
2
4
6
8
10
12
14
16
18
TIME SINCE DISTURBANCE (YR)
COMMUNITY
COCOC-GASH
ACCI-BENE
RHMA-GASH
COLA
ACCI-GASH
POMU
-2
0
2
4
6
8
10
12
14
16
18
20
TIME SINCE DISTURBANCE (YR)

Patterns Among Soil Disturbance Classes

The origin and development of seral vegetation were greatly influenced by the heterogeneity of disturbance intensity. To illustrate this variation, we first compare the patterns of transition among dominant growth-forms, then describe the origin and development of the vegetation strata for each soil disturbance class.

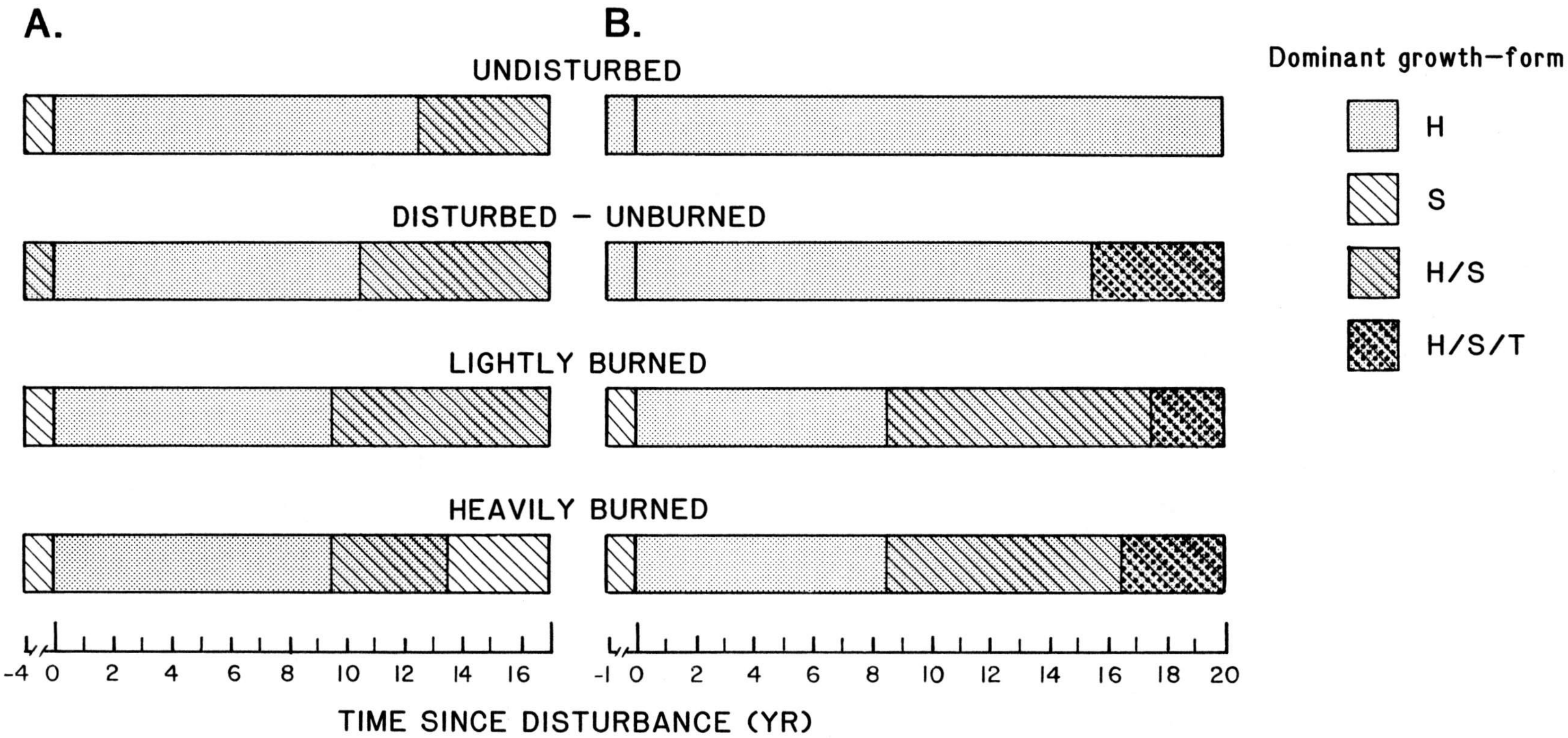
Growth-form phases

The transitions of dominance between growth-forms were gradual among the soil disturbance classes of both watersheds (Fig. II-9). On WS1, the duration of herb layer dominance decreased with intensity of disturbance, ranging from 12 yr in the undisturbed class (representing little mixing of soil with litter and no burning) to 9 yr in the lightly and heavily burned classes (Fig. II-9A). Thereafter, herb and tall shrub strata were co-dominant. A subsequent transition to dominance by shrubs occurred only in the heavily burned class, 14 yr following burning.

On WS3, three basic patterns of structural change were evident among disturbance classes (Fig. II-9B). On undisturbed sites herbs were the dominant growth-form through the entire sere. On disturbed-unburned sites, herbs were dominant for 15 yr, after which all growth-forms were co-dominant. On lightly and heavily burned

Figure II-9. Changes in the dominant growth-form with time for the soil disturbance classes of Watersheds 1 and 3. **A)** WS1, **B)** WS3. A growth-form was considered co-dominant if its cover was 75% that of the dominant growth-form. Dominant growth-form codes: H = herbs and low shrubs, S = tall shrubs, T = trees.

Figure II-9.


A.
B.
UNDISTURBED
DISTURBED – UNBURNED
LIGHTLY BURNED
HEAVILY BURNED
Dominant growth—form
H
S
H/S
H/S/T
-4 0 2 4 6 8 10 12 14 16
-1 0 2 4 6 8 10 12 14 16 18 20
TIME SINCE DISTURBANCE (YR)

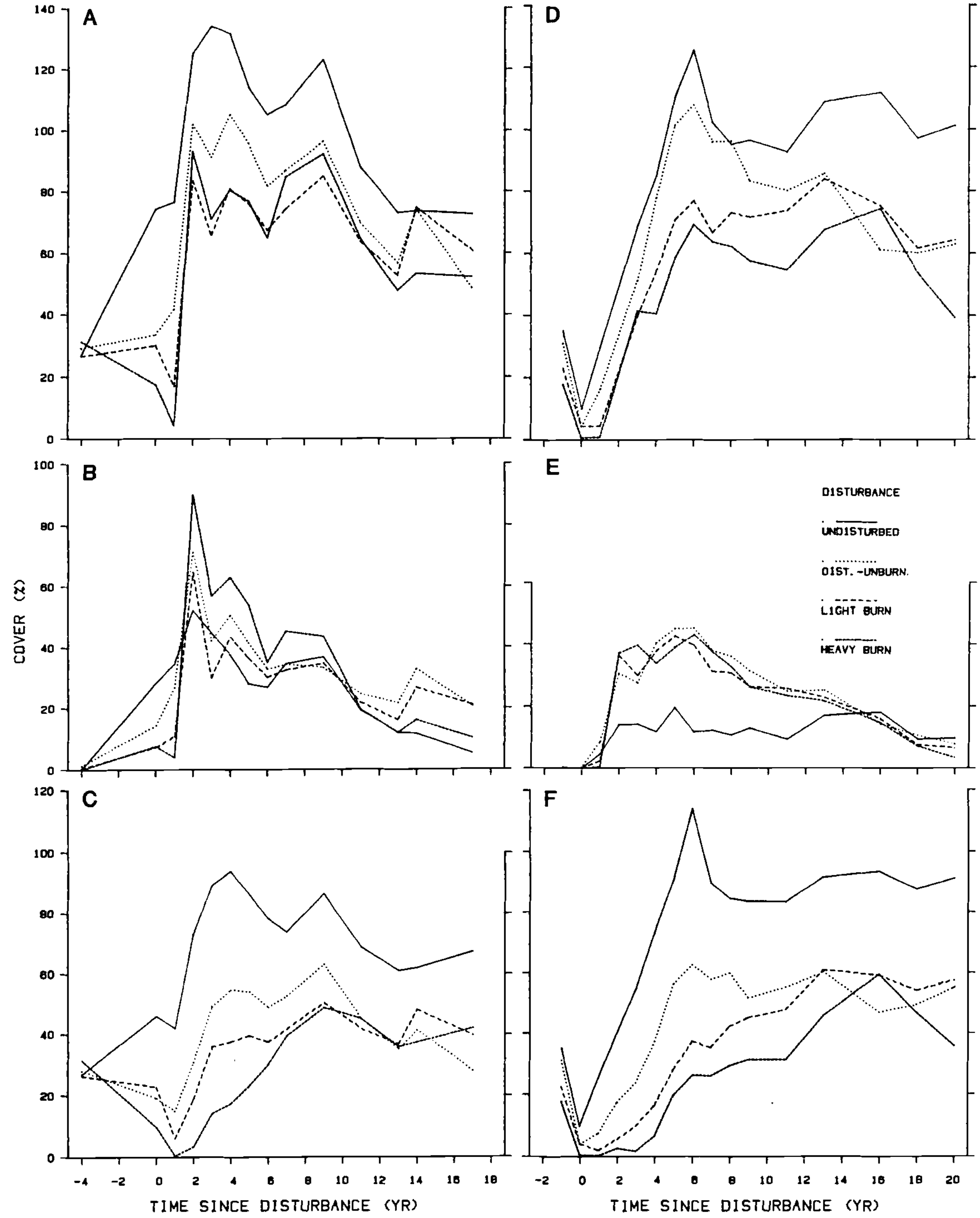
sites, an herb phase (years 1-8) preceded an herb and tall shrub phase (years 9-15). This was followed by co-dominance of all growth-forms (years 16-20).

Herb and low shrub stratum

Early dynamics in the herb and low shrub layer differed dramatically between watersheds (Figs. II-10A and D). On WS1, large differences in herb cover developed among disturbance classes during the extended period of logging (years -4 to 0) (Fig. II-10A). Herb cover increased by 47% in plots that were subsequently classified as undisturbed, but declined by 14% in those that were later heavily burned. In plots to be classsified as disturbed-unburned and lightly burned cover changed minimally. Invading herbs (primarily *Epilobium angustifolium*) were common in all disturbance classes, but were most abundant on undisturbed sites (Fig. II-10B). Changes in residual herb cover, paralleled those of total herb cover--increasing on undisturbed sites and decreasing on heavily burned sites during logging (Fig. II-10C). Initial forest dominants (e.g., *Berberis nervosa*, *Gaultheria shallon*, and *Polystichum munitum*) declined on all but undisturbed sites. Residuals of low initial abundance (e.g., *Linnaea borealis*, *Trientalis latifolia*, *Hieracium albiflorum*, and *Galium triflorum*) expanded in response to canopy removal--to a greater degree on undisturbed than on disturbed or burned sites.

Figure II-10. Changes in additive canopy cover with time in the herb stratum for the soil disturbance classes of Watersheds 1 and 3. **A)** Total herbs and low shrubs on WS1. **B)** Invading herbs and low shrubs on WS1. **C)** Residual herbs and low shrubs on WS1. **D)** Total herbs and low shrubs on WS3. **E)** Invading herbs and low shrubs on WS3. **F)** Residual herbs and low shrubs on WS3.

Figure II-10.


A
B
C
D
E
F
COVER (%)
140
120
100
80
60
40
20
0
DISTURBANCE
UNDISTURBED
DIST.-UNBURN.
LIGHT BURN
HEAVY BURN
-4
-2
0
2
4
6
8
10
12
14
16
18
20
TIME SINCE DISTURBANCE (YR)
TIME SINCE DISTURBANCE (YR)

Following slash burning on WS1, total cover of herbs increased on unburned sites and decreased on burned sites (Fig. II-10A). Invading herbs increased to a greater degree on unburned than on burned sites (Fig. II-10B). *Epilobium angustifolium* remained the principal invader on undisturbed sites; species of lesser importance established on disturbed and burned sites. After burning, residual herbs declined more on burned than on unburned sites (Fig. II-10C). Among the residuals with relatively high pre-burning cover, *Berberis nervosa*, *Linnaea borealis*, and *Galium triflorum* declined on all sites, whereas *Polystichum munitum* and *Gaultheria shallon* declined on all but undisturbed sites.

Total herb cover peaked within 2-3 growing seasons following burning in all disturbance classes on WS1 (Fig. II-10A). Peak cover was inversely related to disturbance intensity, ranging from 84 and 93% on lightly and heavily burned sites to 105 and 134% on disturbed-unburned and undisturbed sites. Peak abundance of invading herbs was proportional to disturbance intensity (Fig. II-10B). Cover ranged from 32% on undisturbed sites to 92% on heavily burned sites. *Epilobium angustifolium* dominated undisturbed sites. *Epilobium paniculatum* and *Senecio sylvaticus* were widespread, but with greatest abundance on burned sites. *Conyza canadensis* and *Montia sibirica* were locally common on heavily burned sites.

The patterns of residual herbs on WS1 contrasted with those of invaders. Both the rate of development and the magnitude of peak cover were inversely proportional to disturbance intensity (Fig. II-

10C). Maximum residual cover occurred 4 yr following burning in the undisturbed class (94%), but was delayed until 9 yr in the disturbed and burned classes (ranging from 49-63% cover). Rapid development on undisturbed sites corresponded with greater recovery of initial dominants. However, at final sampling, residual herb cover in each disturbance class exceeded the corresponding pre-disturbance value, due to the release of initially uncommon forest herbs.

On WS3, the early dynamics of the herb stratum were simpler than on WS1. Reductions due to logging were similar among disturbance classes (Fig. II-10D). However, one growing season after burning, total herb cover ranged from 0.8% on heavily burned sites to 30% on undisturbed sites , primarily due to the response of residuals (Fig. II-10F). Although initial dominants (e.g., *Berberis nervosa*, *Gaultheria shallon*, and *Polystichum munitum*) were widely reduced, sub-dominant species (e.g., *Rubus ursinus*, *Oxalis oregana*, *Galium triflorum*, and *Linnaea borealis*) were released on undisturbed sites.

Post-burning development of the herb layer on WS3 was correlated with disturbance intensity. Total cover peaked for all disturbance classes in year 6, ranging from 74% on heavily burned sites to 125% on undisturbed sites (Fig. II-10D). The rate and magnitude of recovery of residual herbs, varied inversely with disturbance intensity (Fig. II-10F). For example, cover of residuals peaked after 6 yr on undisturbed and disturbed-unburned sites (114 and 62%, respectively) but only after 13 and 16 yr on lightly and heavily burned sites, respectively (60% each). The prominence of residuals on undisturbed sites reflected early expansion of *Rubus ursinus* and *Linnaea borealis*, as well as continuous, two- to three-fold recovery of *Gaultheria shallon* and *Polystichum munitum*. In contrast, on disturbed-unburned sites, *Trientalis latifolia* and *Whipplea modesta* were the principal species contributing to peak residual herb cover.

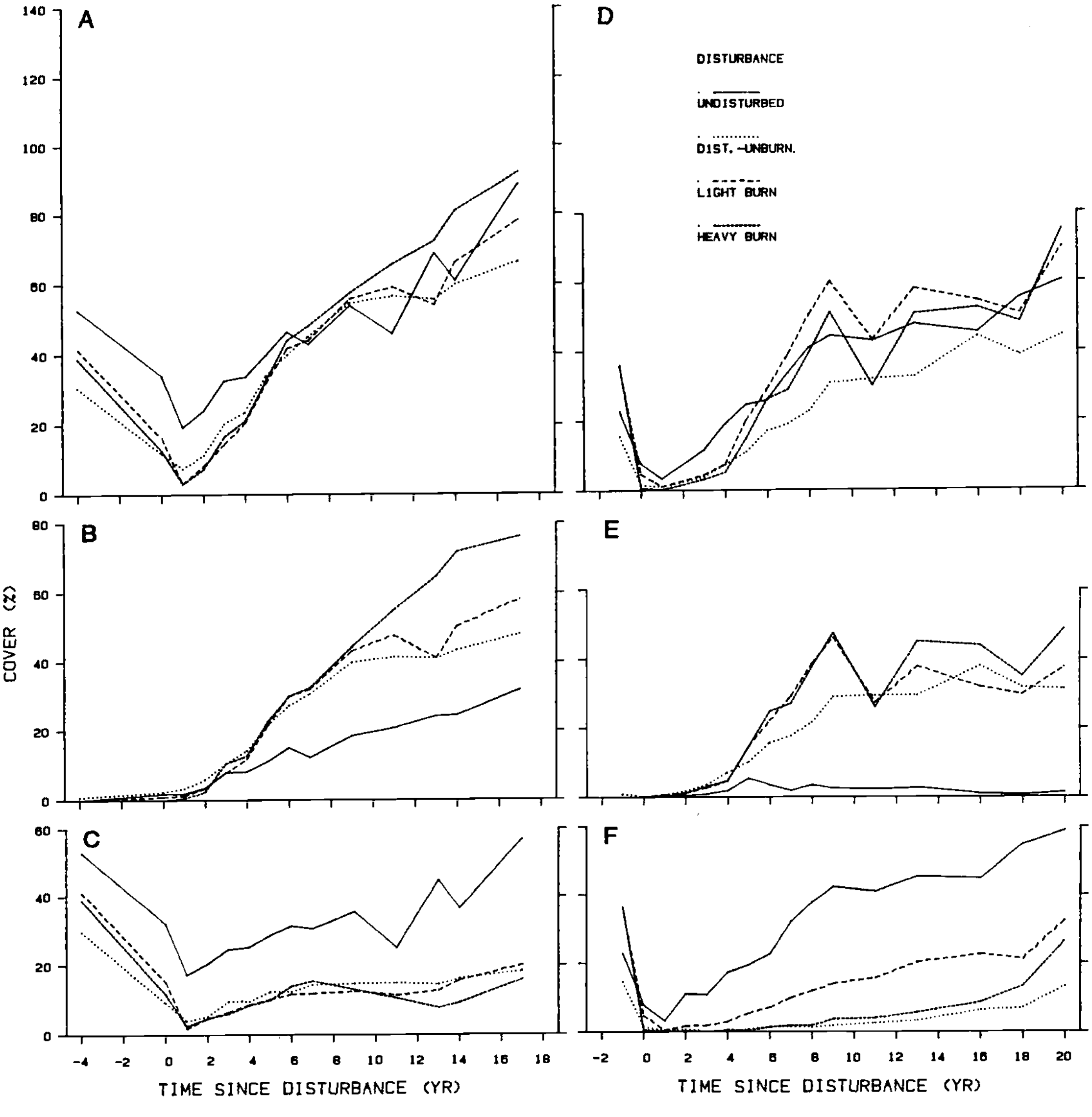
Invading herbs were markedly less abundant on WS3 than on WS1. On undisturbed sites they remained sub-dominant (Fig. II-10E). On disturbed and burned sites invaders were briefly dominant. Here their patterns of abundance were nearly identical, with cover rising rapidly in year 2, peaking at 42-45% within 5-6 yr, and declining slowly to < 10% by year 20. Nevertheless, the spatial and temporal distributions of dominant invaders on WS3 were complex. *Senecio sylvaticus* reached peak abundance on lightly and heavily burned sites in year 2; *Epilobium angustifolium*, on heavily burned sites in year 3; and *E. paniculatum*, on lightly burned sites in year 4.

Tall shrub stratum

The dynamics of the tall shrub layer were largely determined by the intensity of initiating disturbance. Logging and slash burning on both watersheds reduced total shrub cover (principally *Acer circinatum* and *Rhododendron macrophyllum*) in proportion to disturbance intensity (Figs. II-11A and D). Subsequent changes in total shrub cover were fairly similar among disturbance classes,

Figure II-11. Changes in additive canopy cover with time in the tall shrub stratum for the soil disturbance classes of Watersheds 1 and 3. **A)** Total tall shrubs on WS1. **B)** Invading tall shrubs on WS1. **C)** Residual tall shrubs on WS1. **D)** Total tall shrubs on WS3. **E)** Invading tall shrubs on WS3. **F)** Residual tall shrubs on WS3.

Figure II-11.


A
B
C
D
E
F
DISTURBANCE
UNDISTURBED
DIST.-UNBURN.
LIGHT BURN
HEAVY BURN
COVER (%)
140
120
100
80
60
40
20
0
80
60
40
20
0
60
40
20
0
-4
-2
0
2
4
6
8
10
12
14
16
18
TIME SINCE DISTURBANCE (YR)
-2
0
2
4
6
8
10
12
14
16
18
20
TIME SINCE DISTURBANCE (YR)

although invaders were more important on disturbed and burned sites (Figs. II-11B and E) and residuals, on undisturbed sites (Figs. II-11C and F).

On WS1, the rates of expansion for invading shrubs increased with intensity of disturbance. At final sampling, canopy cover ranged from 32% on undisturbed sites to 76% on heavily burned sites (Fig. II-11B). The principal invaders, Ceanothus sanguineus and C. velutinus, dominated burned sites. Rubus parviflorus developed comparatively slowly, assuming co-dominance on unburned sites. Rubus parviflorus also expanded late in the sere on heavily burned sites, but remained less important than the Ceanothus species.

On undisturbed sites of WS1, residuals dominated the tall shrub stratum (Fig. II-11C), as Acer circinatum and Rhododendron macrophyllum returned to pre-disturbance abundance within the sampling period. In contrast, among the disturbed and burned soil classes, residual shrubs showed poor development. Although Corylus cornuta was resilient, recovery of the characteristic species was low. For example, R. macrophyllum was eliminated from heavily burned sites.

On WS3, the disturbed and burned soil classes were also dominated by invading shrubs (Fig. II-11E); the undisturbed class by residuals (Fig. II-11F). On lightly and heavily burned sites, the principal invader, Ceanothus velutinus, expanded rapidly, accounting for the early peak in shrub cover. However, it declined sharply between years 9 and 11, and was gradually replaced by Salix scouleriana on heavily burned sites. On disturbed-unburned sites, the principal invader, *Rubus parviflorus*, increased steadily with time. Few invading shrub species occupied undisturbed sites (Fig. II-11E).

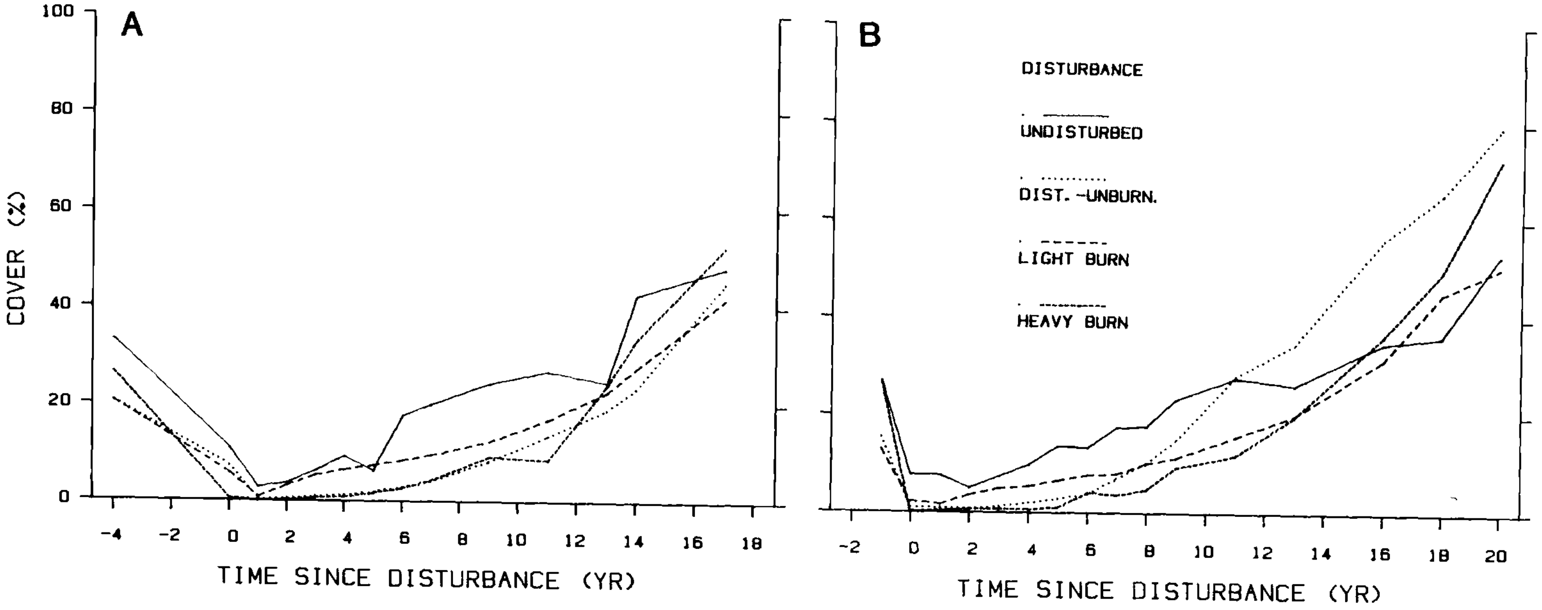
Patterns of residual shrub abundance on WS3, as on WS1, contrasted with those of invaders. Recovery was rapid on undisturbed sites, illustrated by a three-fold expansion in pre-disturbance cover, but slower elsewhere (Fig. II-11F). Nevertheless, residual shrubs recovered almost completely on disturbed-unburned and lightly burned sites, as *Acer circinatum* and *Rhododendron macrophyllum* displayed full canopy regeneration.

Tree stratum

The long-term patterns of tree development showed little direct relation to intensity of disturbance. However, reductions due to logging and burning were greater on disturbed and burned sites than on undisturbed sites (Fig. II-12). On both watersheds, early canopy development was greatest on undisturbed sites, reflecting the local persistence and expansion of *Tsuga heterophylla*. Subsequent patterns of tree abundance were more complex and characterized by fairly high variability. *Pseudotsuga menziesii* reached peak cover in the heavily burned class on WS1, but in the disturbed-unburned class on WS3. Whereas *P. menziesii* dominated all soil disturbance classes on WS1, the undisturbed class on WS3 was dominated by *T. heterophylla*.

Figure II-12. Changes in additive canopy cover with time in the tree stratum for the soil disturbance classes of Watersheds 1 and 3. **A)** Total trees on WS1. **B)** Total trees on WS3.

Figure II-12.


A
B
COVER (%)
100
80
60
40
20
0
-4
-2
0
2
4
6
8
10
12
14
16
18
20
TIME SINCE DISTURBANCE (YR)
DISTURBANCE
UNDISTURBED
DIST.-UNBURN.
LIGHT BURN
HEAVY BURN

DISCUSSION

General Successional Trends

Floristic changes

The changes in species number on Watersheds 1 and 3 are consistent with the hypothesis of initial floristics (Egler 1954). Numerous fugitive colonizers established within 2-3 growing seasons following burning, augmenting a residual flora that largely persisted through disturbance. Subsequent understory development reflected the differential expansion and decline of the dominant residual and invading species.

Differences in the timing of disturbance between watersheds resulted in dramatically different initial responses to logging, despite similar long-term floristic trends. Staggered logging on WS1 promoted increased species richness by providing a long period for recruitment of invaders and reemergence of residuals. Single season harvest on WS3, however, resulted in reduced numbers. Immediate post-logging establishment of invading species was precluded on WS3, as fall seed dispersal preceded winter harvesting. Additionally, emergence of many initially uncommon residuals was delayed until after burning.

The resilience of these plant communities is suggested by the loss of only 7 rather uncommon species. Many species sprouted from adventitious buds on stems, root crowns, rhizomes, tubers, corms, or bulbs. The phenomenon is widespread in ecosystems in which the seral vegetation derives from surviving individuals (Naveh 1975, Gill 1981, Keeley 1981, 1986, Westman 1981, Mallik and Gimingham 1983, Viereck 1983, Christensen 1985, Stickney 1986). In contrast, other forest species did not reappear for 2-11 growing seasons following burning. Some of these species may have established from seed, but others, especially shade-tolerant herbs with sub-surface perennating structures, may have had delayed vegetative emergence. Delay of 3 yr in the emergence of some forest species has been reported following volcanic burial (Griggs 1918, Zobel and Antos 1986). Stickney (1986) also suggests that delayed sprouting of forest species may occcur after severe fire.

Species lost from the sample plots were uncommon; thus, causes of their disappearance cannot be assessed. Nevertheless, they may have been eliminated by fire. Four are closely related to forest herbs in the families Ericaceae and Orchidaceae that have been shown to be fire susceptible (Volland and Dell 1981, Fischer and Clayton 1983, Crane et al. 1983, Rowe 1983). A fifth species, <u>Pinus lambertiana</u>, is also susceptible to fire when it is young (Kilgore 1973).

The marked loss of species late in each sere reflects both the limited life-span of many perennial invaders and the effects of local canopy closure. However, responses to climatic stress also may have influenced species turnover. For example, numerous uncommon forest herbs were absent on WS1 during the dry hydrologic year of 1976-1977 (year 11). This may reflect a sampling artifact (i.e., senescence prior to measurement) or temporary dormancy.

The early establishment and differential loss of species during understory development support the model of initial floristics. Yet, in a strict sense, aspects of the relay floristics model (Egler 1954) were also supported, as new species entered the sample plots during each remeasurement year. However, species invading after the initial period were limited in abundance, perhaps reflecting the reduced number of regeneration sites, or the competitive dominance of established species.

Physiognomic changes

Growth-form phases. A majority of studies of secondary succession in coniferous forests describe an herb-dominated phase of shorter duration than those on WS1 (9 yr) or WS3 (17 yr). For example, Foote (1983) estimated an herb phase of 1-5 yr following fire in *Picea* forests while Viereck (1983) suggested a tree seedling-herb stage of 1-4 yr. Within *Larix*-*Abies* forests of the northern Rocky Mountains, estimates for herb-dominance following clearcutting and burning are 3-7 yr (Stickney 1981). However, after holocaustic fire in *Thuja*-*Tsuga* forests, the period may vary from 4 to > 10 yr (Stickney 1986). Isaac (1940) suggested an average herb phase of 7 yr based on widely collected data from *Pseudotsuga* forests of western Oregon and Washington. Comparisons are tenuous, however, since estimates of growth-form dominance are highly dependent on the assignment of species to understory strata and on the measures of abundance. For example, classification of *Rubus ursinus*, *Berberis nevosa*, or *Gaultheria shallon* as shrubs, would result in dramatically different estimates of herb layer dominance.

The patterns of transition between dominant growth-forms on Watersheds 1 and 3 are not entirely consistent with the classical model describing successive replacement of vegetation layers of increasing stature (Clements 1916, 1928). The trends in growth-form cover on WS1 support the model. However, WS3 has never developed a distinct tall shrub phase due to the limited development of invading shrubs. Whereas *Ceanothus velutinus* and *C. sanguineus* were both prominent on WS1, only the former was abundant on WS3. The limited abundance of *C. sanguineus* on WS3 probably reflected low levels of buried seed. Further, *C. velutinus* declined dramatically only on WS3, following severe frost during the winter of 1972-1973. Kraemer (1977) documented a coincidental response in other cutover areas in the western Cascade Range. That the decline occurred only on WS3, possibly reflects the reduced vigor of older individuals (9 versus 6 yr) or local differences in climate. These contrasts in patterns of abundance for both *Ceanothus* species suggest that dramatic differences in the structural development of understory vegetation, were largely the result of historical and stochastic factors.

Patterns within the herb stratum. A diversity of reproductive strategies may have contributed to rapid pre- and post-burning development of the herb stratum on Watersheds 1 and 3. Prior to burning, invading herbs potentially expanded by three mechanisms: 1) initial recruitment of annual or perennial species from wind-dispersed seed, 2) subsequent establishment of annual or perennial seedlings from on-site seed sources, and 3) vegetative reproduction of perennials. Epilobium angustifolium, the dominant invader during this period, exemplifies all of these mechanisms. Although its prominence following catastrophic disturbance has been attributed to vegetative reproduction of surviving individuals (Moss 1936, Viereck 1973, van Andel 1975, Viereck and Dyrness 1979, Bartos and Mueggler 1981, Crane et al. 1983, Foster 1985), it more commonly spreads vegetatively, following recruitment from wind-dispersed seed (van Andel and Rozema 1974, van Andel 1975, van Andel and Vera 1977, Haeussler and Coates 1986). This pattern is widely observed following slash burning in the central Cascade Range (Kienholz 1929, Ingram 1931, Mueller-Dombois 1965, Gashwiler 1970, Dyrness 1973, Kraemer 1977) and following prescribed burning or wildfire in other northern coniferous systems (Lyon 1971, Johnson and Rowe 1977, Black and Bliss 1978, Stickney 1980, 1981, 1985, 1986, Viereck and Schandelmeier 1980, Van Cleve and Viereck 1981, Foote 1983).

The pre-burning expansion of residual herbs and low shrubs may be associated with similar regenerative mechanisms: recruitment from on- or off-site seed and vegetative reproduction. For example, marked expansion of Hieracium albiflorum, an initally uncommon forest perennial, commonly follows overstory removal (Isaac 1940, Yerkes 1958, Mueller-Dombois 1965, Dyrness 1973) and is attributed to copious, wind-dispersed seed (McLean 1968).

The vigorous above-ground perennation of initially subordinate sub-shrubs, however, was more important to pre-burning expansion of the residual herb group. Release of *Rubus ursinus* has been widely observed following canopy removal within *Pseudotsuga* forests of the Pacific Northwest (Isaac 1940, Neiland 1958, Yerkes 1958, Mueller-Dombois 1965, Bailey 1966, Steen 1966, Gashwiler 1970, Dyrness 1973, Kraemer 1977). Although fruit production may be prolific, and seedlings have been observed following logging (Stewart 1978), its early expansion is probably vegetative. *Linnaea borealis* responds similarly, although its expansion may be limited by the severity of disturbance (McLean 1968, Stark and Steele 1977, Crane et al. 1983, Fischer and Clayton 1983, Rowe 1983, Bradley 1984). Species that sprouted from rhizomes (e.g., *Gaultheria shallon*, *Berberis nervosa*, *Polystichum munitum*) or tubers (e.g., *Trientalis latifolia*), played a smaller role in the pre-burning development of the herb layer.

Many of these regenerative strategies were expressed on WS1 in response to staggered logging. Relative to the single season harvest on WS3, this method facilitated rapid development of the herb and low shrub layer, as both invading and residual species experienced up to 4 yr for establishment and growth prior to burning. Thus, variation in the timing of logging and slash burning played a major role in the early development of seral herb strata.

Following slash burning, the abundance of the invading herb group peaked rapidly, reflecting the early prominence of winter annuals. Following fire in western coniferous forests, dense populations of *Senecio sylvaticus* and *Epilobium paniculatum* commonly establish from copious, wind-dispersed seed (Yerkes 1958, Brown 1963, Bailey 1966, West and Chilcote 1968, Morris 1970, Dyrness 1973, Kraemer 1977, Stewart 1978, Stickney 1981). Their more rapid peak on WS1 relative to WS3, may have reflected an abundance of on-site seed derived from individuals established prior to burning.

Early transition from dominance by invading to residual herbs on both sites was largely due to the dramatic decline of annual invaders. The ephemeral nature of *Senecio sylvaticus* has been attributed to a requirement for high soil fertility associated with recently burned soils and to an inability to compete with perennial invaders such as *Epilobium angustifolium* (West and Chilcote 1968, van Andel and Vera 1977).

The release of initially uncommon forest herbs and sub-shrubs also promoted fairly rapid transition to dominance by residual herbs. Rates of expansion for many of these (e.g., *Rubus ursinus*, *Trientalis latifolia*, and *Whipplea modesta*) accelerated following slash burning, suggesting additional resource availability.

In comparison, original community dominants (e.g., *Gaultheria shallon*, *Berberis nervosa*, and *Polystichum munitum*) showed markedly slower recovery. Regeneration through stem budding and greater investment in below-ground structures and sclerophyllous leaves may have limited potential canopy expansion of the low shrubs. *Polystichum munitum* was least plastic of the community dominants, reflecting its limited spread by rhizomes (Haeussler and Coates 1986). Although it has shown fairly high persistence following disturbance (Kienholz 1929, Isaac 1940, Mueller-Dombois 1965, Stewart 1978) recovery may be limited when light and moisture are drastically altered (Haueussler and Coates 1986).

Original herb layer dominants consistently showed greater long-term recovery on WS3 than on WS1. The greater recovery on WS3 may reflect: 1) a higher proportion of unburned plots on WS3 (50%) than on WS1 (39%), 2) reduced competition from invading tall shrubs, and 3) more favorable environmental conditions, due to the greater edge effect in smaller clearcut units.

Patterns within the tall shrub stratum. Fire may damage the perennating structures of coniferous forest shrubs and inhibit their recovery. However, it commonly enhances the germination and establishment of colonizing species. Thus, invading species often dominate the seral shrub layer following catastrophic fire. Subsequent recovery of the original shrub component is ultimately determined by the relative resistance to burning and by the sprouting ability of residual species.

Invading shrubs may establish by three strategies: 1) from buried seed (e.g., *Ceanothus*, *Ribes*, and *Rubus*), 2) via animal vectors (e.g., *Rubus* and *Ribes*), or 3) via wind-dispersed seed (e.g., *Salix*) (Quick 1956, 1962, Mueggler 1965, Zavitkovski and Newton 1968, Lyon 1971, Lotan et al. 1981, Volland and Dell 1981, Conard et al. 1985). Each strategy was observed on Watersheds 1 and 3. However, the first strategy is especially important in this system, because the dominant invaders, *Ceanothus velutinus* and *C. sanguineus*, establish from a seed bank that may persist for centuries. Densities of *Ceanothus* potentially reach 6 X 10^5

individuals/ha following catastrophic fire (Quick 1956, Gratkowski 1962, Hickey and Leege 1970, Lyon 1971). However, because dispersal from off-site sources is typically limited (Conard et al. 1985, Morgan and Neuenschwander 1985), historical patterns of distribution may largely determine its abundance following disturbance. In this study, variation in the viable seed pool of *C. sanguineus* probably accounted for major long-term differences in the composition of the seral tall shrub strata on Watersehds 1 and 3.

The persistence of seral *Ceanothus* spp. as shrub layer dominants also varies. Prominence for over 3 decades has been suggested for some communities (Gratkowski 1961, Lyon 1971). However, *Ceanothus* may be short-lived where environmental or biotic influences reduce its vigor (Tarry 1968, Zavitkovski and Newton 1968, Furniss and Krebill 1972, Leege and Hickey 1975). In the Oregon Cascade Range, *C. velutinus* may persist for 20-40 yr following catastrophic disturbance (Conard et al. 1985). In this study, a dramatic difference in the longevity of *C. velutinus* between Watersheds 1 and 3 suggests that similar variation may occur at a local scale.

In many ecosystems rapid and complete restoration of residual shrub cover may be attained either vegetatively or from a seed bank (e.g, Mediterranean woodland [Trabaud and Lepart 1980], chaparral and coastal sage scrub [Horton and Kraebel 1955, Hanes 1971, Keeley 1986, Keeley and Keeley 1981, 1984, Malanson and O'Leary 1982], *Calluna* heathland [Mallik and Gimingham 1983, 1985] and boreal forest [Black and Bliss 1978, Viereck and Dyrness 1979, Viereck

1983, AuClair 1983]). In _Pseudotsuga_ forests, however, reproduction of residual shrubs from seed is probably insignificant (Anderson 1967, Russell 1974, Schopmeyer 1974). Consequently, long-term recovery will be limited by the sprouting ability of the dominant residual species. However, recovery of the residual shrub layer may be complex, varying with the principal surviving species, and with the history of disturbance and site environment (e.g., Lyon 1971, Kraemer 1977, Stickney 1986).

The abundance patterns of residual shrubs on Watersheds 1 and 3 exemplify this complex response to disturbance. On WS1, recovery of original cover was limited by the slow development of _Acer circinatum_ and _Rhododendron macrophyllum_, despite the complete regeneration of subordinate species such as _Corylus cornuta_. Based on a linear extrapolation of recent trends, recovery to pre-disturbance levels may require an additional 10 yr. On WS3, however, both _Acer circinatum_ and _Rhododendron macrophyllum_ have completely recovered within 20 yr. Greater recovery on WS3 may reflect the higher proportion of unburned plots, more favorable post-disturbance environmental conditions, and reduced competition from invading shrubs.

Patterns within the tree stratum. Because the relative contributions of artificial and natural regeneration to total understory tree cover are unknown, the patterns of understory tree development are difficult to evaluate. Nevertheless, a rapid transition toward co-dominance by trees was essentially identical in both watersheds, despite distinct histories of seeding and planting.

Plant Community Patterns

The origin and development of understory strata on Watersheds 1 and 3 were correlated with the initial composition and structure of communities rather than with the gradient in available moisture. On WS3, three patterns of physiognomic development emerged, reflecting the widespread recovery of initial community dominants: 1) herb-dominated communities (*Acer* - *Gaultheria* and *Polystichum*) persisted as such; 2) shrub-dominated communities (*Rhododendron* - *Gaultheria* and *Acer* - *Berberis*) rapidly changed from herb to tall shrub prominence; and 3) initially depauperate communities (*Coptis*) moved directly from herb to tree dominance.

Local variation in disturbance intensity also influenced community pattern on WS3. Within the *Polystichum* community, for example, the dramatic release of residual herbs and the paucity of invaders reflected a light disturbance regime (i.e., 72% unburned plots, Table II-4). Within the *Rhododendron* - *Gaultheria* and *Acer* - *Berberis* communities, however, the rapid transition to shrub co-dominance was associated with a relatively severe disturbance regime (i.e., 82% burned plots, Table II-4) that apparently facilitated invasion by *Ceanothus velutinus*. Although *C. velutinus* may express an affinity for dry to mesic sites, disturbance intensity and environment apparently interact in determining its distribution (e.g., Mueggler 1965, Pengelly 1966, Zavitkovski and Newton 1968, Leege and Hickey 1975, Orme and Leege 1976, Conard et al. 1985, Noste 1985).

Table II-4. Summary of sample plot distributions among the plant communities and soil disturbance classes of Watershed 3. **A)** The proportion (%) of plant community plots in each soil disturbance class. **B)** The proportion (%) of soil disturbance class plots in each plant community. See Vegetation section for community abbreviations. Totals for soil disturbance classes may be < 100% because they do not include unclassified plots.

A. Plant communities

	Proportion of plant community plots (%)				
	RHMA-GASH	ACCI-GASH	ACCI-BENE	COLA	POMU
Number of Plots	11	11	10	12	11
Undisturbed	18	9	10	8	36
Disturbed-unburned	0	45	30	50	36
Lightly burned	64	27	50	33	18
Heavily burned	18	18	10	8	9
Total:	100	99	100	99	99

B. Soil disturbance classes

	Proportion of soil disturbance class plots (%)			
	Undisturbed	Disturbed-unburned	Lightly burned	Heavily burned
Number of Plots	10	21	23	7
RHMA-GASH	20	0	30	29
ACCI-GASH	10	24	13	29
ACCI-BENE	10	14	22	14
COLA	10	29	17	14
POMU	40	19	9	14
Total:	90	86	91	100

On WS1, the role of initial community composition and structure in seral community development were largely confounded by variation in two factors: the timing of logging and the distribution of burning. First, the average number of growing seasons betweeen initiation and completion of logging differed among plant communities. Through an examination of individual plot histories, we estimated the length of this period as the sum of the products of the annual harvest (proportion of plots harvested within a community) and the number of growing seasons experienced prior to slash burning (Table II-5). The average number of pre-burning growing seasons ranged from 1.6 yr in the *Acer* - *Gaultheria* community to 3.2-3.3 yr in the *Coptis* and *Polystichum* communities. These differences were largely manifested in the abundance patterns of invading herbs. For example, the elevated cover of invading herbs in the *Coptis* and *Polystichum* communities prior to and immediately following burning (years 0 and 1), was correlated with longer periods of pre-burning expansion.

Second, an uneven distribution of burning intensity on WS1 greatly influenced the physiognomic development of communities. For example, heavily burned plots were absent from the *Corylus* - *Gaultheria* community, but were common in the *Acer* - *Gaultheria* community (Table II-6). Thus, the post-burning prominence of invading herbs in the *Acer* - *Gaultheria* community, was associated with a relatively severe disturbance regime. Local heavy burning also delayed the recovery of residual herbs and stimulated the dramatic expansion of *Ceanothus* spp., facilitating an early

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for

Halpern, C. B. 1987. Twenty-one years of secondary succession in Pseudotsuga forests of the western Cascade Range, Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Page 89, Table II-5--replace with the following:

Table II-5. The proportion of plots experiencing from one to four growing seasons prior to burning, and the corresponding average number of growing seasons for the plant communities and soil disturbance classes of Watershed 1. **A)** Plant communities, **B)** Soil disturbance classes. The average number of growing seasons (X) is calculated as the sum of the products of the annual harvest (proportion of plots) and the number of growing seasons prior to slash burning. See Vegetation section for community abbreviations.

		Proportion of plots (%)				
		Number of growing seasons				
	Number of plots	1	2	3	4	$\overline{X}$ (yr)
A. Plant communities						
COCO-GASH	12	58	33	0	8	1.6
RHMA-GASH	20	15	50	25	10	2.3
ACCI-GASH	7	86	14	0	0	1.1
ACCI-BENE	34	24	44	22	12	2.2
COLA	23	0	48	30	22	2.7
POMU	32	6	22	34	38	3.0
B. Soil disturbance classes						
Undisturbed	11	0	9	27	64	3.5
Disturbed-unburned	40	15	45	15	25	2.5
Lightly burned	70	27	36	27	10	2.2
Heavily burned	10	20	50	20	10	2.2
Watershed average:	131	21	37	23	19	2.4

Table II-5. The proportion of plots experiencing from one to four growing seasons prior to burning, and the corresponding average number of growing seasons for the plant communities and soil disturbance classes of Watershed 1. **A)** Plant communities, **B)** Soil disturbance classes. The average number of growing seasons ($\bar{X}$) is calculated as the sum of the products of the annual harvest (proportion of plots) and the number of growing seasons prior to slash burning. See Vegetation section for community abbreviations.

		Proportion of plots (%)				
		Number of growing seasons				
	Number of plots	1	2	3	4	$\bar{X}$ (yr)
A. Plant communities						
COCO-GASH	12	25	67	0	8	1.9
RHMA-GASH	20	15	25	40	20	2.7
ACCI-GASH	7	43	57	0	0	1.6
ACCI-BENE	34	15	26	35	24	2.7
COLA	23	0	22	30	48	3.3
POMU	32	9	22	13	56	3.2
B. Soil disturbance classes						
Undisturbed	11	0	0	18	82	3.8
Disturbed-unburned	40	15	33	20	32	2.7
Lightly burned	70	14	34	26	26	2.7
Heavily burned	10	20	20	30	30	2.7
Watershed average:	131	13	30	24	33	2.8

Table II-6. Summary of sample plot distributions among the plant communities and soil disturbance classes of Watershed 1. **A)** The proportion (%) of plant community plots in each soil disturbance class. **B)** The proportion (%) of soil disturbance class plots in each plant community. See Vegetation section for community abbreviations. Totals for soil disturbance classes may be < 100% because they do not include unclassified plots.

A. Plant communities

	Proportion of plant community plots (%)					
	COCO-GASH	RHMA-GASH	ACCI-GASH	ACCI-BENE	COLA	POMU
Number of plots	12	20	7	34	23	32
Undisturbed	8	15	0	6	13	6
Disturbed-unburned	25	20	14	29	39	34
Lightly burned	67	60	57	59	35	53
Heavily burned	0	5	29	6	13	6
Total:	100	100	100	100	100	100

B. Soil disturbance classes

	Proportion of soil disturbance class plots (%)			
	Undisturbed	Disturbed-unburned	Lightly burned	Heavily burned
Number of plots	11	40	70	10
COCO-GASH	9	8	11	0
RHMA-GASH	27	10	17	10
ACCI-GASH	0	3	6	20
ACCI-BENE	18	25	29	20
COLA	27	23	11	30
POMU	18	28	24	20
Total:	99	97	98	100

transition to dominance by tall shrubs.

The variation in number of burned plots within a community was not correlated with inherent differences in the tendency of communities to burn. Instead, it appears highly correlated with the distribution of woody debris generated by logging. For example, log cover was fairly uniform in the original forest understory of WS1, but after harvest it ranged from 1% on sites that were subsequently undisturbed, to 34% on sites that were later heavily burned.

Because the origin and development of the tree layer in each community were largely dependent on the success of seeding and planting of Pseudotsuga menziesii, patterns of tree abundance were poorly correlated with those of the initial community. Although residual components (e.g., Tsuga heterophylla, Castanopsis chrysophylla) persisted locally as advanced regeneration or as resprouting individuals, post-disturbance understories were generally dominated by P. menziesii. Nevertheless, the rapid return of a dense tree canopy in the Coptis community was notable on both watersheds. It may reflect the interaction of low competition from a depauperate residual flora and a favorable moisture regime.

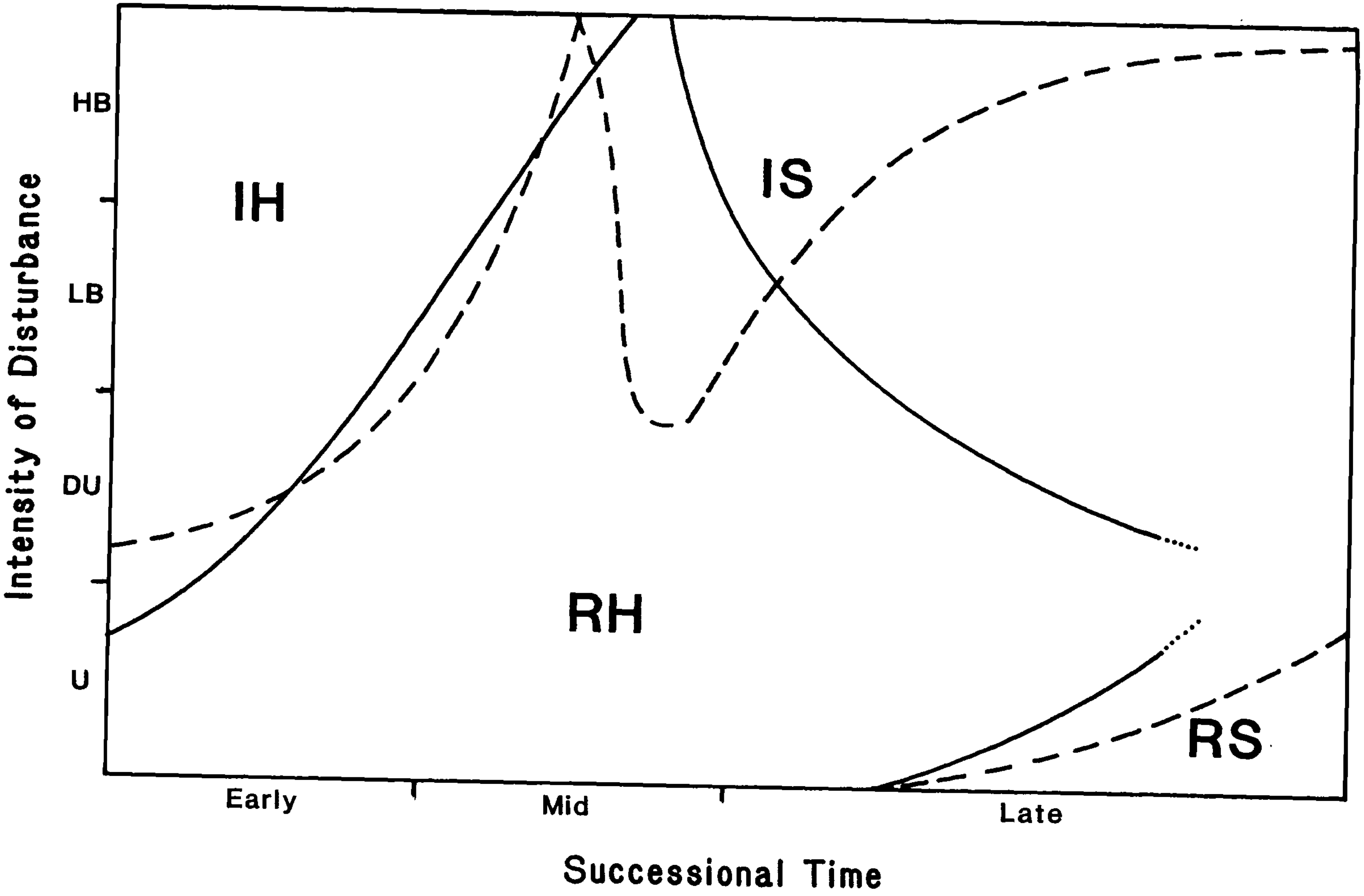
The Influence of Intensity of Disturbance:
A Model of Understory Development

Severity of burning is important when seral vegetation potentially derives from surviving individuals, from a germinating seed bank of species with various temperature optima, or from wind-dispersed species whose establishment is influenced by the availability of mineral soil (Gratkowski 1962, Dyrness 1973, Floyd 1976, Westman 1981, Mallik and Gimingham 1983, Viereck 1983, Christensen 1985). Potentially, the seral vegetation of Pseudotsuga forests is comprised of species with each of these characterisitics. Consequently, where catastrophic disturbance is spatially heterogeneous, successional patterns may vary.

To portray this heterogeneity we have developed a simple descriptive model of early secondary succession in Pseudotsuga forests (Fig. II-13). A two-dimensional vegetation space is defined by gradients of successional time and intensity of disturbance. The space is partitioned into regions representing principal seral groups (i.e., invading herbs, residual herbs, invading shrubs, and residual shrubs). Although any number of seral groups may be present within a region of the mosaic, the model indicates only the dominant forms. The orientation of boundaries indicates the rate of compositional change in time or space: a vertical boundary reflects a rapid successional change, whereas a horizontal boundary suggests a dramatic shift in vegetation composition with a change in disturbance intensity.

Figure II-13. A model of understory development during secondary succession in Pseudotsuga forests. Regions of dominance of principal seral groups are illustrated along gradients of successional time (time since disturbance) and intensity of disturbance. Seral group codes: IH = invading herbs and low shrubs, RH = residual herbs and low shrubs, IS = invading tall shrubs, and RS = residual tall shrubs. The terms early, mid, and late are subjectively defined time intervals. Intensity of disturbance codes: U = Undisturbed, DU = Disturbed-Unburned, LB = Lightly burned, HB = Heavily burned. Solid lines = WS1, dashed lines = WS3.

Figure II-13.


HB
LB
DU
U
IH
IS
RH
RS
Early
Mid
Late
Intensity of Disturbance
Successional Time

The model also illustrates the potential variability in understory development arising from stochastic effects or historical phenomena (e.g., timing of disturbance, variation in initial structure or composition, availability of propagules, fluctuations in climate, or local competitive interactions). The differential distribution of principal seral groups on Watersheds 1 and 3 (shown by the solid and dashed lines, respectively) reflects these factors.

Variation in understory development attributed to the gradient in available moisture is not included in the model. Within predisturbance forest understories, the importance of residual herb or shrub groups is not correlated with the moisture gradient--well-developed herb or shrub strata are widely distributed across the landscape. Further, following disturbance, community patterns suggest that the environmental gradient does not produce a corresponding gradient in the development of residual groups. For example, residuals recover as well in xeric as in mesic and moist communities. Instead, because communities are generally comprised of resilient floras, the seral abundance of a residual group reflects its abundance in the initial community.

The groups of invading herbs and shrubs are also broadly distributed along the moisture gradient within seral *Pseudotsuga* forests. Variation in temperature, soil moisture, or nutrient availability may influence the success of particular species. However, the response of dominant invaders appears more closely tied to the intensity of disturbance (e.g., *Senecio sylvaticus* and *Ceanothus* spp.) or to stochastic factors such as the timing of disturbance (e.g., *Epilobium angustifolium*), the availability of propagules (e.g., *Ceanothus sanguineus*), or the vagaries of weather (e.g., *C. velutinus*). Thus, although the importance of individual residual or invading species may parallel the environmental gradient, the importance of seral groups as a whole, do not.

In the model, invading herbs (IH in Fig. II-13) dominated the disturbed and burned, early-seral sites of both watersheds. On WS1, their greater abundance and persistence on heavily burned sites is illustrated by the sequential prominence of *Montia sibirica*, *Conyza canadensis*, and *Vicia americana* following peaks in the more widespread annuals (e.g., *Senecio sylvaticus*, *Epilobium paniculatum*). Although the duration of dominance by invading herbs increased with disturbance intensity, it was also correlated with a decrease in the abundance of residual herbs.

On the undisturbed sites of WS1, invading herbs were also briefly co-dominant (Fig. II-13), due to the abundance of *Epilobium angustifolium*. Although *E. angustifolium* usually favors burned soils (Ahlgren 1960, Mueggler 1965, Haeussler and Coates 1986), it reached its greatest abundance on WS1 in undisturbed sites because of local variation in the timing of disturbance. Specifically, 82% of the undisturbed plots were harvested during the first year of staggered logging (Table II-5). Thus, early establishment and a prolonged period for vegetative spread of *E. angustifolium* resulted in early co-dominance of undisturbed sites by invading herbs.

Residual herbs and low shrubs played a central role in the development of understories on both watersheds (RH in Fig. II-13), with dominance generally increasing over time, but decreasing with intensity of disturbance. On unburned sites, initially subordinate herbs expanded by a diversity of vegetative strategies: by trailing or freely rooting (e.g., *Rubus ursinus*, *Linnaea borealis*, *Whipplea modesta*, and *Galium triflorum*), by sprouting from tubers (e.g., *Trientalis latifolia*), and by perennating from rhizomes (e.g., *Oxalis oregana*). This expansion probably reflects a temporary release from competition and an increase in resource availability. Similar increases in abundance have been observed following canopy removal or disturbance in other *Pseudotsuga* systems (Isaac 1940, Yerkes 1958, Mueller-Dombois 1965, Steen 1966, Gashwiler 1970, Kraemer 1977).

Within mid- to late-seral sites of both watersheds (Fig. II-13), the prominence of residual herbs reflected the persistence of *Rubus ursinus*, as well as the continuous recovery of initial forest dominants (e.g., *Polystichum munitum*, *Berberis nervosa*, and *Gaultheria shallon*). On WS3, the greater distribution of residual herbs along both gradients of time and disturbance, was associated with the shorter persistence of invading shrubs as well as the greater long-term recovery of initial herb dominants. On early- to mid-seral burned sites, however, the residual herb group was reduced on both watersheds, due to poor development of subordinate residual herbs (Fig. II-13). Species with strategies of above-ground perennation (e.g., *Linnaea borealis* and *Whipplea modesta*) were released on unburned sites, but were largely replaced by species establishing from seed (e.g., *Hieracium albiflorum*) on burned sites.

Invading tall shrubs occupied a larger portion of the successional mosaic on WS1 than on WS3 (IS in Fig. II-13). On WS1 they characterized late-seral sites--both disturbed and burned--displaying earlier prominence and greater abundance with increasing disturbance. In contrast, on WS3, they dominated earlier, but were restricted to burned sites. Local abundance of the dominants, Ceanothus velutinus and C. sanguineus, is commonly associated with the severity of fire (Biswell 1961, Dyrness 1973, Orme and Leege 1976, Conard et al. 1985). Because the buried seeds require cracking of the hilar fissure for germination, higher temperatures result in greater establishment (Gratkowski 1962). Germination may also be stimulated by mechanical scarification, or by elevated soil temperatures associated with insolation--however, subsequent establishment is usually reduced (Pengelly 1966, Hickey and Leege 1970, Orme and Leege 1976).

The abundance patterns of Ceanothus on Watersheds 1 and 3 generally support these observations. However, on WS3, the poorer establishment of C. sanguineus and the dramatic decline of C. velutinus, suggest that seed bank distributions and local climatic fluctuations may ultimately limit the abundance and persistence of invading shrubs following disturbance.

Residual tall shrubs occupied the smallest portion of the successional mosaic on both watershed--undisturbed, late-seral sites (RS in Fig. II-13). Temporal and spatial distributions of this group were fairly similar between watersheds, although differences in initial abundance occasionally confounded post-disturbance patterns. For example, the prominence of residual tall shrubs on undisturbed sites of WS1 may reflect the over-representation of shrub-dominated *Rhododendron* - *Gaultheria* community plots (Table II-6). On the other hand, within the disturbed-unburned sites of WS3, low initial abundance of residual tall shrubs precluded their late-seral dominance (Fig. II-13), despite complete canopy recovery.

Sprouting from adventitious buds at the bases of stems may afford the dominant residuals (e.g., *Acer circinatum* and *Rhododendron macrophyllum*) moderate resistance to fire, although the range of reponse varies considerably (Bailey 1966, Steen 1966, Anderson 1969, Gashwiler 1970, Dyrness 1973, Kraemer 1977). However, because their development following burning is slow compared to invading species (e.g., *Ceanothus velutinus* and *C. sanguineus*), dominance by residual shrubs prior to canopy closure may be limited to unburned sites.

Our model portrays the temporal and spatial distribution of broad vegetation groups during early secondary succession in *Pseudotsuga* forests. Because it is based on the life history traits of the dominant residual and invading species in these systems, its application should be limited to communities comprised of these species (i.e., those in the central western Cascade Range of Oregon). Additionally, we have not included the transitions to understory tree dominance, as the patterns observed were largely dependent on the success of artificial regeneration. Although it portrays the dynamics of seral vegetation initiated by clearcut logging and slash burning, the model probably has broader applicability to forest seres initiated by wildfire.

Our results illustrate that the successional dynamics of broad groups of understory vegetation are a complex consequence of the interactions between initial composition and structure, intensity of disturbance, and stochastic and historical phenomena. A more complete understanding of structural and compositional change lies in the response of individual species to disturbance. A companion paper (Halpern 1987) addresses the dynamics of these species populations.

Chapter 3

SPECIES PATTERNS DURING TWENTY-ONE YEARS OF SECONDARY SUCCESSION IN FORESTS OF THE WESTERN CASCADE RANGE, OREGON

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ABSTRACT

Patterns of abundance were observed and described for vascular plant species during 21 yr of secondary succession in two clearcut and burned *Pseudotsuga* watersheds in the western Cascade Range of Oregon. 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, successional changes were characterized by gradual shifts in the abundance of generally persistent species.

Eleven types of population patterns (species groups) were identified. The interactions of life history traits and disturbance explain the temporal trends of the most common species. Within the invading species groups, the timing of initial establishment, as well as the timing and magnitude of peak abundance, were correlated with the origin of propagules, the phenology of the life cycle, and

the potential for vegetative expansion. Temporal distributions were also influenced by stochastic and historical factors. Contrasting patterns between watersheds reflected differences in the histories of logging and slash burning.

Within the residual species groups, the temporal patterns of abundance reflected numerous factors, including initial species distributions, resistance to logging and burning disturbance, mode of reproduction, morphological characteristics, and spatial variation in disturbance intensity. These observations suggest that succession in Pseudotsuga systems may encompass deterministic components, founded in the life history traits of the available species, as well as historical and stochastic components.

INTRODUCTION

The sequential replacement of organisms in response to the provision of resources by disturbance is the central concept of succession. Although the processes by which species enter, develop, and depart from a community have been studied for decades, ecologists remain divided on the mechanisms which drive succession. There are two contending viewpoints: 1) a holistic perspective emphasizing simple species relationships and replacement sequences leading to predictable, stable climax communities (e.g., Clements 1916, Margalef 1963, Odum 1969, Whittaker 1975) and 2) a reductionist perspective emphasizing the importance of stochastic and other external influences which result in complex and unpredictable successional sequences (e.g., Gleason 1927, Egler 1954, Drury and Nisbet 1973, Pickett 1976, Connell and Slatyer 1977). It is becoming clear from empirical studies, however, that sequences of species replacement are a complex consequence of deterministic, as well as stochastic and historical factors (Cattelino et al. 1979, Miles 1979, Noble and Slatyer 1980, MacMahon 1980, 1981, Horn 1981, Pickett 1982, Finegan 1984, Walker and Chapin 1986).

Much of the confusion and controversy in successional literature has arisen from the interpretation of static observations. Successional theory has largely developed from studies in which stands of different ages are arranged chronologically to portray temporal sequences. Interpretations of these chronosequences, however, are limited by assumptions that predisturbance vegetation, environment, and post-disturbance influences are uniform among sites. As a consequence, species patterns ostensibly associated with successional age, may be confounded by historical or stochastic phenomena.

To separate the effects of successional age from those due to stochastic or site-specific factors, studies based on the repeated observation of permanent plots have been employed. Permanent plot studies may not be successful, however, if sampling is short-term, or if observations are infrequent. Information on the dynamics of short-lived species or on populations with episodic fluctuations may be misinterpreted or lost. Yet, it is clear that such phenomena are frequent and important (e.g., in grasslands [Watt 1960, 1970, Albertson and Tomanek 1965, van den Bergh 1979, van der Maarel 1978, 1981], salt marshes [Beeftink 1979, ter Borg 1979] and heathlands [Lippe et al. 1985]).

In this paper, I examine the patterns of species abundance during 21 yr of succession in two clearcut and burned *Pseudotsuga* forests in the western Cascade Range of Oregon. The study contains one of the longest and most complete permanent plot records of understory development during secondary forest succession. The dynamics of similar species populations have been observed within permanent plots in other western coniferous forests (e.g., Isaac 1940, Steen 1966, Morris 1970, Lyon 1971, 1984, Kraemer 1977, Stickney 1980, 1981, 1985, 1986). However, in many of these studies, an understanding of the origin and persistence of species is limited by the absence of pre-disturbance abundance data, infrequent sampling, or short-term observation (but see Lyon 1984, Stickney 1986).

In this paper, I examine the temporal patterns of species' abundance following catastrophic disturbance, using a detailed record of their frequency of occurrence (constancy) and canopy cover. Pre-disturbance abundance data form a basis for evaluating the expansion or decline of original forest species and for the invasion of others. Estimates of the rates and magnitudes of population change through time are obtained from frequent post-disturbance remeasurements. Furthermore, because original forest plots were classified by plant community and subsequently by disturbance intensity, spatial as well as temporal dynamics of species are revealed.

The patterns illustrate the nature of early community development and provide empirical support for the view that succession reflects deterministic, as well as historical and stochastic, factors. The deterministic component in this system is founded in the life history traits of species in relation to disturbance. Their ultimate expression, however, reflects the initial composition of communities, the availability of propagules, variation in the timing and distribution of disturbance, and local fluctuations in weather.

STUDY AREA

Physical Environment

The study was conducted within two, 100 ha watersheds of the H. J. Andrews Experimental Forest, 80 km east of Eugene, Oregon, on the western slope of the central Cascade Range. Watersheds 1 and 3 (WS1 and WS3) typify the mature, dissected topography of the region, with steep slopes and downward trending 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). The soils are colluvial in nature, derived from pyroclasitc 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, yet only 6% falls between June and August. Average minimum temperatures range from -5.5°C in January to 11.9°C in August and average maxima range from 5.5°C in January to 23.3°C in July (Bierlmaier and McKee in press). Although snowfall is common, snowpacks rarely persist longer than 1-2 weeks.

Vegetation

The vegetation of the study sites is typical of the surrounding *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Prior to logging, forests were comprised of dominant, old-growth *Pseudotsuga menziesii* (300-500 yr old) and *Tsuga heterophylla* in a range of size and age classes. Mature stands of *P. menziesii* (125 yr old) were also present. Sub-canopy and understory tree species included conifers such as *Taxus brevifolia*, *Thuja plicata*, and *Pinus lambertiana* and hardwoods such as *Alnus rubra*, *Acer macrophyllum*, *Castanopsis chrysophylla*, and *Cornus nuttallii*.

Six forest understory communities were arrayed along a complex gradient of moisture and topographic position. They are characterized by species with broad ecological amplitude and typify sites of similar elevation and topography throughout the experimental forest. The communities are closely related to associations of the *Pseudotsuga menziesii* and *Tsuga heterophylla* series of Hemstrom et al. (1985). Characteristics of these communities are presented in Table III-1. Detailed descriptions of community composition, structure, and distribution have been presented elsewhere (Rothacher et al. 1967, Dyrness 1973, Hawk and Dyrness 1973, Halpern 1987).

Table III-1. Characteristics of the six forest understory communities of Watersheds 1 and 3. Communities are arranged in order of increasing available moisture.

Plant community	Topographic position and aspect	Dominant growth-form(s)	Dominant species	Corresponding plant association (Hemstrom et al. 1985)
Corylus cornuta - *Gaultheria shallon*	ridgetops, south-facing upper-slopes	tall shrubs	*Corylus cornuta*, *Acer circinatum*, *Berberis nervosa*	*Pseudotsuga menziesii* / *Berberis nervosa*
Rhododendron macrophyllum - *Gaultheria shallon*	ridge-tops, mid-slope benches	tall shrubs	*Rhododendron macrophyllum*, *Gaultheria shallon*	*Tsuga heterophylla* / *Rhododendron macrophyllum* - *Gaultheria shallon*
Acer circinatum - *Gaultheria shallon*	mid- to upper-south-facing slopes	herbs and low shrubs, (tall shrubs)	*Acer circinatum*, *Gaultheria shallon*	*Tsuga heterophylla* / *Berberis nervosa* - *Gaultheria shallon*
Acer circinatum - *Berberis nervosa*	mid- to lower-slopes	tall shrubs	*Acer circinatum*	*Tsuga heterophylla* / *Berberis nervosa*
Coptis laciniata	mid- to lower-slopes	trees, (herbs and low shrubs)[1]	*Berberis nervosa*, *Coptis laciniata*, *Linnaea borealis*	*Tsuga heterophylla* / *Berberis nervosa* (shade phase)
Polystichum munitum	bottom-slopes, steep north- to east-facing slopes, seeps	herbs and low shrubs	*Polystichum munitum*, *Acer circinatum*	*Tsuga heterophylla* / *Polystichum munitum*

---

[1] depauperate understory

History of Disturbance

Although both watersheds were logged and broadcast burned, aspects of the timing and distribution of disturbances differed between sites. The entire 96 ha of WS1 was harvested over a 4 yr period--between fall 1962 and summer 1966--using a skyline cable to transport logs to a single landing at the mouth of the watershed. Slash was broadcast burned in October 1966. On WS3, however, 3 stands of 5, 9, and 11 ha (one quarter of the watershed) were harvested during the 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 aerially 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, two-year-old *P. menziesii* were planted. Again, in April 1971, two- and three-year old trees were planted within 40 ha of the south-facing slope. On WS3, all clearcut units were planted with three-year-old *P. menziesii* between March and May 1964.

METHODS

Field Sampling

Permanently staked sample plots of 2 X 2 m were established in forest understories during the summer of 1962, prior to clearcut logging. 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. The sampling protocol is presented in detail in Halpern (1987). Forest understories were initially sampled during summer 1962, prior to disturbance. Following logging, plots were relocated or reestablished from field notes and resampled. Both watersheds were broadcast burned during fall, plots were again relocated, and resampled the ensuing growing season. Post-disturbance remeasurements were conducted annually from 1967-1973 on WS1 and from 1964-1972 on WS3. Thereafter, sampling generally occurred in alternate years.

Data Reduction and Analysis

To assess the influence of initial community characteristics and the intensity of initiating disturbance on species patterns, we grouped sample plots by two criteria. First, each plot was assigned to one of six plant communities based upon the initial classification developed for forest understories (see Vegetation section). Second, immediately following slash burning, each plot was subjectively assigned to one of four soil disturbance classes based on the following classification (Tarrant 1956, Dyrness et al. 1957, Dyrness 1973):

1. Undisturbed. The soil surface appeared similar to that prior to disturbance, 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 no evidence of fire.
3. Lightly burned. Surface litter was charred by fire but was not completely removed.
4. Heavily burned. Surface litter was completely consumed by intense fire exposing a highly colored mineral soil.

The computer programs CONDENSE and DATAEDIT of the Cornell Ecology Program Series (Gauch 1973, Gauch and Singer 1982) and additional programs developed at Oregon State University (B. G. Smith unpublished programs) were used to reduce and summarize species data. The frequency of occurrence in sample plots (constancy) and the mean percent cover (± 1 S.E.) for all species were calculated for each watershed and for each plant community and disturbance class within each watershed.

RESULTS AND DISCUSSION

The successional dynamics of species may be envisioned as changes in their frequency of occurrence (constancy) and canopy cover with time. Species comprising the seral flora of Watersheds 1 and 3 displayed a diversity of such temporal changes, as illustrated by their broadly overlapping curves of both constancy and cover. Although these changes were essentially continuous in nature, groups of species exhibited similar patterns of response. I identified a total of 11 such population patterns, grouping species according to four criteria:

1. Seral origin (invader or residual): Invaders were defined as species absent from undisturbed forest communities or restricted to locally disturbed microsites, whereas residuals were defined as species characterizing undisturbed forest communities regardless of their abundance (Dyrness 1973).

2. Phase of peak abundance: Early- (0-4 yr), mid- (5-10 yr), or late-seral (> 10 yr following disturbance).

3. Magnitude of abundance (dominant or sub-dominant): Dominant species were defined as those which exhibited canopy cover > 5% during any growing season; the remaining species were considered as sub-dominant.

4. Duration of dominance: Short (1-2 yr), moderate (3-5 yr), or long (> 5 yr).

A summary of group characteristics and representative species are presented in Table III-2.

Table III-2. Summary of abundance characteristics for 11 seral species groups. Codes for growth-forms are: H = herb and low shrub, S = tall shrub, and T = tree. See text (Results and Discussion) for explanation of codes for peak abundance characteristics and duration of dominance. Population patterns are not plotted for species enclosed in parentheses.

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

I illustrate the dynamics of each species group in graphs of constancy and mean canopy cover for representative species, plotted as a function of time since disturbance. Because the watersheds experienced chronologically different histories of logging and slash burning, a standardized time axis facilitates the comparison of pattern between sites. Thus, pre-disturbance samples occur at times "-4" and "-1" for WS1 and WS3, respectively; times "0" and "1" represent the growing seasons following completion of logging and following slash burning for both watersheds.

Although a total of 196 species comprised the seral flora of Watersheds 1 and 3, for simplicity and clarity I consider only the most common species--those with constancy > 20% or canopy cover > 1% for one or more growing seasons. Taxonomy and nomenclature follow Hitchcock and Cronquist (1973).

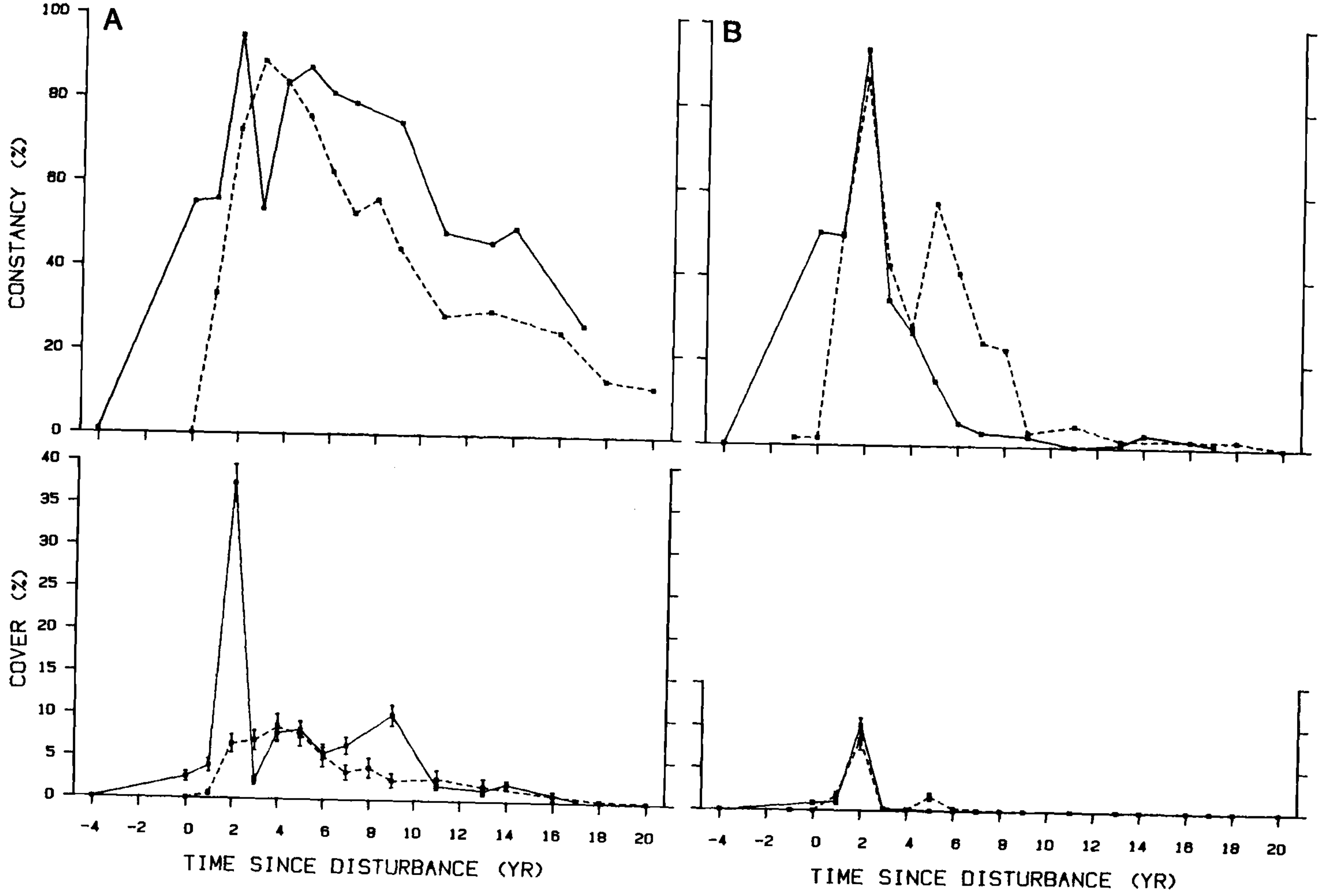
Population Patterns

Invading species groups

1. _Group I1 species_. Species of the I1 group were the first to peak in abundance, although their rapid expansion was transient (Fig. III-1). They included 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. III-1A) and _S. sylvaticus_ (Fig.

Figure III-1. Changes in constancy and mean canopy cover with time for species of the I1 group on Watersheds 1 and 3. **A)** Epilobium paniculatum, **B)** Senecio sylvaticus. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-1.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III-1B), 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 the cover, it declined more slowly, especially within the population of *E. paniculatum* on WS1.

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. Open regeneration sites are required for propagules disseminated at this time. The availability of these sites on WS1 and their absence on WS3 are reflected in the dramatic difference in post-logging (year 0) frequency of occurrence of these annuals (Fig. III-1). On WS1, although total cover was rather low, both *S. sylvaticus* and *E. paniculatum* occupied > 50% of the sample plots. Due to staggered harvesting, germination sites were available for 1-3 yr prior to burning (varying with location). On WS3, however, winter logging succeeded seed dispersal and thus precluded their establishment prior to burning. Differences in the post-logging establishment of annuals may also influence their post-burning abundance. For example, the markedly greater cover of *E. paniculatum* on WS1 than on WS3 (Fig. III-IA), may have reflected a greater abundance of on-site seeds--those derived from individuals established prior to burning.

A similar relationship between the timing of disturbance and the availability of propagules is important in the early dynamics of old field seres (Bonck and Penfound 1945, Keever 1950, 1979, 1983, Levin 1966, Bazzaz 1968, Pickett 1982).

The most striking characteristics of both annual populations were their ephemeral dominance (more dramatically observed on WS1 than on WS3) and their prominence on burned microsites. Both phenomena have been widely observed following fire in western coniferous forests (Yerkes 1958, Brown 1963, Bailey 1966, Morris 1970, Dyrness 1973, Kraemer 1977, Stewart 1978, Stickney 1981). Peak abundances typically coincide with the second growing season due to the timing of seed availability and the tendency to burn 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) a poor competitive ability compared with perennials such as _E. angustifolium_ which, once established, are more efficient in nutrient uptake (van Andel and Vera 1977). Whether _E. paniculatum_ shares these characteristics is unclear. That it displayed a protracted period of recruitment (Fig. III-1A), however, suggests that _E. paniculatum_ may be less limited by nutrient requirements and competition from associated species than _S. sylvaticus_.

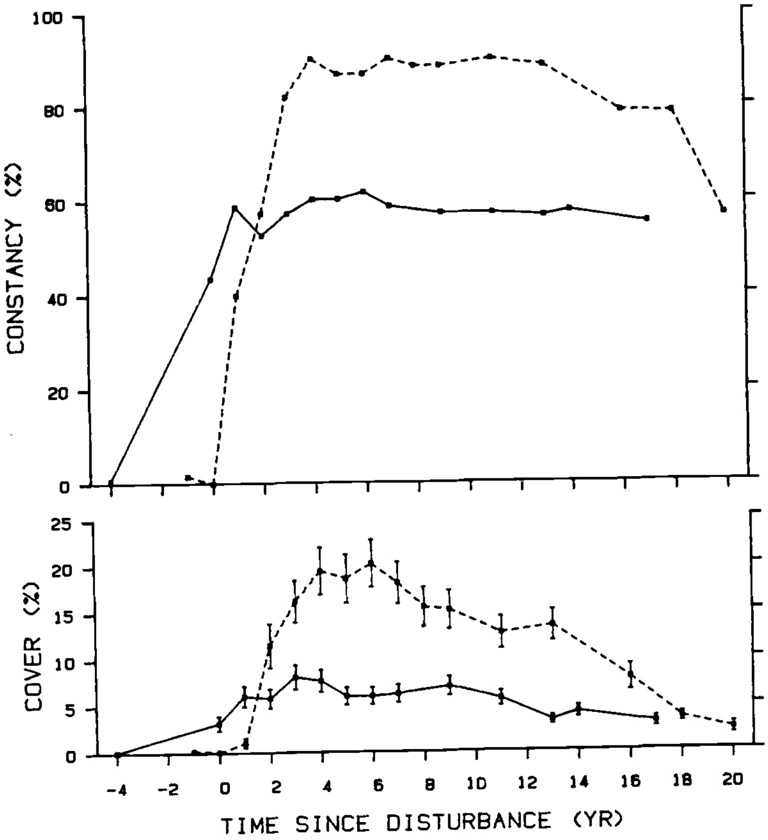
2. _Group I2 species_. A single, perennial colonizer, _Epilobium angustifolium_, characterized this species group. Its establishment and expansion were relatively rapid and widespread on both watersheds, although temporally displaced between sites due to

differences in disturbance history (Fig. III-2). Constancy peaked in year 1 on WS1 and in year 4 on WS3, 5 yr after the initiation of logging on each watershed. Mean canopy cover increased similarly, but peaked 2 yr later on each site. Subsequent changes in constancy were minimal during the mid- to late-seral periods, whereas cover declined slowly. Thus, *E. angustifolium* persisted as a dominant herb through a major portion of both seres.

The long-term dynamics of *E. angustifolium* suggest a complex reproductive and competitive response following disturbance. A widely distributed perennial herb, its abundance following catastrophic disturbance has been attributed to vegetative reproduction of surviving individuals (Moss 1936, Viereck 1973, Viereck and Dyrness 1979, Bartos and Mueggler 1981, Foster 1985, Stickney 1986) and to establishment from copious wind-borne seed (Lyon 1971, Dyrness 1973, Johnson and Rowe 1977, Black and Bliss 1978, Hill and Stevens 1981, Van Cleve and Viereck 1981, Haeussler and Coates 1986, Stickney 1986). Its prominence on Watersheds 1 and 3 likely derived from multiple mechanisms. Initial establishment was primarily from off-site wind dispersed seed. Subsequent increases in constancy and cover, however, were probably more complex. Vegetative propagation commonly dominates following initial seedling establishment (Ingram 1931, van Andel and Rozema 1974, van Andel 1975, van Andel and Vera 1977). Nevertheless, recruitment of seed from off-site and local sources probably occurred in adjacent, open microsites and, particularly on WS1, where areas were harvested during subsequent seasons of logging.

Figure III-2. Changes in constancy and mean canopy cover with time for *Epilobium angustifolium* (I2 group) on Watersheds 1 and 3. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-2.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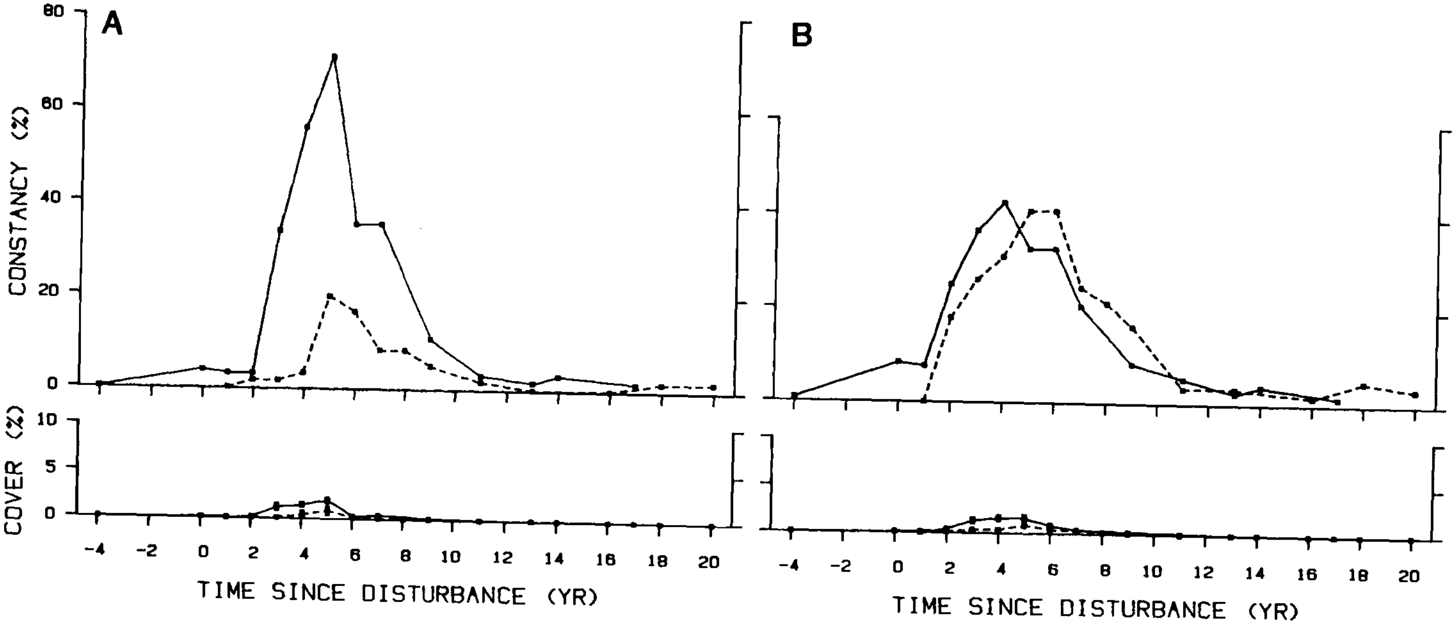
TIME SINCE DISTURBANCE (YR)

The resistance of *E. angustifolium* to catastrophic disturbance was also evident on WS1. Individuals which developed during the period of staggered harvesting displayed vigorous sprouting from rhizomes following burning, a response which reflects the depth of its perennating buds (Moss 1936). On WS3, in contrast, establishment of *E. angustifolium* was insignificant prior to burning (Fig. III-2) due to the timing of disturbance and of seed dispersal. Harvesting occurred after fall seed dissemination, limiting its development during the following growing season (year 0). Although the early dynamics of *E. angustifolium* on Watersheds 1 and 3 reflected differing histories of disturbance, subsequent trends in constancy and cover were similar, including its long-term persistence within both open and shaded communities.

3. *Group I3 species*. The species representing this group comprised a suite of sub-dominant, invading herbs which achieved greatest abundance between years 3 and 5 (Fig. III-3). All were wind-dispersed members of the family Compositae, including the biennials *Cirsium vulgare* and *Lactuca serriola* and the short-lived perennials *Agoseris grandiflora*, *C. arvense*, *C. brevistylum*, and *Gnaphalium microcephalum*. Although the annual, *Agoseris heterophylla*, was also observed, it was fairly uncommon. The *Agoseris* (Fig. III-3A) and *Cirsium* species (Fig. III-3B) were each treated as single taxa due to the difficulty in identifying first year rosettes to species. Trajectories of constancy and canopy cover for all taxa were typically bell-shaped curves--although comparatively flattened for cover--with long reduced tails. Maximum

Figure III-3. Changes in constancy and mean canopy cover with time for species of the I3 group on Watersheds 1 and 3. **A)** *Agoseris* spp., **B)** *Cirsium* spp. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-3.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TIME SINCE DISTURBANCE (YR)

constancy (20-70%) coincided with peak canopy cover (1-3%) (Fig. III-3). The species as a group were consistently most abundant within the lightly and heavily burned soil classes and within the *Acer* - *Gaultheria* community.

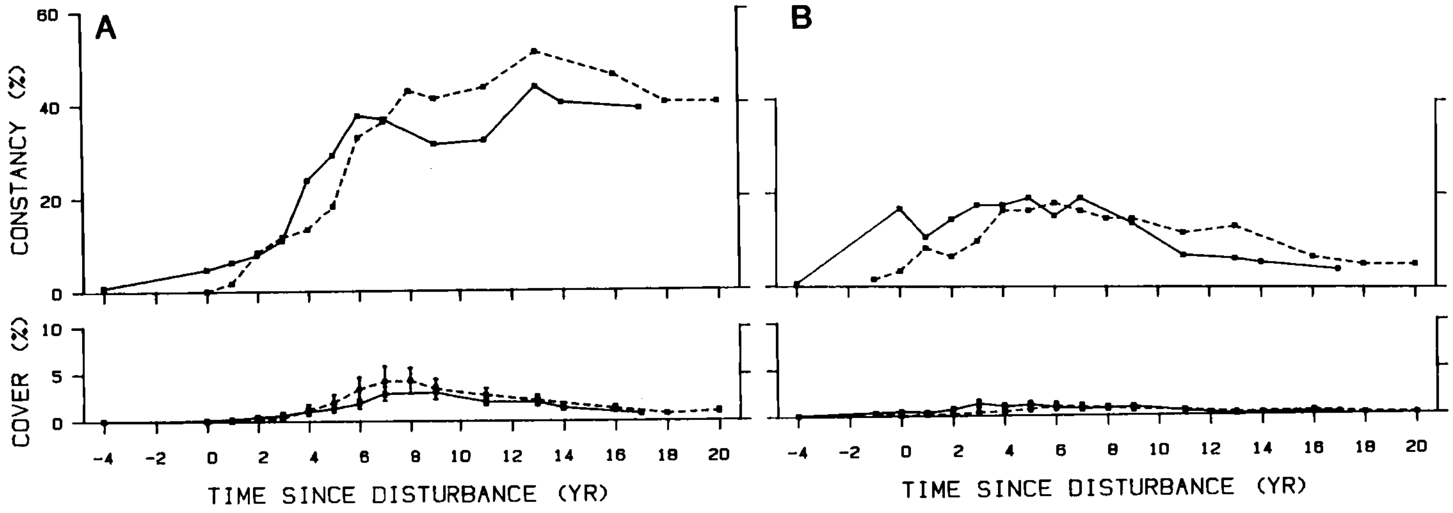
Population patterns within the I3 group were displaced temporally relative to those of the I1 group. Abundances were also consistently lower than those of co-occurring dominant invading species groups. Their delayed development and subordinate status may have reflected the interaction of numerous endogenous and exogenous factors, including the relationship between life history traits and the timing of disturbance, morphological constraints, and historical or stochastic elements. The developmental cycles of biennial and short-lived perennial species are typically slower than those of winter annuals. Additionally, the transition from vegetative rosettes to upright and flowering individuals may be highly dependent on resource availability (Peterson and Bazzaz 1978, Kelly 1985). Therefore, following fall disturbance, biennial populations recruited from late-summer, wind-borne seed would not display maximum abundance until at least 3 yr after slash burning. Furthermore, the root and shoot morphologies of species in this group may limit their potential for lateral spread compared with long-lived rhizomatous perennials such as *Epilobium angustifolium*. Thus, it appears that annual increases in mean canopy cover of I3 species may be dependent on continuous recruitment as on the expansion of established individuals.

Historical and stochastic factors may also restrict the abundance of these populations. For example, local seed rain may vary temporally in relation to the changing composition of source populations (surrounding clearcuts, roadbanks, and other disturbed areas) or spatially due to the vagaries of dispersion (Rabinowitz and Rapp 1980). However, variation or periodicity in the seed crop associated with climatic trends or intrinsic factors are probably less common among these fugitive species than among large seeded groups such as shrubs and trees (e.g., Franklin 1974, Davies 1976, Eis 1973, 1976, Waller 1979). In fact, biennial herbs tend to produce greater numbers of seeds than do either herbaceous annuals or perennials (Salisbury 1942, Fenner 1985). That a majority of the biennial and short-lived perennial species of Watersheds 1 and 3 were most abundant during the early- to mid-seral periods, supports the concept that biennial species are typically found in the transitional stage between an initial, open, disturbed phase and a subsequent closed, competitive phase (Fenner 1985).

4. *Group I4 species*. This group was characterized by an array of sub-dominant, invading herbs and shrubs displaying greatest abundance between years 3 and 9 (Fig. III-4). Two principal trends in constancy were evident--a broad, shallow, bell-shaped curve for taxa such as *Rubus leucodermis* (Fig. III-4B), *Vicia americana*, and *Bromus* spp. and a moderate increase to a plateau for species such as *Anaphalis margaritacea* (Fig. III-4A) and *Collomia heterophylla*. Trajectories of canopy cover for all taxa were typified by flattened bell-shaped curves with maxima < 5% and with long persistent tails. Thus, species of the I4 group were distinguished from those of the

Figure III-4. Changes in constancy and mean canopy cover with time for species of the I4 group on Watersheds 1 and 3. **A)** Anaphalis margaritacea, **B)** Rubus leucodermis. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-4.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TIME SINCE DISTURBANCE (YR)

I3 group by slower rates of expansion and extinction and by generally later peak development. As a group, I4 species showed little consistent relationship with site characteristics, although the most common species, *A. margaritacea* and *R. leucodermis*, showed greatest development within the mesic to moist communities.

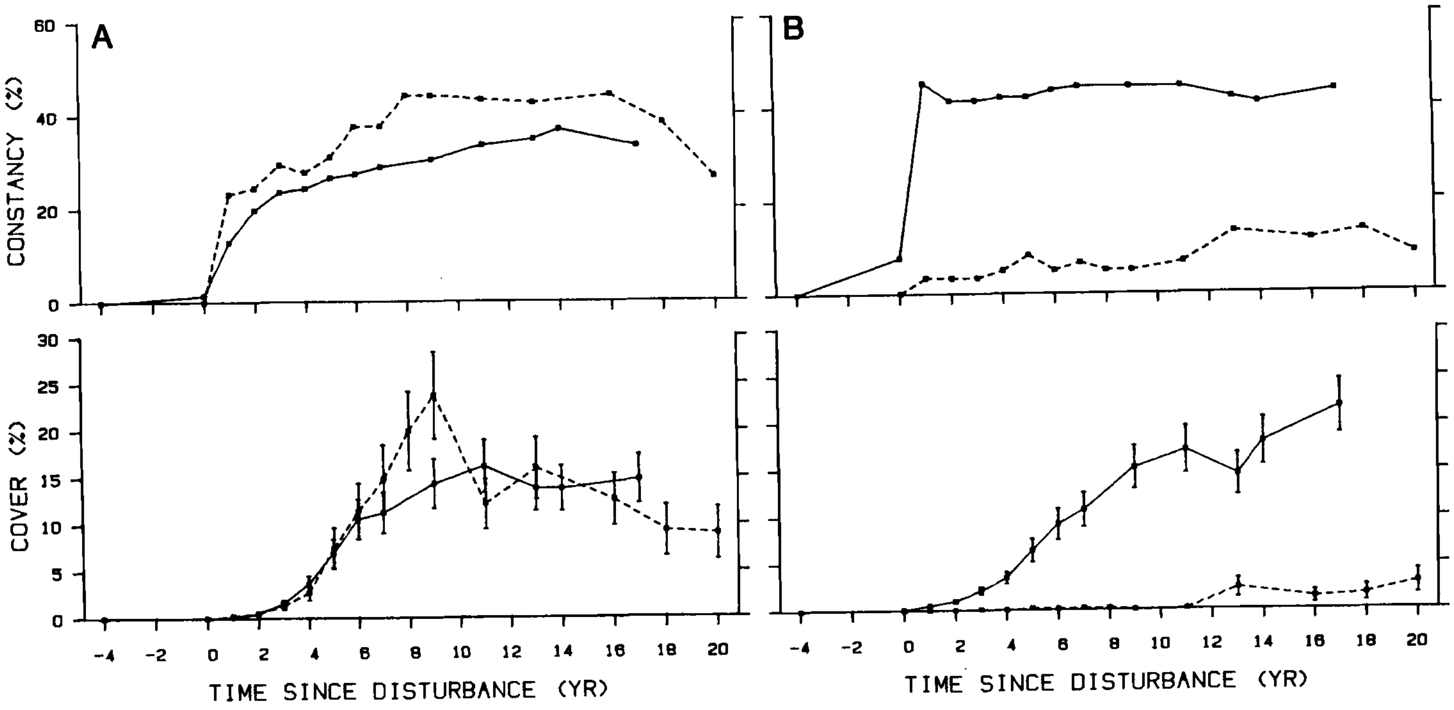
The long-term changes in constancy for these perennials suggest slow continuous entrance into sample plots and greater longevity or shade tolerance than species of the I3 group. Yet, because the data are not demographic, I am unable to distinguish among the regenerative strategies of species which reproduce both sexually and vegetatively. For example, although *A. margaritacea* and *R. leucodermis* are rhizomatous perennials, both produce prolific seed. Thus, gradual increases in their frequency of occurrence in plots may have represented continuous recruitment of seedlings or lateral growth of adjacent individuals. Seeds of *A. margaritacea* are wind-dispersed; although initial establishment was most likely by this mechanism, buried viable seeds (of indeterminate age) have also been found both within old-growth and seral forest communities (Kellman 1974). *Rubus leucodermis* may have originated from buried seed or from fleshy fruits dispersed by animals. Although species in the genus *Rubus* typically form a persistent seed bank (Olmsted and Curtis 1947, Livingston and Allessio 1968, Kellman 1970, Marks 1974, Moore and Wein 1977, Graber and Thompson 1978, Hill and Stevens 1981, Naka and Yoda 1984), the longevity of buried seeds of *R. leucodermis* is unknown. Additionally, original individuals of *R. leucodermis*--which occurred locally on disturbed microsites--may have persisted through disturbance.

5. Group I5 species. Represented by the tall shrubs, *Ceanothus velutinus* and *C. sanguineus*, this invading group dominated the mid- to late-seral periods (Fig. III-5). Recruitment was most rapid immediately following slash burning, although scattered individuals were observed following the completion of logging on WS1 (year 0). Constancy increased rapidly between years 0 and 2 and more slowly through the remainder of the sere, although *C. sanguineus* (Fig. III-5B) was much less common on WS3. 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, *C. velutinus* (Fig. III-5A) peaked more sharply, declined rapidly between years 9 and 11, and rather slowly thereafter. The importance of both species increased with intensity of disturbance. Peak cover on heavily burned sites was 3-5 times greater than that on undisturbed sites. The patterns of abundance within initial plant communities were, however, less distinct.

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 X 10^5 - 6 X 10^5 viable seeds/ha (Gratkowski 1962, Hickey and Leege 1970, Lyon 1971) may persist in the soil for centuries. Elevated temperatures stimulate germination by cracking the hilar fissure, promoting the absorption of moisture (Gratkowski 1962). Germination also may be stimulated by mechanical scarification or by elevated soil

Figure III-5. Changes in constancy and mean canopy cover with time for species of the I5 group on Watersheds 1 and 3. **A)** Ceanothus velutinus, **B)** Ceanothus sanguineus. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-5.



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TIME SINCE DISTURBANCE (YR)
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temperatures associated with insolation, although subsequent establishment is usually much poorer (Pengelly 1966, Hickey and Leege 1970, Orme and Leege 1976). Emergence is typically enhanced by a cold stratification period following burning, although immediate recruitment has also been observed (Orme and Leege 1976). Thus, _Ceanothus_ typically establishes during the first growing season after stratification; subsequent emergence decreases rapidly with time (Cronemiller 1959, Orme and Leege 1976). Changes in the pre- and post-burning constancy of _Ceanothus_ on Watersheds 1 and 3, support these observations.

The relative abundance of seral _Ceanothus_ species is commonly correlated with the intensity of burning (Biswell 1961, Dyrness 1973, Orme and Leege 1976, Conard et al. 1985). The greatest rates of germination typically result from fall burns which are characterized by low humidities and relatively dry litter. Regardless of the season of disturbance, greater germination also results from locally high concentrations of fuel. Interestingly, 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 and with that documented elsewhere (Biswell 1961, Orme and Leege 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 paucity of _C. sanguineus_ on

WS3 may similarly suggest variation its historical distribution, although at a significantly coarser scale.

Differences in the long-term dynamics of *Ceanothus* on Watersheds 1 and 3 emphasize the complex nature of its 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. Undoubtedly these were influential on Watersheds 1 and 3 (Halpern 1987).

The longevity of *Ceanothus* may vary significantly, although it appears, in part, to be a function of competition from associated trees (Zavitkovski and Newton 1968, Hickey and Leege 1970, Conard et al. 1985). In the Oregon Cascade Range, the functional life span of *C. velutinus* is estimated as 20-40 yr (Conard et al. 1985). However, environmental and biotic influences may reduce the vigor of *Ceanothus* individuals, promoting earlier senescence. These include injury to root crowns from snow loading (Zavitkovski and Newton 1968), stem dieback following severe frost (Young and Payne 1948, Stickney 1965, Leege and Hickey 1975, Kraemer 1977), herbivory by ungulates and insects (Hickey and Leege 1970, Wittinger et al. 1977), and fungal infection (Tarry 1968, Zavitkovski and Newton 1968). On WS3, the precipitous decline in canopy cover of *C. velutinus* between years 9 and 11 (Fig. III-5A) represents one such phenomenon. Coincidental with the canopy dieback documented by Kraemer (1977), it may be a consequence of severe winter frost during 1972-1973 (years 9-10). The apparent absence of dieback on

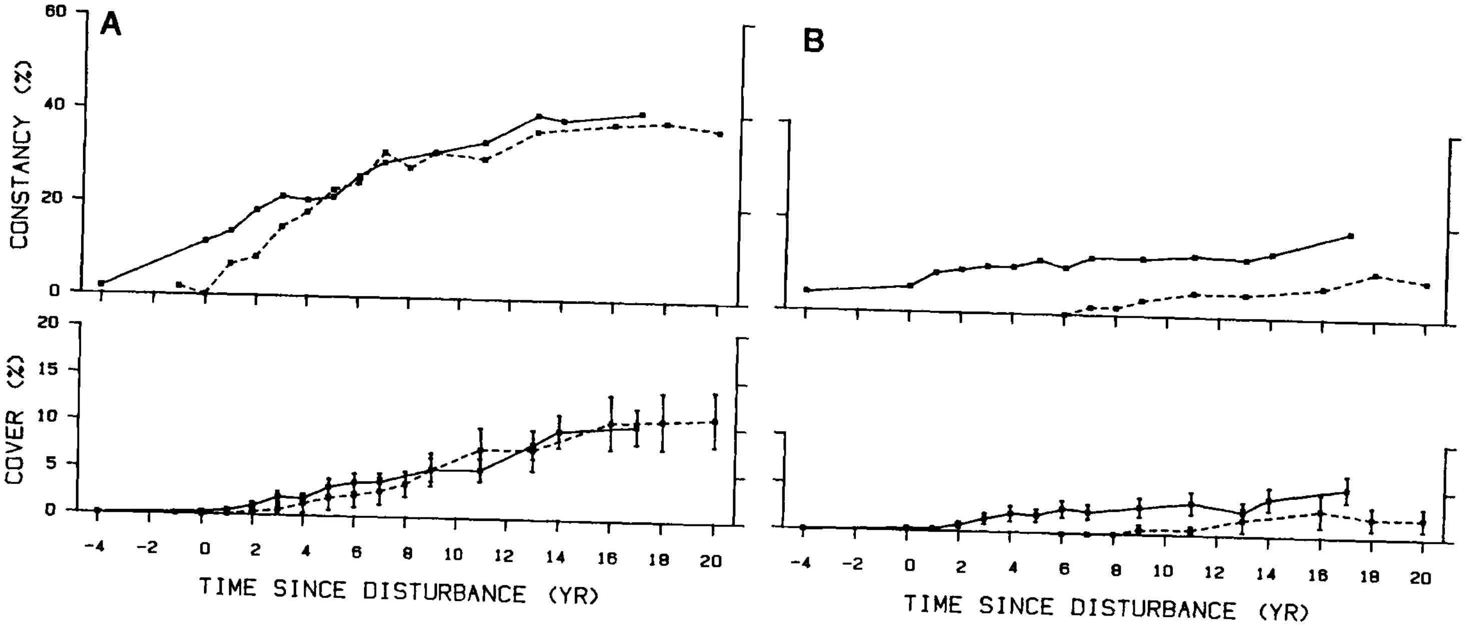
WS1 is puzzling. It may reflect the greater vigor of younger individuals on that site, or differences in local weather conditions. Nevertheless, the contrast illustrates the potential influence of stochastic events on the long-term dynamics of species populations.

6. Group I6 species. These species were invading perennials of various growth-forms which achieved dominance late in the sere. The most abundant species included the fern, *Pteridium aquilinum* (Fig. III-6B), and the tall shrub, *Rubus parviflorus* (Fig. III-6A), 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 15-40%, while peak cover averaged between 3 and 11%. These long-terms trends suggest that I6 species may exhibit the greatest longevity of any colonizers observed.

Similar post-disturbance patterns of abundance for *Rubus parviflorus* and *Pteridium aquilinum* have been described for other seral forests of the Cascade Range (Isaac 1940, Kraemer 1977) and the northern Rocky Mountains (Zamora 1975, Irwin and Peek 1979, Stickney 1980, 1986). Interestingly, the latter populations may derive from surviving forest understory individuals, unlike the colonizers of Watersheds 1 and 3. Although both *R. parviflorus* and *P. aquilinum* were observed in the initial forest plots of Watersheds 1 and 3, they were rare, restricted to disturbed microsites (Dyrness 1973). Thus, the contribution of surviving individuals to the long-term dynamics of these species was probably small.

Figure III-6. Changes in constancy and mean canopy cover with time for species of the I6 group on Waterhseds 1 and 3. **A)** *Rubus parviflorus*, **B)** *Pteridium aquilinum*. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-6.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Species of the I6 group on Watersheds 1 and 3 possess numerous modes of origin: 1) buried viable seeds (e.g., *R. parviflorus* and *P. emarginata*), 2) animal dispersed seeds (e.g., *R. parviflorus* and *P. emarginata*), and 3) wind-dispersed seeds and spores (e.g., *S. scouleriana* and *P. aquilinum*). Although the longevity of *R. parviflorus* seed is unknown, it may be abundant within forest soils of the *Tsuga heterophylla* zone and may be stimulated by soil disturbance, canopy removal, or fire. Estimates of buried viable seed from stands in coastal British Columbia and the Oregon Coast Range averaged between 6.2 X 10^4 and 2.4 X 10^5 individuals/ha (Kellman 1970, Stewart 1978). Reproduction of *P. 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, spore viability may be greatly diminished several years after dispersal (Conway 1949). Germination also appears to be limited within established colonies or under closed vegetation (Hauessler and Coates 1986).

Extensive lateral expansion from established rhizomes may explain the persistent increase in constancy and canopy cover of both perennials. This regenerative strategy has been widely observed for *R. parviflorus* (Mueggler 1965, Wright 1972, Lyon and Stickney 1976, Volland and Dell 1981, Cholewa and Johnson 1983, Crane et al. 1983, Hauessler and Coates 1986, Stickney 1986) and for *P. aquilinum* (Summerhayes and Williams 1926, Ingram 1931, McCulloch 1942, McMinn 1951, Watt 1955, Mueller-Dombois 1965, Fletcher and Kirkwood 1979, Hobbs and Gimingham 1984, Hobbs et al. 1984, Hauessler and Coates 1986).

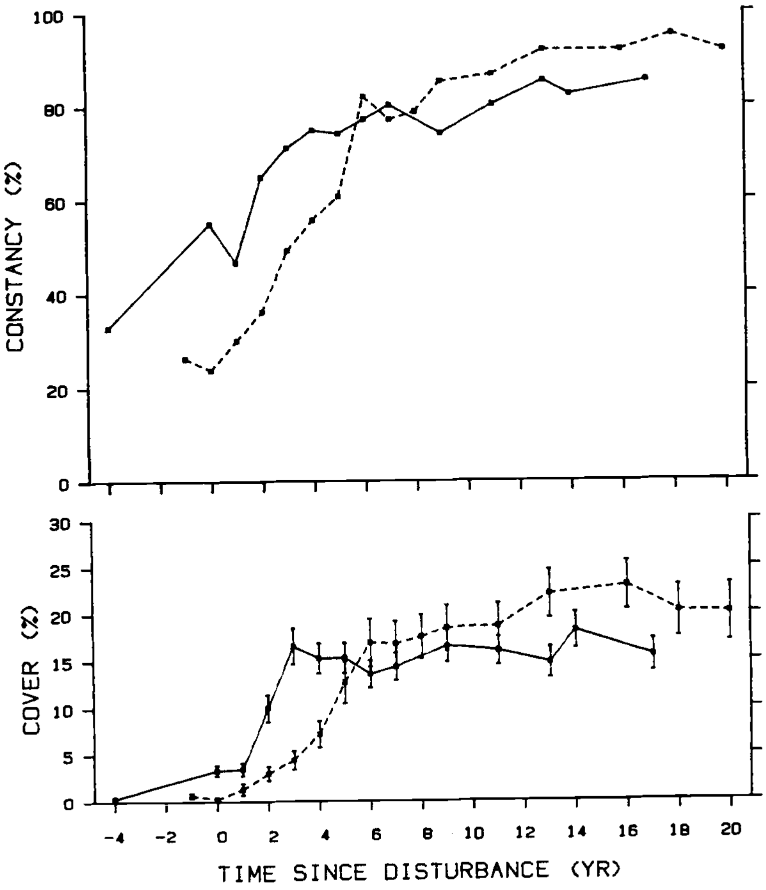
The slower increase in constancy and cover of *R. parviflorus* (Fig. III-6A) relative to *Ceanothus* spp. (Fig. III-5), suggests an inherently slower rate of growth. However, it may also indicate that establishment of *R. parviflorus* is partly dependent on animal-dispersed seed. Hauessler and Coates (1986) suggest that germination of newly deposited seed may be 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 (Potzger and Potzger 1950, Bazzaz 1968, McDonnell and Stiles 1983). The establishment of these species appears to be temporally related to the availabilty of suitable animal habitat, vertical structure, or sources of food.

Residual species groups

1. *Group R1 species*. A native trailing blackberry, *Rubus ursinus*, was the only species in this group. An inconspicuous member of the undisturbed forest understory, populations expanded dramatically following disturbance and remained prominent through both seres (Fig. III-7). Constancy increased rapidly to 75 and 82% within 4 and 6 yr following burning on Watersheds 1 and 3, respectively, and continued to rise, although more slowly, through final sampling. Mean canopy cover increased rapidly to 16% after 3

Figure III-7. Changes in constancy and mean canopy cover with time for *Rubus ursinus* (R1 group) on Watersheds 1 and 3. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-7.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TIME SINCE DISTURBANCE (YR)

yr on WS1 and to 17% after 6 yr on WS3. Subsequent changes in cover varied 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 intensity of disturbance. Together with the annual and perennial colonizers of the I1 and I2 groups, R. ursinus dominated the herb stratum as early as 2-5 yr following disturbance, exhibiting the earliest expansion of any forest residual.

The release of R. ursinus has been widely observed following catastrophic disturbance in Pseudotsuga forests of the Pacific Northwest (Isaac 1940, Neiland 1958, Yerkes 1958, Mueller-Dombois 1965, Bailey 1966, Steen 1966, Gashwiler 1970, Dyrness 1973, Kraemer 1977). Rapid increases in constancy and cover on Watersheds 1 and 3 were achieved primarily through the above-ground perennation of trailing and climbing stems. 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. It showed vigorous vegetative spread on all substrates including logs, stones and stumps; among associated herb and low shrub species; and vertically into the crowns of tall shrubs and trees. Although seedlings have been observed following logging (Stewart 1978) and its post-disturbance fruit production may be prolific, the longevity of buried seeds and the role of sexual reproduction in its expansion are unknown. Current trends in constancy and cover suggest that R. ursinus may persist as a dominant component of the herb stratum until it is again supressed by canopy closure.

2. *Group R2 species*. Three subordinate forest herbs and sub-shrubs, *Trientalis latifolia*, *Whipplea modesta*, and *Hieracium albiflorum*, represented this group (Fig. III-8). Their release resembled that of *R. ursinus*. For example, long-term trends in constancy were similar to *R. ursinus*--increasing rapidly for 4-6 yr following disturbance and fluctuating near peak levels through final sampling. The R2 species had a different pattern of canopy cover, however, with broad bell-shaped curves and elongate tails. Peak abundances ranged from 4-12% between years 4 and 9. These species patterns resembled those of the I4 group (Fig. III-4), although the latter were generally less abundant.

Differences in the regenerative strategies of species of the R2 group were reflected in their response to disturbance. *Whipplea modesta* (Fig. III-8B), a trailing sub-shrub which freely roots at the nodes (Hitchcock and Cronquist 1973), was most abundant within the two unburned soil classes and uncommon within the heavily burned class. Its susceptibility to fire probably reflects the position of its perennating structures. *Trientalis latifolia* (Fig. III-8A) displayed a greater range of response, expanding within all soil disturbance classes, although progessively later with increased disturbance. Its perennating structures are short, thickened, tubers, presumably less sensitive to fire. The relative role of reproduction by seed is unknown for both of these species.

In contrast to these patterns, *Hieracium albiflorum* (Fig. III-8C) exhibited its greatest abundance on heavily burned sites. Although its resistance to fire is rather poor due to the exposure

Figure III-8. Changes in constancy and mean canopy cover with time for species of the R2 group on Watersheds 1 and 3. **A)** *Trientalis latifolia*, **B)** *Whipplea modesta*, **C)** *Hieracium albiflorum*. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-8.

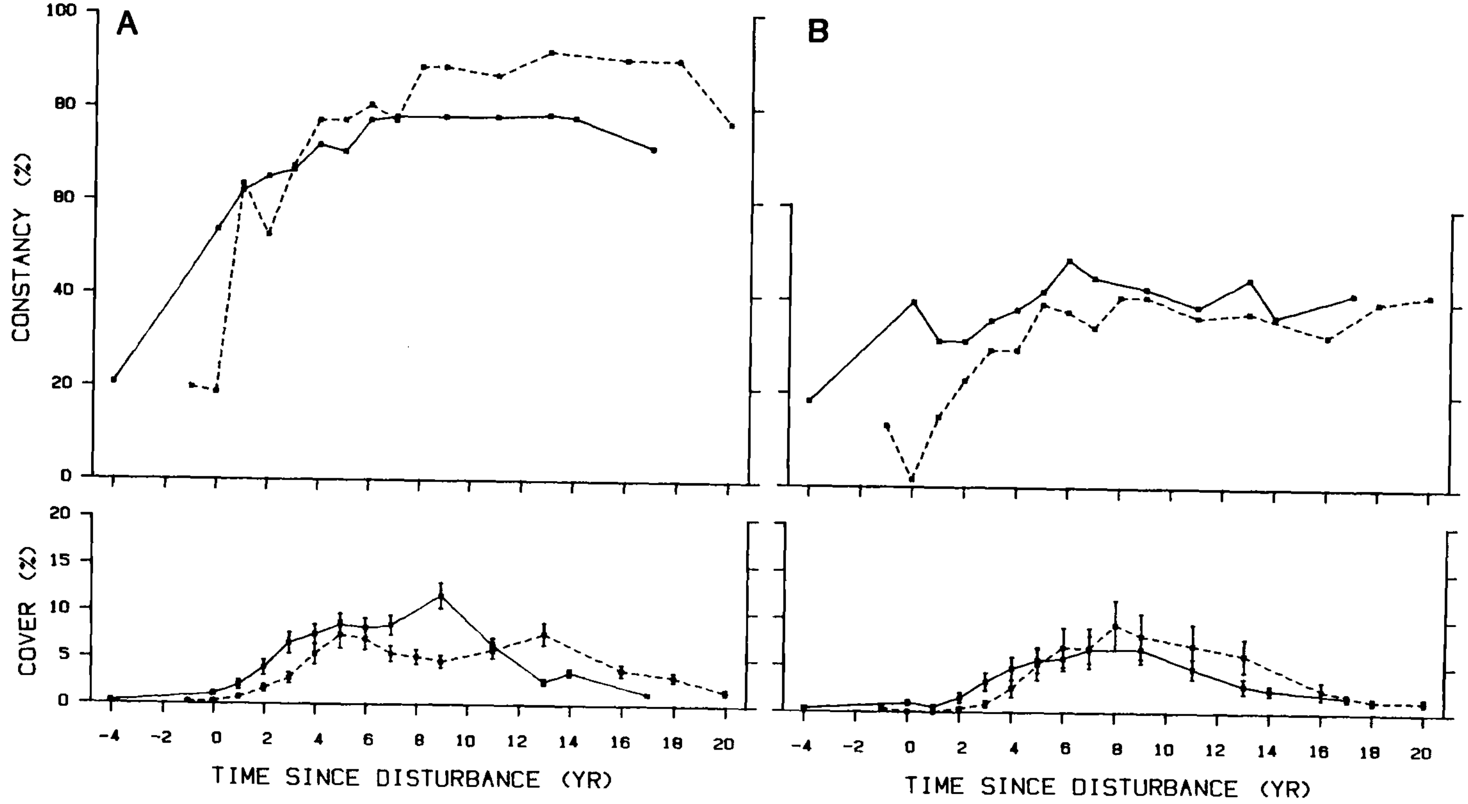
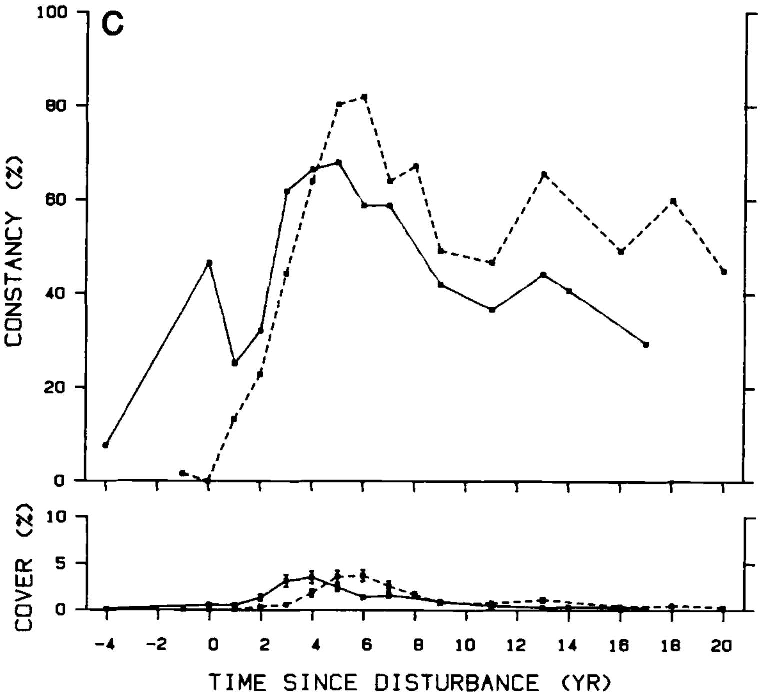

A
B
100
80
60
40
20
0
CONSTANCY (%)
20
15
10
5
0
COVER (%)
-4
-2
0
2
4
6
8
10
12
14
16
18
20
TIME SINCE DISTURBANCE (YR)
TIME SINCE DISTURBANCE (YR)

Figure III-8. (Continued).



of a short, caudex-like rhizome, its principal means of reproduction is through recruitment by copious, wind-borne seed (McLean 1968). Thus, establishment is likely to be greatest on heavily burned soils, where regeneration sites are abundant. The period of elevated abundance of *H. albiflorum* was earlier and of shorter duration on both watersheds than that of the previous R2 species. This suggests that although the site conditions promoting the germination and establishment of wind-borne seed were enhanced on heavily burned soils, the period of recruitment and expansion was limited.

3. *Group R3 species*. This group was comprised of the initial understory dominants on Watersheds 1 and 3. These included herb and low shrub species (e.g., *Gaultheria shallon*, *Polystichum munitum*, and *Berberis nervosa*); tall shrub species (e.g., *Acer circinatum*, *Rhododendron macrophyllum*, and *Corylus cornuta*); and tree species (e.g., *Tsuga heterophylla*) (Fig. III-9). Population patterns were typified by dramatic reductions in response to logging and slash burning, followed by parallel recovery in constancy and cover. Immediate reductions from logging and slash burning were dramatic. Subsequent recovery was continuous, but varied among species. By the late-seral period, R3 species were again co-dominant within portions of both watersheds.

The long-term dynamics of R3 species were complex, both spatially and temporally, reflecting initial distributions and variation in intensity of disturbance. However, two principal trends characterized their patterns of recovery: 1) constancy and

Figure III-9. Changes in constancy and mean canopy cover with time for species of the R3 group on Watersheds 1 and 3. **A)** *Acer circinatum*, **B)** *Polystichum munitum*, **C)** *Gaultheria shallon*, **D)** *Rhododendron macrophyllum*. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-9.

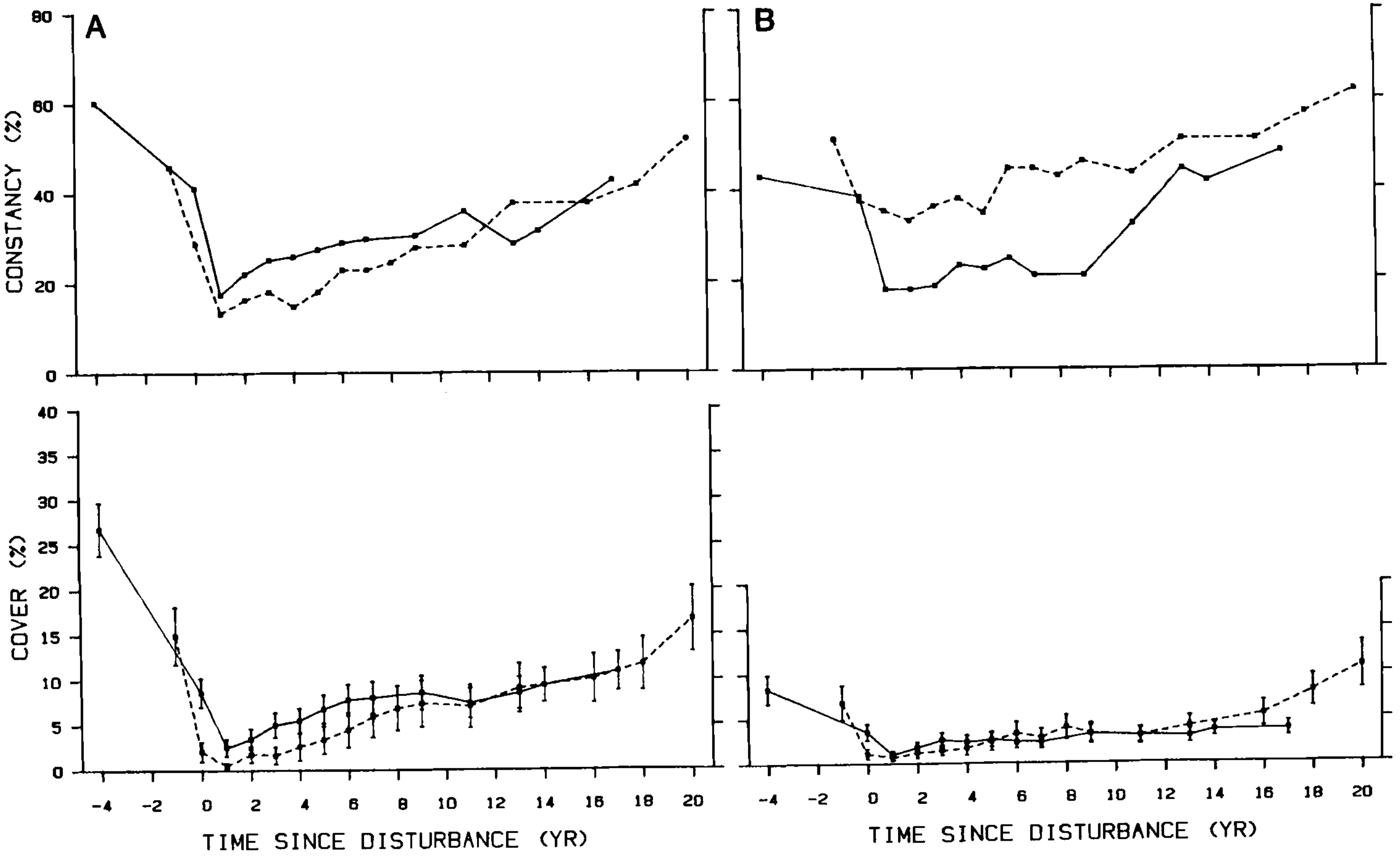
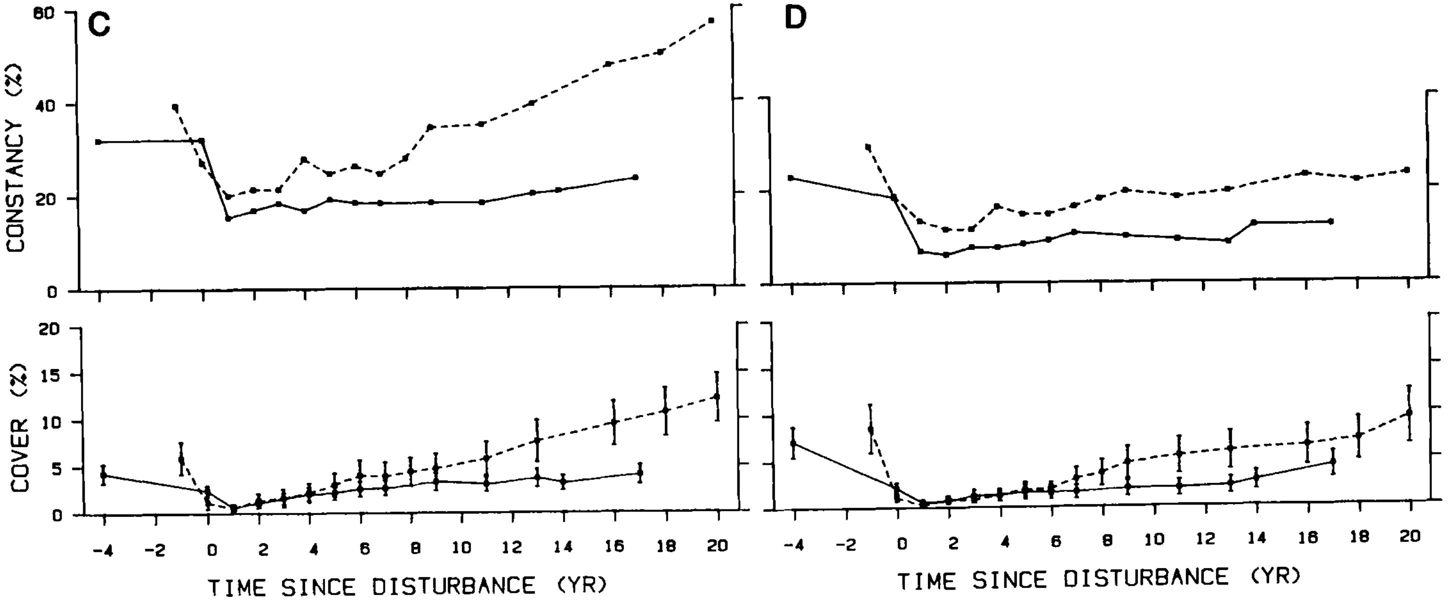

A
B
CONSTANCY (%)
0
20
40
60
80
COVER (%)
0
5
10
15
20
25
30
35
40
-4
-2
0
2
4
6
8
10
12
14
16
18
20
TIME SINCE DISTURBANCE (YR)

Figure III-9. (Continued).



cover were generally proportional to initial community values and 2) long-term recovery was inversely proportional to the intensity of disturbance.

Vegetative reproduction dominated post-disturbance recovery for both herb and shrub species. Sprouting from adventitious buds at the bases of stems and along rhizomes may afford these species moderate resistance to fire (Sabhasri 1961, McLean 1968, Volland and Dell 1981, Haeussler and Coates 1986). Observational studies within similar ecosystems suggest that these understory dominants display greater recovery on unburned than burned sites, although responses vary (Bailey 1966, Steen 1966, Anderson 1969, Gashwiler 1970, Kraemer 1977). However, little information is available from controlled experiments or from long-term observation of species response to disturbance. The role of sexual reproduction in initiating post-disturbance populations is unknown for most forest understory species. Seed reproduction has been reported as poor in *A. circinatum* (Anderson 1967, Russel 1974, Schopmeyer 1974) and *G. shallon* (Sabhasri 1961, Haeussler and Coates 1986), however.

4. *Group R4 species*. A diversity of subordinate forest species displaying relatively minor changes in overall abundance comprised this group (Fig. III-10). The most common species represented an array of growth-forms, including herbs (e.g., *Viola sempervirens* and *Coptis laciniata*), deciduous shrubs (e.g., *Vaccinium parvifolium*), and sclerophyllous trees (e.g., *Castanopsis chrysophylla*). Additional species included the herbs, *Oxalis oregana* and *Rubus nivalis*, and the deciduous hardwood trees, *Acer macrophyllum* and

Figure III-10. Changes in constancy and mean canopy cover with time for species of the R4 group on Watersheds 1 and 3. **A)** *Coptis laciniata*, **B)** *Vaccinium parvifolium*, **C)** *Viola sempervirens*, **D)** *Castanopsis chrysophylla*. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-10.

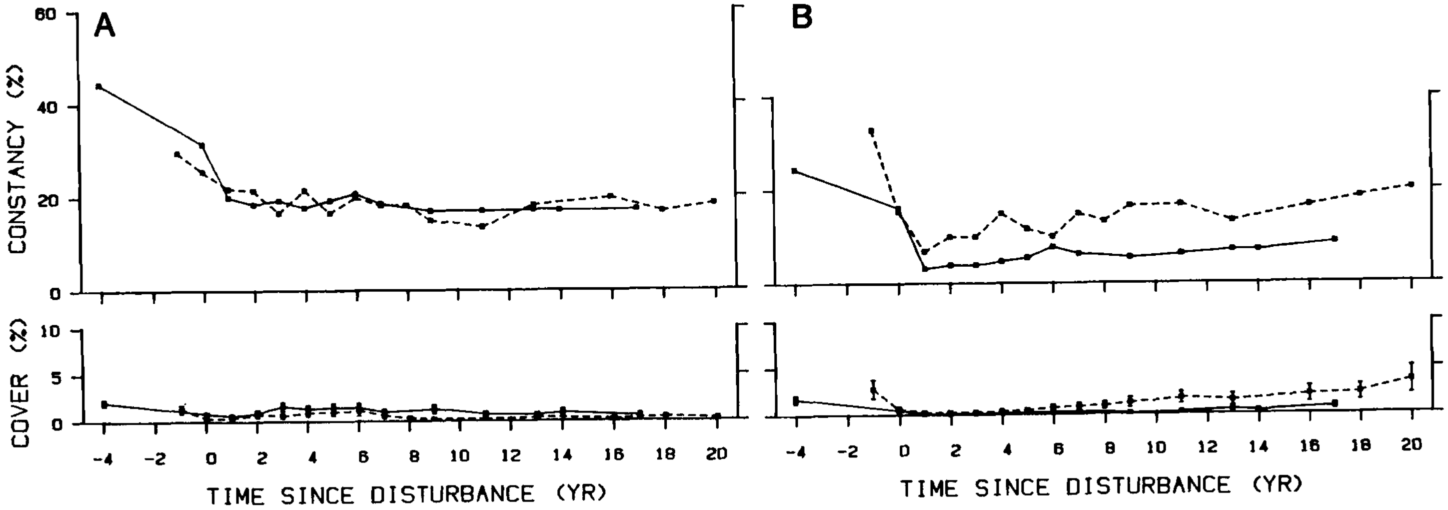
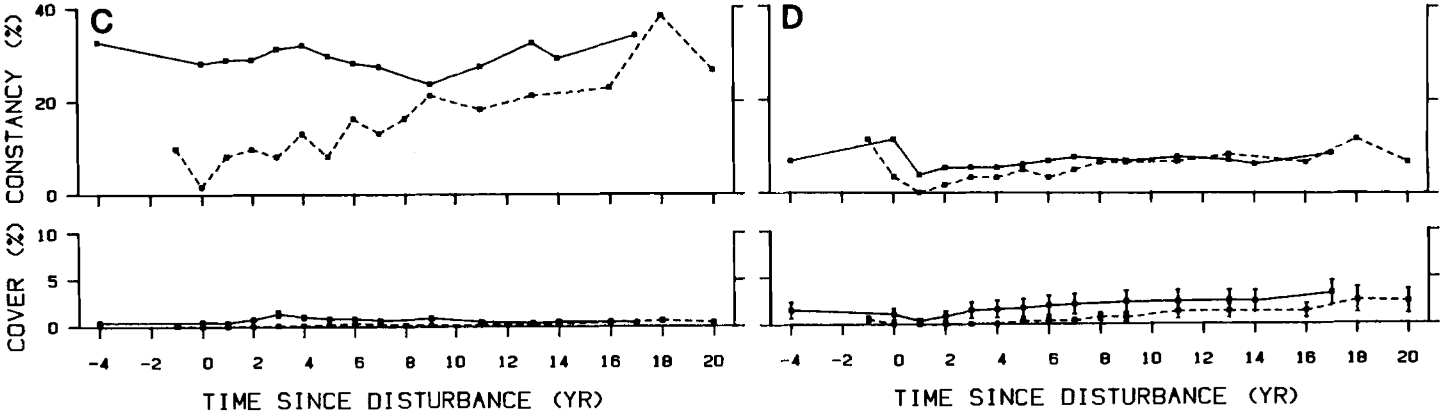


Figure III-10. (Continued).



Cornus nuttallii. While logging and burning initially reduced the constancy and cover of each species, subsequent changes in abundance varied. Whereas constancy increased for *Viola sempervirens* (Fig. III-10C), *Vaccinium parvifolium* (Fig. III-10B), and *Castanopsis chrysophylla* (Fig. III-10D) on WS3, it remained rather stable for *Coptis laciniata* (Fig. III-10A) on WS3 and for all species on WS1. Changes in canopy cover were generally less pronounced. Among the clearest trends, however, were gradual, continuous increases in the cover of *Vaccinium parvifolium* on WS3 and of *Castanopsis chrysophylla* on both sites.

The post-disturbance distributions of *Vaccinium parvifolium* and *Castanopsis chrysophylla* reflected their initial distributions--the former displayed greater recovery within the moist communities and the latter, within the drier communities. Stem sprouting afforded both shrub species moderate resistance to fire. Thus, with the exception of heavily burned sites, post-disturbance distributions generally remained similar to those of the initial forest understory. The dynamics of the herb populations, by contrast, were more correlated with differences in disturbance intensity than with initial distributions. *Coptis laciniata* was briefly released on undisturbed sites but greatly reduced on burned sites. Although *Viola sempervirens* was not reduced by burning, its expansion was restricted to undisturbed sites.

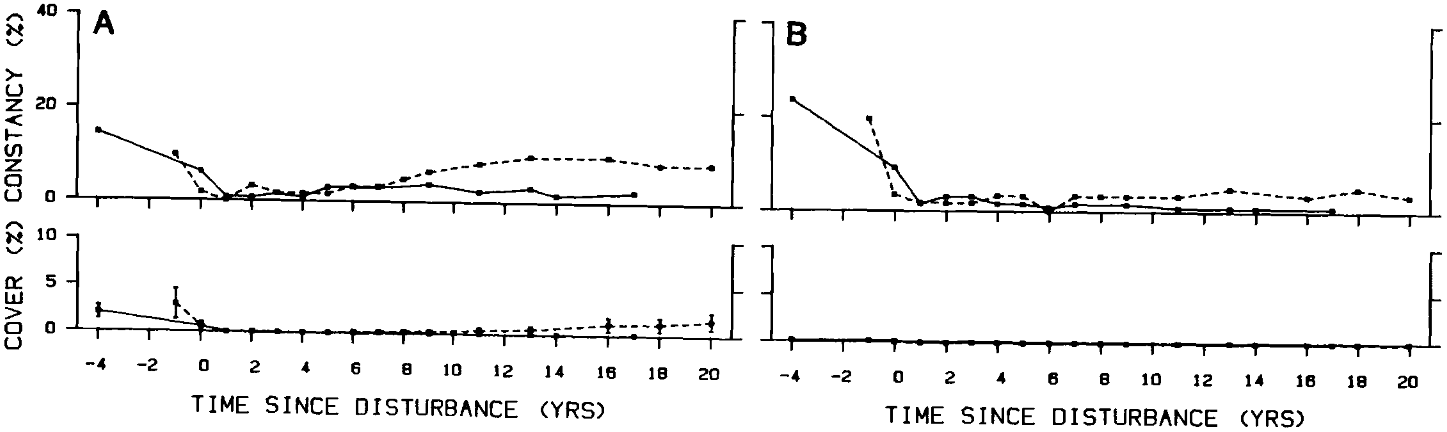
The subordinate seral role of R4 species may reflect interactions between growth-habit (morphological) characteristics and initial or historical factors. For example, *Vaccinium* *parvifolium* and *Castanopsis chrysophylla* appear moderately resistant to burning as they sprout from adventitious buds. However, relative to the trailing and rhizomatous species of the previous residual groups, both shrubs possess a limited potential for lateral growth. Compounded with their initially sparse distributions, this morphological constraint may have restricted their seral abundance on Watersheds 1 and 3. The importance of reproduction by seed to their post-disturbance dynamics is unknown.

The seral 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 presumably affords them little resistance to fire. Thus, clonal spread may be expected only within unburned microsites. Vegetative expansion was apparent on Watersheds 1 and 3, although not to the extent of the more vigorous sub-shrubs, *Rubus ursinus* and *Whipplea modesta*. Second, the abundance of R4 herbs may be limited simply by their small stature in an herb layer dominated by a diversity of erect herbs and sub-shrubs.

5. *Group R5 species*. This group encompassed a variety of uncommon but characteristic forest species which, unlike those of the previous residual groups, displayed minimal post-disturbance recovery (Fig. III-11). Among the most frequent species were the ericaceous sub-shrub, *Chimaphila umbellata*, and the coniferous tree, *Thuja plicata* (the latter occurring as suppressed understory individuals). Additional herb and tree species included *Goodyera*

Figure III-11. Changes in constancy and mean canopy cover with time for species of the R5 group on Watersheds 1 and 3. **A)** *Thuja plicata*, **B)** *Chimaphila umbellata*. Solid line represents Watershed 1, dashed line represents Watershed 3. Vertical bars represent ± 1 SE.

Figure III-11.



oblongifolia, *Synthyris reniformis*, and *Taxus brevifolia*. Predisturbance constancies which ranged from 10-24% declined to between 0 and 3% following slash burning. Although the post-disturbance dynamics of individual species varied, canopy cover typically persisted at trace levels.

The species comprising the R5 group showed broad susceptibility to disturbance. *Chimaphila umbellata* (Fig. III-11B) 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. Similarly, *Thuja plicata* (Fig. III-11A) was absent from the sample plots of WS3 in year 1 and its reappearance was delayed for 8-9 yr within the moist *Coptis* and *Polystichum* communities. Although scattered individuals probably survived disturbance in protected microsites, long-term recovery of the tree species will largely depend on regeneration by seed. Its greater post-disturbance abundance on WS3 likely reflected the more pronounced edge effect associated with smaller cutting units. Bordering seed sources were closer, facilitating dispersal. Nevertheless, the long-term patterns on both watersheds suggest that, relative to the vegetative recovery of other residual groups, this process is intrinsically slow.

Others report the absence of fire resistance in herbs belonging to the R5 group (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). Therefore, vegetative recovery will depend primarily upon the scattered individuals which survive within undisturbed microsites.

General Conclusions

The process of secondary succession on Watersheds 1 and 3 was revealed as an array of individualistic species responses. The temporal patterns of abundance of species were a series of broadly overlapping, unimodal curves of constancy and canopy cover which differed in time of initiation, duration, and magnitude. The temporal displacement of populations suggests that species are responding variously to changing stresses and resource availability, similar to interpretations of the spatial nature of the plant community. That individualistic species responses characterize both the temporal and the spatial dimensions of communities was initially posed by Gleason (1917); the concept is becoming increasingly apparent (e.g., Whittaker 1969, 1975, Drury and Nisbet 1973, Gomez-Pompa and Vazquez-Yanes 1974, Horn 1974, Pickett 1976, 1982, Glenn-Lewin 1980).

Succession was characterized by the changing abundances of persistent species rather than by sequential invasions and discrete replacements. Curves of constancy and cover on Watersheds 1 and 3 revealed that a majority of both dominant and subordinate species established within 1-2 yr following disturbance and occurred on sample plots throughout the sere. Although some populations displayed dramatic variations in abundance during particular phases, nearly all species exhibited rather slow extinctions. Early invasion and subsequent sorting of species through differential growth and mortality support Egler's (1954) initial floristics model. Originally developed for old field succession, the concept has found broad application in secondary forest seres (Cremer and Mount 1965, Johnson and Rowe 1977, Trabaud and Lepart 1980, AuClair 1983, Abrams and Dickmann 1984, Foster 1985, Stickney 1986).

Succession on Watersheds 1 and 3 represented a temporal continuum of species pattern. Detailed examinations of the individual response of species among communities and disturbance classes revealed that their long-term patterns were distinct, both temporally and spatially. Although species were placed within groups, the general types of response they portrayed were subjectively chosen to emphasize similarities in their patterns of abundance. These similarities commonly derived from characteristics of parallel life cycles. For example, among the invading groups, species of the I1 group were all winter annuals, species of the I3 group were biennials and short-lived perennials, and species of the I6 group 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.

Although a majority of the common species were easily assigned to one of the 11 population patterns, others were not, further supporting the concept of a temporal continuum of species pattern.

For example, Linnaea borealis, a frequent but subordinate trailing sub-shrub, had a cover pattern resembling that of the R2 group and a constancy pattern similar to that of the R3 group. These divergent trends resulted from extreme spatial variation in its development--dramatic expansion of surviving individuals on undisturbed sites, but widespread elimination on disturbed and burned sites. Although its potential for lateral spread may exceed that of Whipplea modesta, the location of its perennating buds makes L. borealis particularly sensitive to burning (McLean 1968, Crane et al. 1983, Rowe 1983, Bradley 1984).

The explanation of abundance patterns of individual species and groups of species following disturbance on the basis of life history characteristics, is a common approach to successional analysis (Cattelino et al. 1979, Noble and Slatyer 1980, Botkin 1981, Pickett 1982, Hobbs et al. 1984, Walker et al. 1986). However, this is rendered difficult by the paucity of information on the life history of common understory species in Pseudotsuga forests (e.g., relative roles of sexual and vegetative reproduction, longevity of seed bank propagules, and life spans). Our uncertainty about the causes of changing abundance in populations clearly points to the need for more research on the autecology of these species. However, where aspects of the natural history of species are understood, they do support interpretations of the population trends. For example, the interaction between the timing of disturbance and the dispersal of seeds of the I1 species, the stimulating response of fire on buried seeds of the I5 species, and the regeneration by sprouting of forest perennials of the R3 group, were evident in their respective population patterns.

The numerous paths of dispersal, establishment and expansion which many seral species possess is a major constraint in interpreting their dynamics. Variation among these characteristics in response to biotic or abiotic factors, may influence the sequence of species replacements during succession (Cattelino et al. 1979, Noble and Slatyer 1980, Hobbs et al. 1984). In this study, the origins and mechanisms of species development were largely hidden since demographic data were not available. Almost certainly, multiple modes of regeneration occurred simultaneously. For example, establishment of Epilobium angustifolium from seed probably continued in open microsites throughout the sere, whereas expansion in closed communities was probably limited to perennation of rhizomes following initial establishment. Similarly, resprouting of forest residuals may have been common on undisturbed and moderately disturbed sites, whereas reproduction on heavily burned sites may have been largely by seed.

Despite the diversity of potential developmental paths, it is striking that the abundance patterns of many seral species were similar on both watersheds. This suggests that, to a degree, the successional process initiated by catastrophic disturbance in these systems has a deterministic component which is founded in the life history attributes of the available species. However, there were also differences in species distributions between watersheds (e.g., Ceanothus spp. and Epilobium spp.). Factors contributing to these differences included variation in: 1) logging and burning disturbance, 2) initial distribution of forest understory species and buried viable seeds, and 3) post-disturbance dispersal of propagules. A complete understanding of such phenomena is often limited in observational studies. However, these studies do illustrate their potential importance in the dynamics of individual populations and communities.

This study provides a unique and detailed record of the dynamics of species during early secondary succession in *Pseudotsuga* forests, despite its descriptive nature. Features of the temporal and spatial distribution of species are described that are not apparent in short-term or chronosequence studies. They reflect the life histories of species, as well as the effects of stochastic or historical factors. These patterns support the view that succession is a complex process resulting from the interaction of species' strategies with the vagaries of history and environment.

Chapter 4

EARLY SUCCESSION IN PSEUDOTSUGA FORESTS: A METHOD FOR CHARACTERIZING ALTERNATE PATHWAYS

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ABSTRACT

Vegetation changes following catastrophic disturbance commonly follow a variety of pathways. Alternate successional sequences reflect variation in numerous factors, including initial composition and structure, intensity of disturbance, availability of propagules, and random events. Successional changes were studied for 21 yr in two logged and burned *Pseudotsuga* watersheds in the western Cascade Range of Oregon. Detrended correspondence analysis (DCA) was used to assess the successional pathways of six forest communities exposed to a gradient in disturbance intensity.

Ordinations through time for plant communities revealed a pattern of rapid floristic change away from initial composition, followed by gradual, unidirectional return common to all communities. The primary ordination axis represented a temporal gradient, with the most rapid changes in species composition

occurring within two growing seasons after logging and slash burning. Early, but transient, convergence of successional pathways was more common on mesic to dry sites, reflecting the floristic similarity of pre-disturbance communities and the broad distribution of colonizers. Discrete sequences were observed on moist sites, reflecting more distinct residual and colonizing floras.

Ordinations of composite samples representing four intensities of logging and burning disturbance, indicated that compositional change increased with disturbance intensity. Alternate successional sequences were dominated by residual species on minimally disturbed sites and by alternate suites of invading species on moderately disturbed and on burned sites. Ordinations of subsets of the data revealed that changes in disturbance intensity within individual plant communities also resulted in alternate pathways. These additionally revealed the influence of historical factors and random events in succession.

Euclidean distances in ordination space between pre- and post-disturbance samples were used to compare community resistance (maximum displacement of composition) and resilience (degree of recovery). Differences in the resistance and resilience of communities were greatest between the depauperate Coptis and well-developed Polystichum communities. Both measures also varied inversely with intensity of disturbance. Although rates of recovery vary, the widespread resilience of communities derives from the ability of forest dominants to resprout following burning. Variation in the immediate and long-term response to disturbance, reflects the complex interaction between species life history, disturbance intensity, and local stochastic factors.

INTRODUCTION

The response of communities to disturbance is central to the study of vegetation change. Catastrophic disturbances such as clearcut logging or wildfire profoundly influence the composition and structure of vegetation. Entire plants or plant parts may be removed or displaced, physical environments are often drastically altered, and below-ground resources are commonly redistributed. In ecosystems subject to fire, the species contributing to a post-disturbance flora derive from three principal sources: propagules dispersed from off-site sources, propagules persisting on the site, and resprouting individuals that survive disturbance (Naveh 1975, Lyon and Stickney 1976, Noble and Slatyer 1980, Gill 1981, Hobbs et al. 1984). However, their ultimate contribution to the post-disturbance community is a complex consequence of the nature of the disturbance (e.g., its intensity, duration, or areal extent), the character of the vegetation (e.g., the initial composition or structure), the local environmental conditions (e.g., moisture, temperature, or nutrients), the influence of herbivory, and the effects of chance (e.g., the timing of disturbance, or subsequent fluctuations in weather). Thus, in many ecosystems, successional sequences initiated by disturbance may follow alternate pathways (Noble and Slatyer 1977, 1980, Lubchenco and Menge 1978, Cattelino et al. 1979, Sousa 1979, 1984b, Turner 1983, Abrams et al. 1985, Olson 1985).

The species which comprise a community possess two mechanisms for persistence through disturbance. First, they may simply resist change. Second, if altered by disturbance, they may possess the ability to readjust or to recover. Resistance to a disturbance such as fire may be imparted by thick bark or dormancy at the time of disturbance. Readjustment or recovery from fire may occur by sprouting from subterranean organs, reestablishment from buried seed or from seeds stored in the canopy, or dispersal of propagules from off-site sources. The degree to which component species possess these properties thus determines the relative displacement of the community by disturbance, as well as the rate and extent to which initial composition and structure are restored.

In this paper I examine the long-term response of Pseudotsuga forest communities to catastrophic disturbance. My objectives are two-fold: first, to illustrate the multiplicity of successional paths that characterize understory development prior to canopy closure and second, to compare the relative resistance and resilience of initial forest communities. The data presented derive from 22 yr of observation of permanent plots within clearcut and burned Pseudotsuga forests in the western Cascade Range of Oregon. Initiated prior to disturbance in 1962, the study provides one of the longest and most detailed records of understory development in the low elevation montane forests of the Pacific Northwest.

Because long-term successional data such as these are inherently complex, the nature of species response and community development are often difficult to describe and to interpret. An approach to reducing the complexity employs the ordination of data from the sequential observation of permanent plots. The successive positions of samples within the resulting ordination field thus represent temporal changes in community composition. The technique has been previously used to compare the dynamics of communities within grasslands (Hopkins 1968, van der Maarel 1969, Austin 1977, Swaine and Greig-Smith 1980, Austin et al. 1981, Polley and Collins 1984, Aarssen and Turkington 1985, Belsky 1986), heathlands (Hobbs and Gimingham 1984), and coastal sage scrub (Westman and O'Leary 1986). In this study I use detrended correspondence analysis (DCA) ordination to examine the successional pathways of six forest understory communities exposed to a gradient in disturbance intensity. The patterns revealed by the ordination of selected subsets of the data were used to answer the following questions:

1) How do successional pathways vary among initial plant communities or among sites exposed to different intensities of disturbance?

2) How do successional paths within particular plant communities vary with intensity of disturbance? Conversely, how do successional paths vary with initial composition, following a disturbance of a particular intensity?

3) Is there evidence for compositional convergence or divergence?

4) Do rates and directions of compositional change vary with time? Are there periods of fluctuating or stable species composition?

The results of DCA ordination may also be employed to compare the relative resistance and resilience of communities. A diversity of terms and measures have been advanced to address these complex responses of communities to disturbance (e.g., Margalef 1969, Connell and Sousa 1983, Holling 1973, Sutherland 1974, 1981, Orians 1975, Cairns and Dickson 1977, Westman 1978, 1985, Pimm 1984, Westman and O'Leary 1986). Similarity indices are often used to measure the temporal changes in species composition initiated by disturbance and to express the relative displacement or recovery of communities (e.g., Westman 1978, Sousa 1980, Smedes and Hurd 1981, Leps et al. 1982, Westman and O'Leary 1986). However, few studies have applied distances in ordination space to this end (but see Bloom 1980, Westman and O'Leary 1986). In this study I use the Euclidean distances between pre- and post-disturbance samples in ordination space to measure initial community displacement and long-term recovery. The approach provides a conceptually and computationally simple method for comparing the relative resistance and resilience of communities. Two principal questions are addressed:

1) How does the maximum community displacement (i.e., its resistance) vary with initial composition or with intensity of disturbance?

2) How does the long-term recovery of community composition (i.e., its resilience) vary with initial composition or with intensity of disturbance?

STUDY AREA

Physical Environment

The study areas are two watersheds of the H. J. Andrews Experimental Forest on the western slope of the central Cascade Range, 80 km east of Eugene, Oregon. Watersheds 1 and 3 (WS1 and WS3) are typical of the mature, dissected topography of the region. Elevations range from 442 to 1082 m and slopes average > 50% (Rothacher et al. 1967). Oriented in a NNW direction, the watersheds bound two of the lowermost tributaries to Lookout Creek which drains the entire experimental forest.

The soils of both sites derive from parent materials of tuffs and breccias, although basalts and andesites are also present. Characterized by poor profile development, soils are loamy and moderately stony, overlying extensive colluvial deposits. Soil porosity and water storage capacity are fairly high (Dyrness 1969).

The climate of the region is maritime with mild, wet winters and warm, dry summers. Annual precipitation averages 2302 mm (principally rain), yet only 6% falls between June and August (Bierlmaier and McKee in press). Temperatures range from an average minimum of -5.5°C in January and 11.9°C in August to an average maximum of 5.5°C in January and 23.3°C in July. Although snowfall is common, accumulations are typically small and do not persist.

Vegetation

The vegetation of Watersheds 1 and 3 is typical of that of the surrounding *Tsuga heterophylla* zone (Franklin and Dyrness 1973). Prior to disturbance, forest canopies were dominated by a mixture of old-growth (300-500 yr) and mature (125 yr old) *Pseudotsuga menziesii*. The climax species, *Tsuga heterophylla*, varied in size and age and dominated the sub-canopy and regeneration layers. Other widely distributed tree species included *Taxus brevifolia*, *Cornus nuttallii*, and *Acer macrophyllum*. *Castanopsis chrysophylla* and *Pinus lambertiana* were restricted to dry, upper slopes and ridgetops, whereas *Thuja plicata* was locally common along moist, lower slopes. Overstory canopy cover (> 8 m) averaged 62 and 58% while understory tree cover (< 8 m) averaged 59 and 42% on Waterheds 1 and 3, respectively.

The initial forest vegetation was composed of six understory plant communities arrayed along a complex gradient of moisture and topographic position. These communities were typical of sites of similar elevation and topography throughout the experimental forest and are closely related to associations of the *Pseudotsuga menziesii* and *Tsuga heterophylla* series of Hemstrom et al. (1985). Although the communities were characterized by species with broad ecological amplitude, the abundance of the understory dominants not only corresponded with variations in environment, but also reflected overstory canopy characteristics and local stand history. Brief descriptions of the communities are included in Table IV-1.

Detailed information on the composition, structure, and distribution of these communities has been presented elsewhere (Rothacher et al. 1967, Dyrness 1973, Hawk and Dyrness 1973, Halpern 1987).

Table IV-1. Characteristics of the six forest understory communities of Watersheds 1 and 3. Communities are arranged in order of increasing available moisture.

Plant community	Topographic position and aspect	Dominant growth-form(s)	Dominant species	Corresponding plant association (Hemstrom et al. 1985)
Corylus cornuta - *Gaultheria shallon*	ridgetops, south-facing upper-slopes	tall shrubs	*Corylus cornuta*, *Acer circinatum*, *Berberis nervosa*	*Pseudotsuga menziesii* / *Berberis nervosa*
Rhododendron macrophyllum - *Gaultheria shallon*	ridge-tops, mid-slope benches	tall shrubs	*Rhododendron macrophyllum*, *Gaultheria shallon*	*Tsuga heterophylla* / *Rhododendron macrophyllum* - *Gaultheria shallon*
Acer circinatum - *Gaultheria shallon*	mid- to upper-south-facing slopes	herbs and low shrubs, (tall shrubs)	*Acer circinatum*, *Gaultheria shallon*	*Tsuga heterophylla* / *Berberis nervosa* - *Gaultheria shallon*
Acer circinatum - *Berberis nervosa*	mid- to lower-slopes	tall shrubs	*Acer circinatum*	*Tsuga heterophylla* / *Berberis nervosa*
Coptis laciniata	mid- to lower-slopes	trees, (herbs and low shrubs)[1]	*Berberis nervosa*, *Coptis laciniata*, *Linnaea borealis*	*Tsuga heterophylla* / *Berberis nervosa* (shade phase)
Polystichum munitum	bottom-slopes, steep north- to east-facing slopes, seeps	herbs and low shrubs	*Polystichum munitum*, *Acer circinatum*	*Tsuga heterophylla* / *Polystichum munitum*

[1] depauperate understory

METHODS

Field Methods

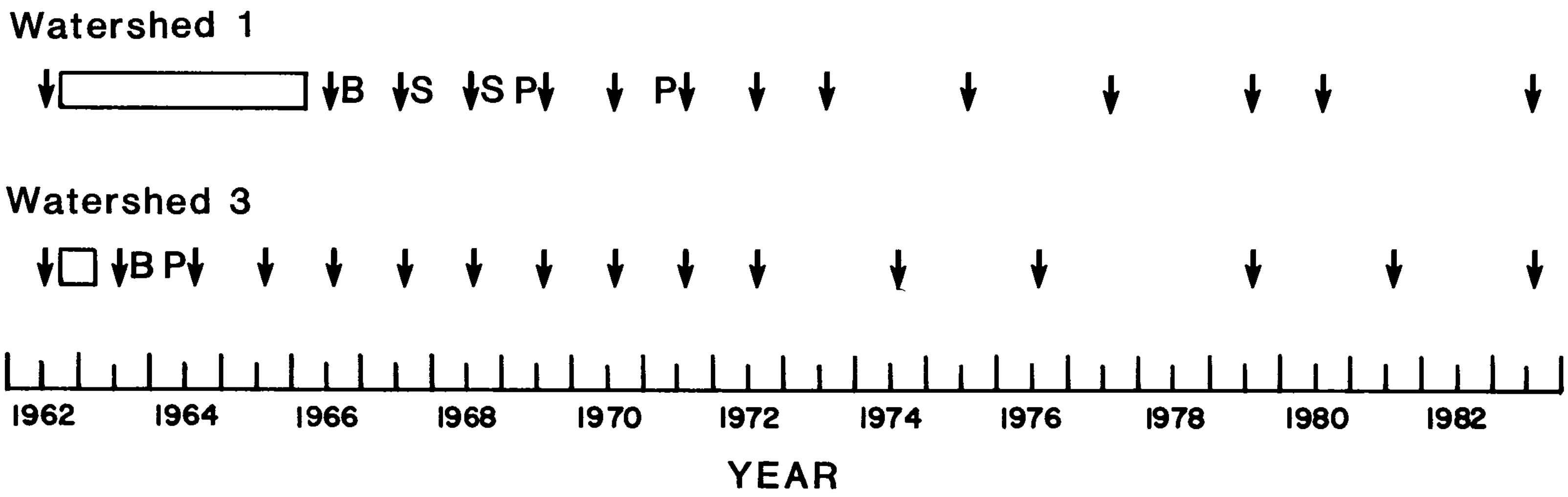
Permanently staked sample plots of 2 X 2 m were established along transects of both watersheds during the summer of 1962, prior to logging. A total of 131 plots represented 6 transects on WS1; 61 plots represented 10 transects on WS3. The position of the initial plot on each transect was determined randomly and the remaining plots were placed at slope-corrected intervals of 30.5 m. Each plot was assigned to one of six plant communities based upon the initial classification of forest understories (see previous Vegetation section).

The timing and distribution of logging and burning disturbance and of artificial regeneration varied within and between watersheds (Fig. IV-1). The entire 96 ha of WS1 was clearcut over a period of 4 yr (fall 1962-summer 1966) and slash was broadcast burned in October 1966. In contrast, on WS3, 3 stands of 5, 9, and 11 ha (one quarter of the watershed) were clearcut during a single season (winter 1962-1963) and slash was burned the following fall (September 1963).

Forest understories were initially sampled during summer 1962, prior to disturbance. Within each plot visual estimates of projected canopy cover (%) were made for each vascular plant species < 6 m tall. Details of the sampling protocol have been presented in Halpern (1987). Vascular plant nomenclature and taxonomy follow

Figure IV-1. The history of disturbance and artificial regeneration on Watersheds 1 and 3. Arrows indicate sampling years. Open bars indicate periods of logging. B = slash burning. S = aerial seeding of *Pseudotsuga menziesii* (all of WS1 seeded in 1967, 10 ha in 1968). P = planting of *P. menziesii* (WS1: 1969 = entire watershed planted with 2 yr old trees; 1971 = 40 ha, 2 and 3 yr old trees. WS3: each clearcut unit, 3 yr old trees.)

Figure IV-1.


Watershed 1
B
S
S P
P
Watershed 3
B P
1962
1964
1966
1968
1970
1972
1974
1976
1978
1980
1982
YEAR

Hitchcock and Cronquist (1973).

Following the completion of logging, plots were relocated or reestablished from field notes and resampled. The watersheds were then broadcast burned. Plots were again relocated and assigned to one of four soil disturbance classes based on the following classification (Tarrant 1956, Dyrness et al. 1957, Dyrness 1973):

1. Undisturbed. The soil surface appeared similar to that prior to disturbance, with minimal mixing of soil and litter and with no evidence of fire.

2. Disturbed - Unburned. Disturbance from logging was evident as litter was removed or mixed with mineral soil; however, there was no evidence of fire.

3. Lightly burned. Surface litter was charred by fire but was not completely removed.

4. Heavily burned. Surface litter was completely consumed by intense fire exposing a highly colored mineral soil.

Plots were resampled the first growing season following slash burning on both sites (1967 on WS1, 1964 on WS3) (Fig. IV-1). Post-disturbance remeasurements were continued annually through 1973 on WS1 and through 1972 on WS3. Thereafter, sampling generally occurred during alternate years.

Data Reduction and Analysis

Ordination analysis

Composite samples were formed representing the average cover of each species within each 1) plant community, 2) soil disturbance class, and 3) permutation within the community-by-disturbance class matrix, for each sampling year. Constructed from a complete species-by-samples-by-dates data matrix using the computer program DATAEDIT of the Cornell Ecology Program Series (Gauch 1973, Singer 1980, Gauch and Singer 1982), the composite samples were used as input for the ordination analysis.

Ordinations were performed using DECORANA, a FORTRAN program for detrended correspondence analysis (DCA) (Hill 1979, Hill and Gauch 1980). Within each ordination field, points representing the same composite sample in successive years were connected sequentially to form successional trajectories (e.g., Fig. IV-2). The closed circle initiating each trajectory represents the average composition prior to disturbance, whereas the second and third points represent the composition during the growing seasons following completion of logging and following slash burning, respectively. The remaining points correspond with subsequent years of sampling (see Fig. IV-1 for sampling schedule). The arrows aid in identifying the direction of change through time and coincide with average composition at final sampling--17 yr after burning on WS1 and 20 yr after burning on WS3 (e.g., Figs. IV-2A and B).

Unlike other ordination techniques, the distances between samples along DCA axes (measured as standard deviation, or sd, units) represent equivalent changes in species composition (Hill 1979, Hill and Gauch 1980).

Measures of resistance and resilience

For this system, resistance was defined as inversely proportional to the maximum deviation of post-disturbance species composition from that of the pre-disturbance vegetation. Resilience was defined as the degree of recovery of composition by final sampling. I used the Euclidean distance (ED) in ordination space to measure the compositional dissimilarity between an initial community sample (time 0) and a post-disturbance sample (time x). Scores of the pre- and post-disturbance samples along DCA Axis i, s_{0i} and s_{xi}, respectively, were weighted by the eigenvalue, A_i, of Axis i. Thus,

$$ED = [\sum_{i=1}^{4} A_i (s_{0i} - s_{xi})^2]^{1/2},$$

Examples of changes in sample dissimilarity with time are presented only for WS1. The pre-disturbance sample (ED = 0) was plotted at time "-4" (because logging occurred over 4 yr) and the samples following logging and burning were plotted at times "0" and "1", respectively, and so on for subsequent growing seasons. Thus, resistance is estimated by the maximum Euclidean distance between the initial and the post-disturbance composite samples, while resilience is estimated as the Euclidean distance between the initial and final sample. Both estimates vary inversely with Euclidean distance.

RESULTS AND DISCUSSION

Ordination of composite samples through time reveals the diversity of pattern in succession (e.g., Figs. IV-2 and IV-3). Nevertheless, common trends underlie all sample trajectories. The immediate response to disturbance was a dramatic, rapid floristic change away from initial composition. The positions of samples in years 1 and 2 reflect widespread reduction in the abundance of forest understory dominants, including herbs and low shrubs (e.g., *Berberis nervosa*, *Gaultheria shallon*, and *Polystichum munitum*); tall shrubs (e.g., *Acer circinatum*, *Rhododendron macrophyllum*, and *Corylus cornuta*); and trees (e.g., *Tsuga heterophylla*, *Taxus brevifolia*, and *Thuja plicata*). Further, they coincide with the prominence of fugitive annuals (e.g., *Senecio sylvaticus* and *Epilobium paniculatum*) which peaked rapidly on most sites 2 yr after burning.

Subsequent changes reflect less dramatic shifts in the abundance of rather persistent invading and residual species (Halpern 1987) with various degrees of return to initial composition. For example, over time the dominant colonizing species changed gradually from annual (e.g., *S. sylvaticus* and *E. paniculatum*) to herbaceous biennial and perennial (*Cirsium* spp., *Agoseris* spp., and *E. angustifolium*) to woody perennial growth-forms (e.g., *Ceanothus velutinus*, *C. sanguineus*, and *Rubus parviflorus*). Coincidentally, initially uncommon forest herbs and sub-shrubs showed transient (e.g., *Hieracium albiflorum*, *Linnaea borealis*, *Trientalis latifolia*, and *Whipplea modesta*) or persistent (e.g., *Rubus ursinus*) release. Initial understory dominants developed relatively slowly, with varying degrees of recovery to pre-disturbance levels.

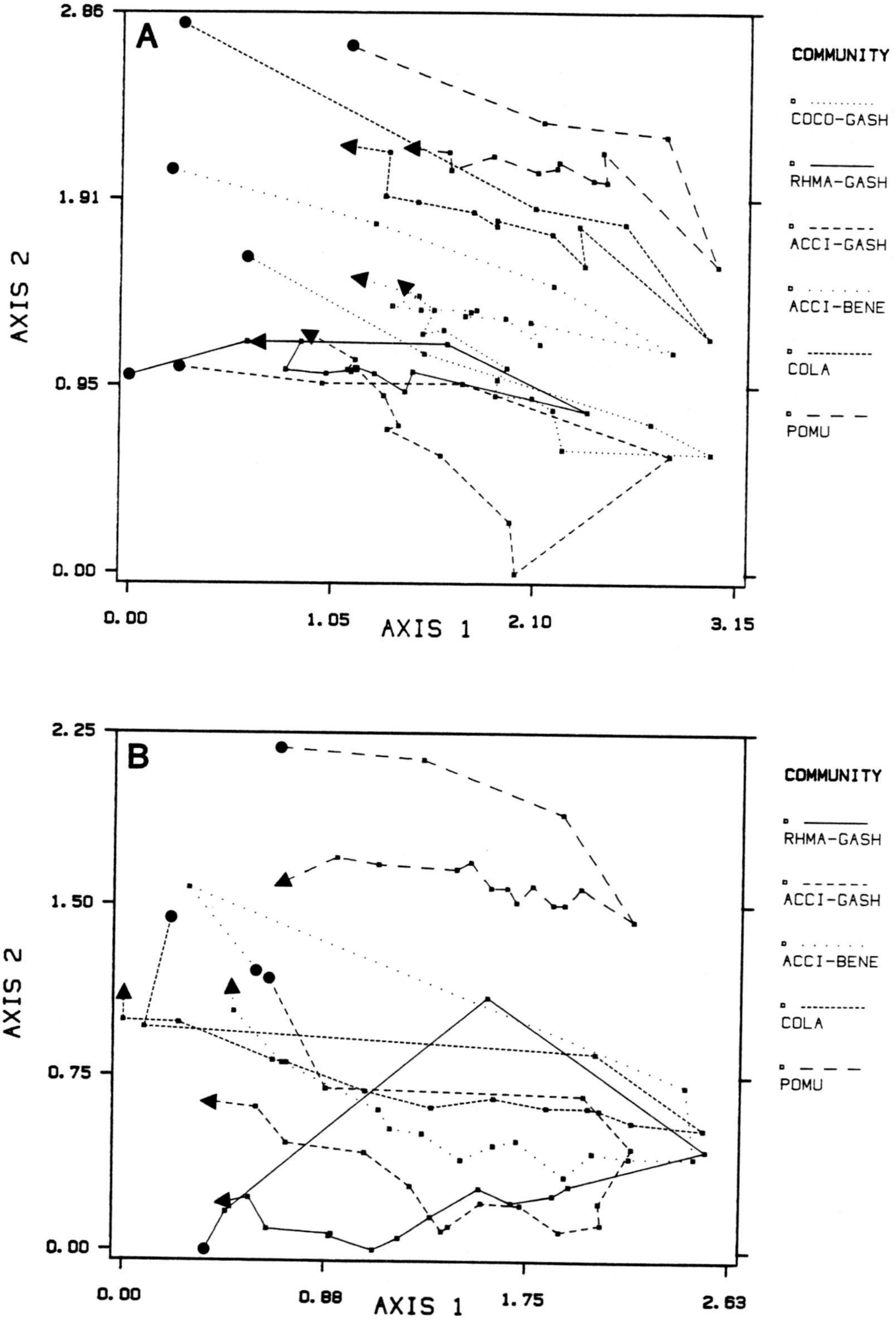
Plant Community Patterns

Convergent, as well as discrete, paths of development were observed in ordinations of plant community samples for both watersheds (Fig. IV-2). Positions of the pre-disturbance samples suggest that Axis 2 coincides with the complex moisture gradient (decreasing from top to bottom) along which initial forest communities were arrayed.

Convergent successional trajectories were particularly evident on WS3 (Fig. IV-2B). Communities representing dry (*Rhododendron* - *Gaultheria* and *Acer* - *Gaultheria*) and mesic sites (*Acer* - *Berberis* and *Coptis*) show strikingly similar changes in composition for 10 yr following burning. Early convergence may be a consequence of the small floristic differences which separated the mesic to dry forest communities, as well as of the broad ecological amplitude of dominant invaders within this portion of the environmental gradient (Halpern 1987). Colonizing species with wide distributions include annuals (e.g., *Senecio sylvaticus* and *Epilobium paniculatum*), herbaceous perennials (e.g., *E. angustifolium*), and woody perennials (e.g., *Ceanothus velutinus*). Subsequent divergence of successional

Figure IV-2. Detrended correspondence analysis (DCA) ordination through time of composite samples representing the initial plant communities of Watersheds 1 and 3. **A)** Watershed 1, **B)** Watershed 3. Lines connect the same composite sample in subsequent years. Closed circles represent the initial forest communities; arrows coincide with the final sample and indicate the direction of change through time. See Fig. IV-1 for the sampling dates for intervening years. Community abbreviations: COCO-GASH = *Corylus-Gaultheria*, RHMA-GASH = *Rhododendron-Gaultheria*, ACCI-GASH = *Acer-Gaultheria*, ACCI-BENE = *Acer-Berberis*, COLA = *Coptis*, POMU = *Polystichum*.

Figure IV-2.


A
2.86
1.91
0.95
0.00
AXIS 2
0.00
1.05
2.10
3.15
AXIS 1
COMMUNITY
COCO-GASH
RHMA-GASH
ACCI-GASH
ACCI-BENE
COLA
POMU
B
2.25
1.50
0.75
0.00
AXIS 2
0.00
0.88
1.75
2.63
AXIS 1
COMMUNITY
RHMA-GASH
ACCI-GASH
ACCI-BENE
COLA
POMU

trajectories accompanies the decline of invading species groups and recovery of initial forest dominants to pre-disturbance levels (e.g., *Rhododendron macrophyllum*, in the *Rhododendron* - *Gaultheria* community, *Acer circinatum* in the *Acer* - *Berberis* community, and *Gaultheria shallon* in the *Acer* - *Gaultheria* community). The positions of late-seral samples suggest return toward pre-disturbance composition (Fig. IV-2B).

In comparison, successional trajectories for moist site communities were more discrete. For example, within the *Polystichum* community of WS1 (Fig. IV-2A), post-disturbance samples were distinguished by invading and residual species with a local affinity for moist sites. These included annual (e.g., *Montia sibirica*) and perennial invaders (e.g., *Anaphalis margaritacea*, *Rubus parviflorus*), as well as initially subordinate (e.g., *Trientalis latifolia*, *Oxalis oregana*, and *Vancouveria hexandra*) and dominant forest herbs (e.g., *Polystichum munitum*). On WS3, the successional sequence for *Polystichum* sites (Fig. IV-2B) additionally reflected the dramatic release of *Linnaea borealis* and *Galium triflorum*. On both watersheds, trajectories for this community were further distinguished by the limited development of *Ceanothus velutinus*, the principal colonizing shrub of mesic and dry sites.

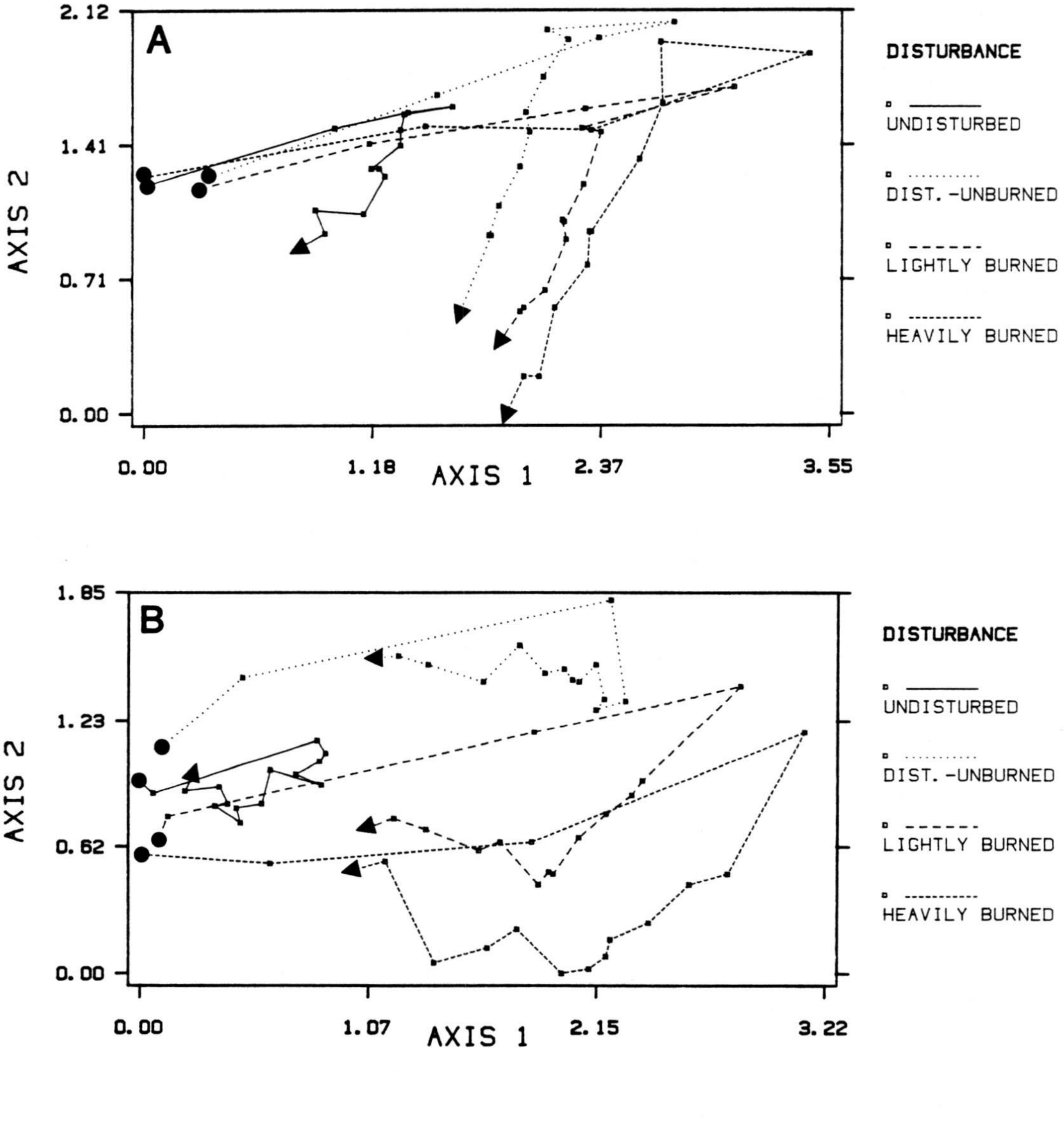
Thus, pronounced changes in composition typify the response of all communities to disturbance. Initial forest dominants are rapidly but temporarily replaced by annual and perennial colonizers. Subsequent convergence depends both on the similarity of initial composition and on the ecological amplitude of invaders. Although convergence is common, it is transient, as gradual decline of invaders and persistent recovery of initial dominants return communities toward pre-disturbance composition. Discrete paths of succession occur where the initial flora is distinct and where invaders show greater community fidelity.

Soil Disturbance Class Patterns

The intensity of initiating disturbance profoundly influences the rate and direction of successional change. Ordinations through time of composite samples, representing soil disturbance classes, revealed increasing rates of change with disturbance intensity (Fig. IV-3). At its ends, Axis 1 contrasts pre-disturbance forest sites (left) with early-seral burned sites (right). For example, on WS1 (Fig. IV-3A), the positions of lightly and heavily burned sites 2 yr following burning, coincide with the maximum abundance of the wind-dispersed colonizers, *Senecio sylvaticus* and *Epilobium paniculatum*. Their prominence on burned sites 2 growing seasons after slash burning reflects 1) copious, local seed production, 2) the interaction of a winter annual life cycle with the timing of disturbance, and 3) an affinity for high soil fertility associated with recent burns (West and Chilcote 1968). The contemporaneous position for undisturbed sites (those with little soil disturbance and no fire), reflects the persistence of initial forest species and the local development of *Epilobium angustifolium*. Because a

Figure IV-3. DCA ordination through time of composite samples representing the soil disturbance classes of Watersheds 1 and 3. **A)** Watershed 1, **B)** Watershed 3. See Fig. IV-2 for details.

Figure IV-3.


A
2.12
1.41
0.71
0.00
AXIS 2
0.00
1.18
2.37
3.55
AXIS 1
DISTURBANCE
UNDISTURBED
DIST.-UNBURNED
LIGHTLY BURNED
HEAVILY BURNED
B
1.85
1.23
0.62
0.00
AXIS 2
0.00
1.07
2.15
3.22
AXIS 1
DISTURBANCE
UNDISTURBED
DIST.-UNBURNED
LIGHTLY BURNED
HEAVILY BURNED

majority of undisturbed plots were harvested during the first season of staggered logging (Halpern 1987), this rhizomatous perennial established relatively early from wind-dispersed seed and showed dramatic vegetative expansion.

Subsequent compositional changes among disturbance classes differed between watersheds, reflected in different paths of recovery of initial composition. On WS1, composite samples uniformly progress downward along the second axis (Fig. IV-3A). On WS3, however, all successional trajectories are directed toward pre-disturbance points (Fig. IV-3B) and the second axis simply segregates alternate floristic sequences initiated by different intensities of disturbance.

Compositional changes along Axis 2 of the WS1 ordination coincide with a gradual physiognomic transition from herb-dominated to tall shrub-dominated understories (Fig. IV-3A). The increasing trajectory length with intensity of disturbance, coincides with the differential distribution of residual and invading tall shrub species among soil disturbance classes. For example, initial forest dominants (e.g., *Acer circinatum* and *Rhododendron macrophyllum*) reoccupied the undisturbed soil class, sprouting from adventitious stem buds. In contrast, invading shrubs dominated the disturbed and burned soil classes. *Rubus parviflorus* characterized disturbed-unburned sites, germinating from a seed bank or from newly deposited seed (Haeussler and Coates 1986). *Ceanothus velutinus* and *C. sanguineus*, stimulated to germinate by fire (Gratkowski 1962), dominated lightly and heavily burned sites. Thus, similar changes in vegetation structure developed through alternate floristic paths.

Although invading shrubs species on WS3 generally showed the same affinities for disturbed and burned soil as on WS1, widespread recovery of residuals occurred on all sites. Additionally, successional trajectories on WS3 (Fig. IV-3B) suggest that, unlike on WS1 (Fig. IV-3A), the relative recovery of disturbed and burned soil classes was not related to the intensity of disturbance. Distances were similar between initial and final composite samples for the three disturbed and burned soil classes. Furthermore, minor fluctuations in the mid- to late-seral positions of undisturbed samples on WS3 (Fig. IV-3B), suggest a temporary stability in composition closely resembling that of the initial forest understory. The differences in recovery between watersheds are partly explained by three observations (Halpern 1987):

1. Invading herbs and tall shrubs showed distinctly greater importance on WS1 than on WS3. Principal differences included the prominence of *Epilobium paniculatum* on WS1, the long-term persistence of *Ceanothus sanguineus* and *C. velutinus* on WS1, and the poor development of *C. sanguineus* on WS3.

2. The abundance of invaders on WS1 varied directly with the intensity of disturbance, reflecting the distributional patterns of annual (e.g., *Senecio sylvaticus* and *E. paniculatum*) and woody perennial species (e.g., *C. sanguineus* and *C. velutinus*). Their total abundance on WS3, in contrast, was notably similar among disturbed and burned soil classes.

3. Complete recovery of initial community dominants was limited

to undisturbed sites on WS1, but was widespread among disturbed and burned sites on WS3. Here, the most resilient species included low shrubs (e.g., *Gaultheria shallon* and *Berberis nervosa*) and tall shrubs (e.g., *Acer circinatum*).

Interactions of Initial Composition and Disturbance Intensity

Vegetation changes may also reflect the combined influence of initial composition and intensity of disturbance. Multiple successional paths arising from this interaction are revealed in ordinations of selected subsets of the data. Several examples from WS1 are provided.

Polystichum munitum community

Succession in the *Polystichum* community of WS1 reflected the differential response of the dominant invading and residual species to variation in disturbance. As a consequence, successional trajectories represented variation in compositional change with disturbance intensity (Fig. IV-4). On undisturbed seral sites, for example, dominance rapidly shifted from invading to residual growth-forms. Early prominence of *Epilobium angustifolium* was followed by dramatic release of the trailing sub-shrub, *Whipplea modesta*, and subsequent recovery of the initial community dominant, *Polystichum munitum*.

In contrast, trajectories on heavily burned sites were persistently dominated by invaders--initially by annuals (e.g., *Senecio sylvaticus*, *Epilobium paniculatum*, and *Montia sibirica*); secondarily by biennials and small statured perennials (e.g.,

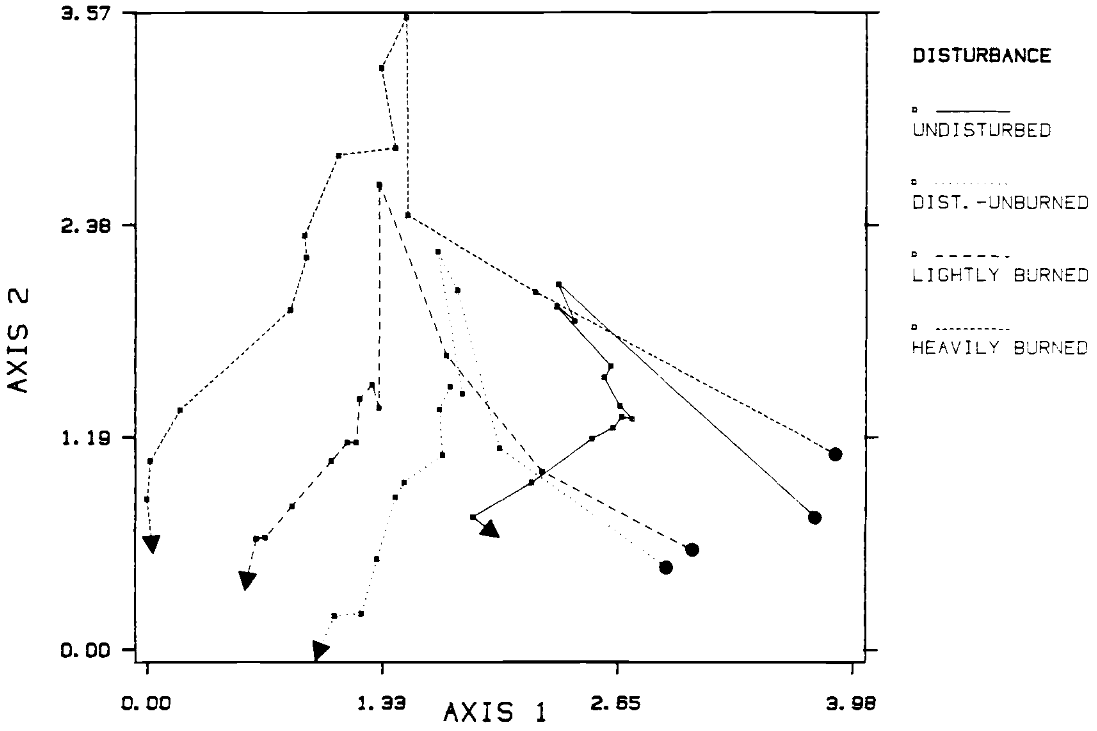


Figure IV-4. DCA ordination through time of composite samples experiencing four intensities of disturbance within the Polystichum munitum community of Watershed 1. See Fig. IV-2 for details.

Agoseris spp., Anaphalis margaritacea, and Rubus leucodermis); and subsequently by tall, woody perennials (e.g., Ceanothus velutinus, C. sanguineus, and Rubus parviflorus). Although subordinate forest herbs (e.g., Trientalis latifolia, Galium triflorum, Hieracium albiflorum, and Rubus ursinus) also showed periods of release, community dominants were either greatly reduced (e.g., Polystichum munitum) or eliminated (e.g., Tsuga heterophylla, Berberis nervosa and Coptis laciniata).

Undisturbed sites

Undisturbed community samples on WS1 maintained their initial floristic character through time (Fig. IV-5). Successional trajectories are variously directed, occupying relatively small, discrete zones within the ordination field. Distances encompassing each trajectory are consistently shorter than distances separating them. Additionally, there is little evidence for a distinct temporal or environmental gradient, in contrast with the response of communities to the average disturbance regime (Fig. IV-2A). Although the principal ordination axes have little ecological meaning, the plant communities are, nevertheless, well segregated by floristic differences.

These successional trends reflect three basic patterns among the principal species groups. First, invading species--most noticeably the fugitive annuals--played a minor role on undisturbed

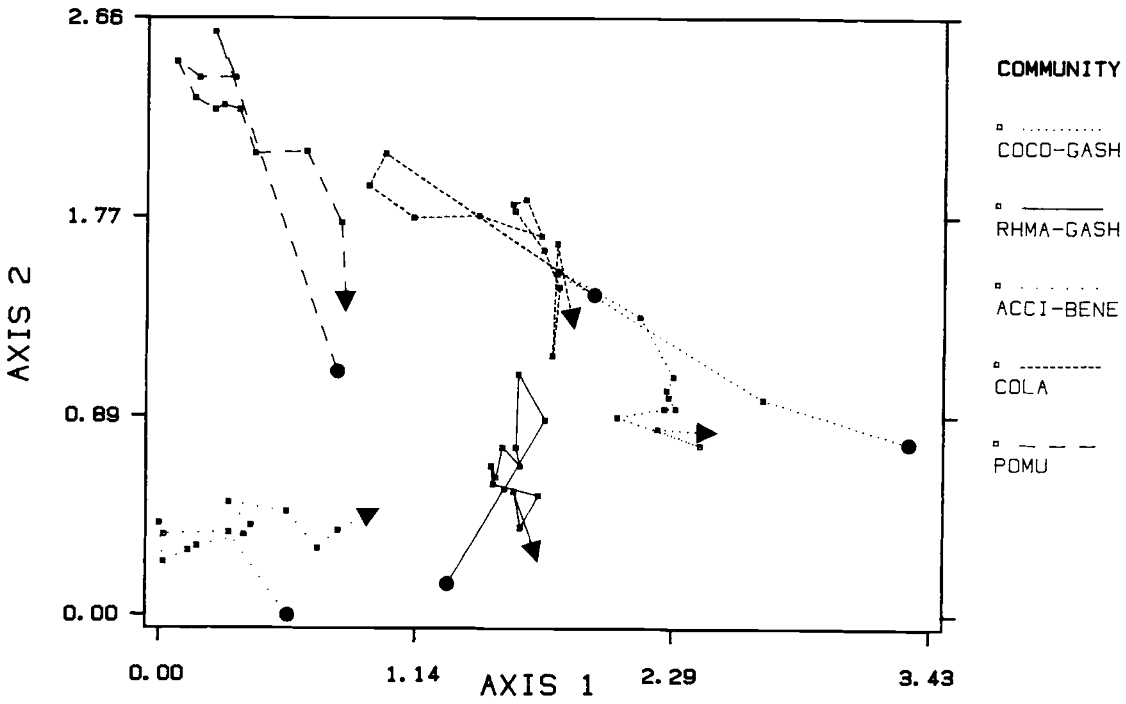


Figure IV-5. DCA ordination through time of composite samples representing the initial plant communities within the undisturbed soil class of Watershed 1. Community abbreviations: COCO-GASH = Corylus-Gaultheria, RHMA-GASH = Rhododendron-Gaultheria, ACCI-GASH = Acer-Gaultheria, ACCI-BENE = Acer-Berberis, COLA = Coptis, POMU = Polystichum. See Fig. IV-2 for details.

sites. Second, initial community dominants persisted through disturbance and recovered moderately to rapidly (e.g., _Acer circinatum_ and _Rhododendron macrophyllum_, and _Polystichum munitum_), or in many instances, expanded beyond pre-disturbance abundance (e.g., _Berberis nervosa_, _Gaultheria shallon_, _Corylus cornuta_, _Coptis laciniata_, and _Tsuga heterophylla_). Third, subordinate residuals showed local, transient release. Among these species, _Achlys triphylla_ was largely restricted to the _Corylus_ - _Gaultheria_ community, _Galium triflorum_ to the _Acer_ - _Berberis_ community, and _Trientalis latifolia_ to the _Acer_ - _Berberis_ and _Polystichum_ communities. Thus, discrete successional paths reflect temporary, local expansion of sub-dominant species, as well as rapid return of initial composition and structure.

Lightly burned sites

Paths of community succession within the lightly burned sites of WS1 emphasized the dramatic influence of fire on community composition and structure (Fig. IV-6). Burning resulted in a significant, and often persistent, reduction in cover of forest residuals and it initiated seres dominated by invading species.

Alignment of pre-disturbance communities along Axis 2 roughly coincides with the principal environmental gradient of available moisture. Following disturbance, however, seral communities display rapid floristic changes leading, in some instances, to brief periods

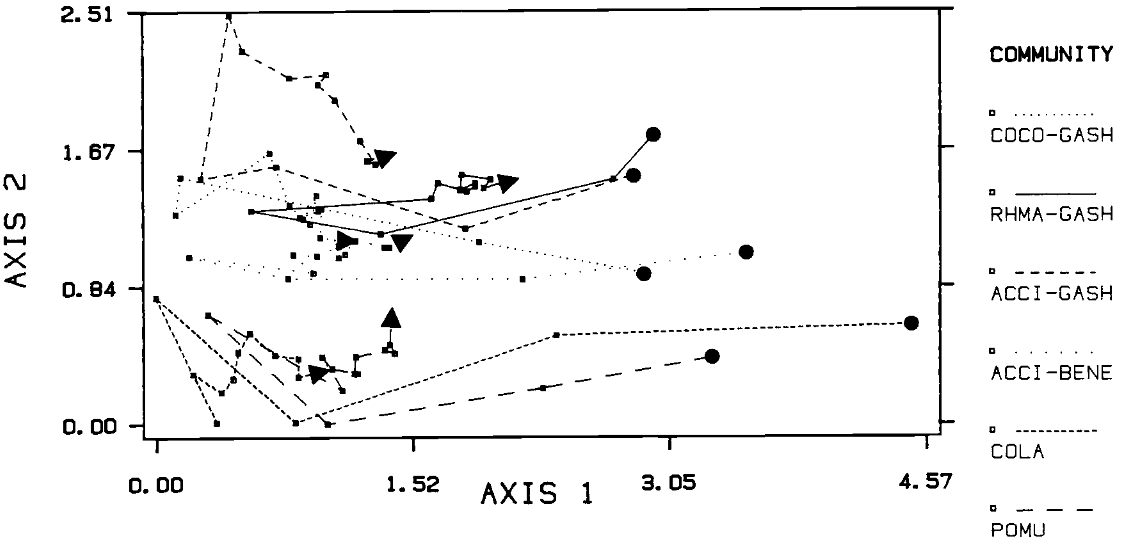


Figure IV-6. DCA ordination through time of composite samples representing the initial plant communities within the lightly burned soil class of Watershed 1. Community abbreviations: COCO-GASH = Corylus-Gaultheria, RHMA-GASH = Rhododendron-Gaultheria, ACCI-GASH = Acer-Gaultheria, ACCI-BENE = Acer-Berberis, COLA = Coptis, POMU = Polystichum. See Fig. IV-2 for details.

of convergence in different regions of the evironmental gradient (e.g., *Acer* - *Gaultheria* with *Corylus* - *Gaultheria* and *Coptis* with *Polystichum* during years 1-2). Early convergence reflects the rapid and pervasive establishment of invading annuals (e.g., *Senecio sylvaticus* and *Epilobium paniculatum*) in response to burning. The separation of mesic-xeric and moist communities at this time, however, is partially explained by local expansion of *E. angustifolium* on moist sites. Vigorous, rhizomatous spread of this perennial invader occurred prior to burning, as a majority of the *Coptis* and *Polystichum* plots were harvested during the first season of staggered logging (Halpern 1987).

Successional trajectories subsequently diverge due to differences among communities in the invasion and replacement of species. For example, otherwise uncommon annual (e.g., *Conyza canadensis*), and perennial invaders (e.g., *Lathyrus polyphyllus*, *Vicia americana*, and *Arctostaphylos columbiana*) dominated the *Acer* - *Gaultheria* community. In the *Coptis* community, other perennial invaders (e.g., *Equisetum arvense*, *Epilobium watsonii*, and *Ribes* spp.) were locally abundant. The most abundant invaders (e.g., *Ceanothus velutinus*, *C. sanguineus*, and *Rubus parviflorus*) displayed distinct community affiliations, despite their broad distribution among lightly burned sites. Subordinate forest herbs, released by disturbance (e.g., *Rubus ursinus*, *Whipplea modesta*, *Trientalis latifolia*, and *Symphoricarpos mollis*), also showed community fidelity, contributing to divergence of trajectories.

The distance separating pre-disturbance and final composite samples for lightly burned communities (Fig. IV-6) suggests that recovery of initial composition was poor relative to that on undisturbed sites (Fig. IV-5), particularly in the depauperate *Coptis* community. Although light burning potentially limits the regeneration of numerous forest dominants, several species recovered locally and, occasionally, expanded beyond initial levels. These included *Berberis nervosa* and *Gaultheria shallon* (in the *Rhododendron* - *Gaultheria*, *Acer* - *Gaultheria*, and *Acer* - *Berberis* communities) and *Corylus cornuta* (in the *Corylus* - *Gaultheria* community). While the recovery of *B. nervosa* and *G. shallon* following fire appears highly variable, *C. cornuta* characteristically resprouts vigorously from the base (Buckman 1964, Tappeiner 1971, Johnston and Woodward 1985, Haeussler and Coates 1986). The relative proximity of initial and final samples for these communities suggests their greater recovery (Fig. IV-5).

Measures of Resistance and Resilience

Resistance and resilience are complex measures of the immediate and long-term response of communities to disturbance. Both properties reflect characteristics of the initial community and of the disturbance itself. Examples from WS1 illustrate the influence of disturbance intensity and initial composition on the resistance and resilience of communities.

Intensity of disturbance

The resistance and resilience of vegetation on WS1 were inversely related to the intensity of disturbance (Fig. IV-7). Maximum compositional dissimilarity occurred in year 2, when fugitive annuals reached peak canopy cover. Varying inversely with the maximum dissimilarity, resistance reflects the relative persistence of initial species' canopies through disturbance (or their immediate post-disturbance regeneration) and the extent of exclusion of invading species. Sprouting of stems and rhizomes affords moderate resistance to disturbance to a majority of the initial dominants in *Pseudotsuga* understories (Sabhasri 1961, Volland and Dell 1981, Haeussler and Coates 1986). Nevertheless, the removal of above-ground structures appears directly related to fire intensity. For example, species such as *Polystichum munitum* commonly survive intense fire, but may be absent above-ground for several years following burning (Haeussler and Coates 1986).

In contrast, the concomitant establishment of fugitive annuals is enhanced by fire. The availability of germination sites on mineral soil increases with disturbance intensity. Further, species such as *Senecio sylvaticus* display an affinity for the high soil fertility associated with recent burns (West and Chilcote 1968).

Resilience, the relative similarity of composition between initial and final samples, also declined with intensity of disturbance (Fig. IV-7), as recovery of residuals decreased and persistence of invaders increased with disturbance intensity. The

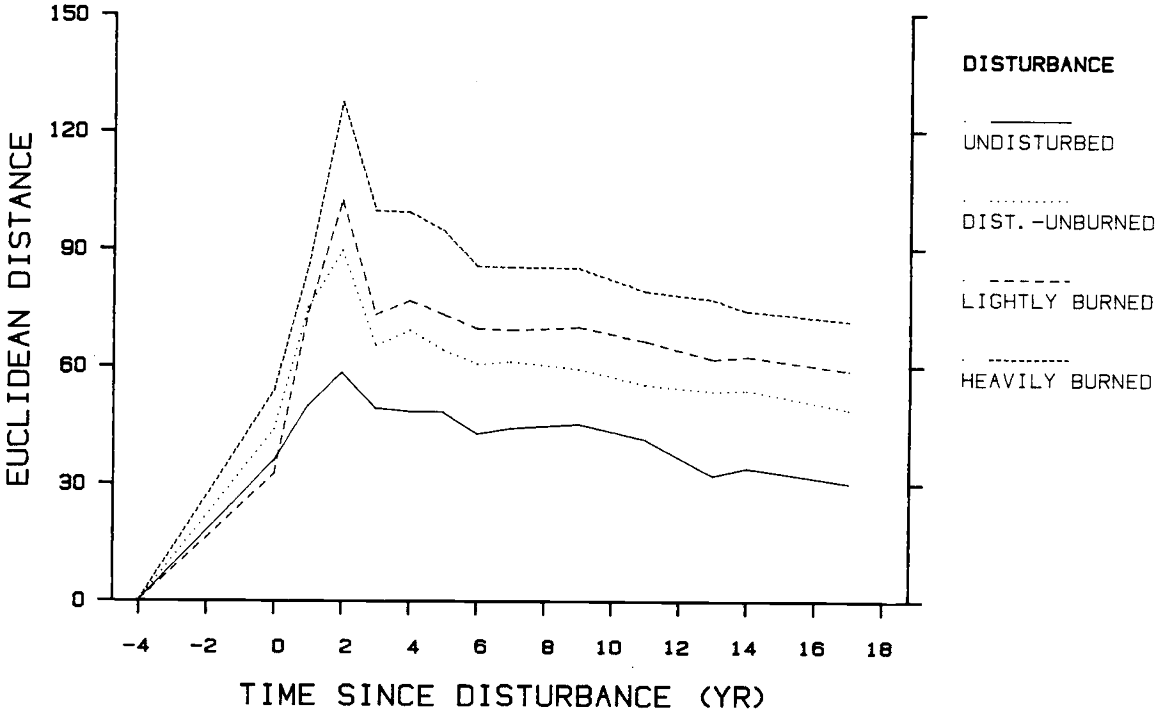


Figure IV-7. Changes in Euclidean distance with time for the soil disturbance classes of Watershed 1. See text for details.

recovery of understories within *Pseudotsuga* forests is typically dependent upon the vegetative reproduction of surviving individuals, as reproduction from seed appears poor (Anderson 1967, Russel 1974, Schopmeyer 1974, Sabhasri 1961, Haeussler and Coates 1986). Although basal sprouting of species such as *Acer circinatum* and *Gaultheria shallon* may be stimulated even after heavy burning, rates of recovery are typically lower than on unburned sites (Bailey 1966, Steen 1966, Anderson 1969, Kraemer 1977, Haeussler and Coates 1986).

Measures of resilience also reflect the persistence of invading species. Both the magnitude, and duration, of dominance of the principal invading shrubs, *Ceanothus sanguineus* and *C. velutinus*, increased with disturbance intensity. Because its buried viable seed requires cracking of the hilar fissure for germination (Gratkowski 1962), *Ceanothus* typically increases in density with intensity of burning (Biswell 1961, Dyrness 1973, Orme and Leege 1976, Conard et al. 1985). At final sampling on WS1, total *Ceanothus* cover ranged from 11% on undisturbed sites to 57% on heavily burned sites (Halpern 1987). This contrast may reflect reduced competition from residuals on heavily burned sites, as well as differences in initial establishment.

Plant communities

Plant communities were similar both in their average resistance and resilience (Fig. IV-8) due to common patterns of early invasion and long-term recovery. Colonizing annuals with broad ecological distributions dominated all communities within 2 growing seasons following burning. Similarly, initial forest dominants slowly, but persistently, recovered following an initial rapid decline; relative abundances at final sampling were proportional to original abundances.

The greatest difference in resistance and resilience occurred between the *Coptis* and *Polystichum* communities, reflecting their initial composition and structure. The *Coptis* community was associated with dense sub-canopies of *Tsuga heterophylla*, and understories were extremely depauperate. Herb and shrub cover averaged 12 and 2%, respectively. Invading species and initially subordinate residuals dominated post-disturbance communities, whereas the limited abundance of forest dominants resulted in poor long-term recovery. In contrast, initial understories of the *Polystichum* community were rich and structurally complex, with herb and shrub cover averaging 53 and 33%, respectively. Although invaders briefly dominated the post-disturbance flora, residuals were also abundant. Surviving individuals served as centers for vegetative expansion, promoting relatively rapid community recovery.

The measures of resistance and resilience presented above represent the response of communities to the average level of

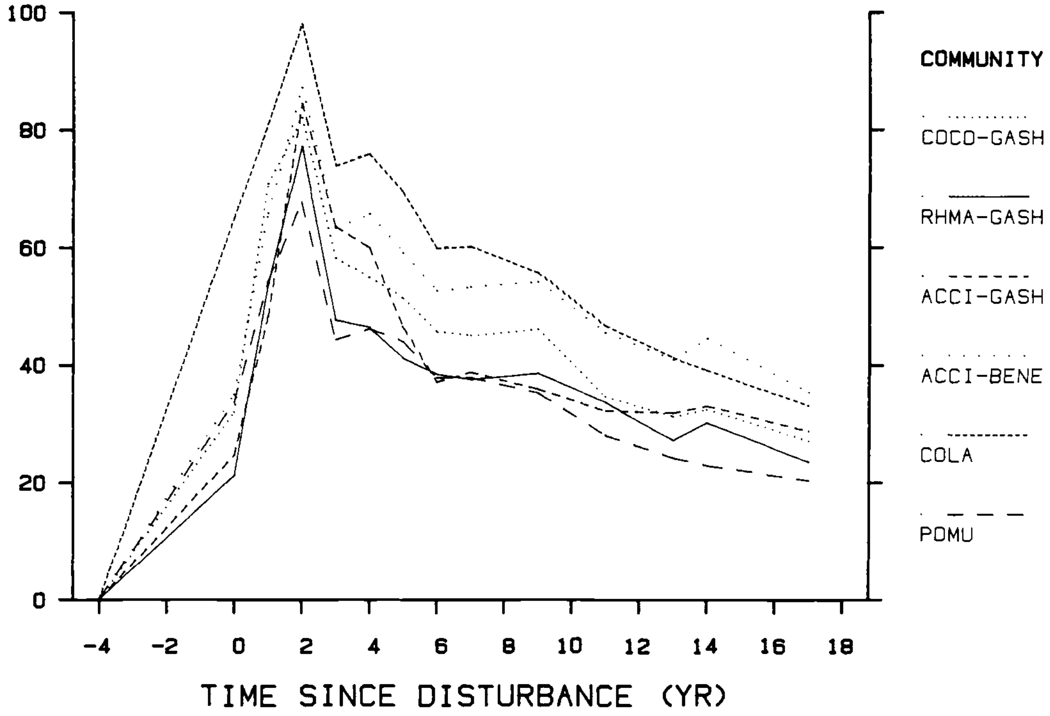


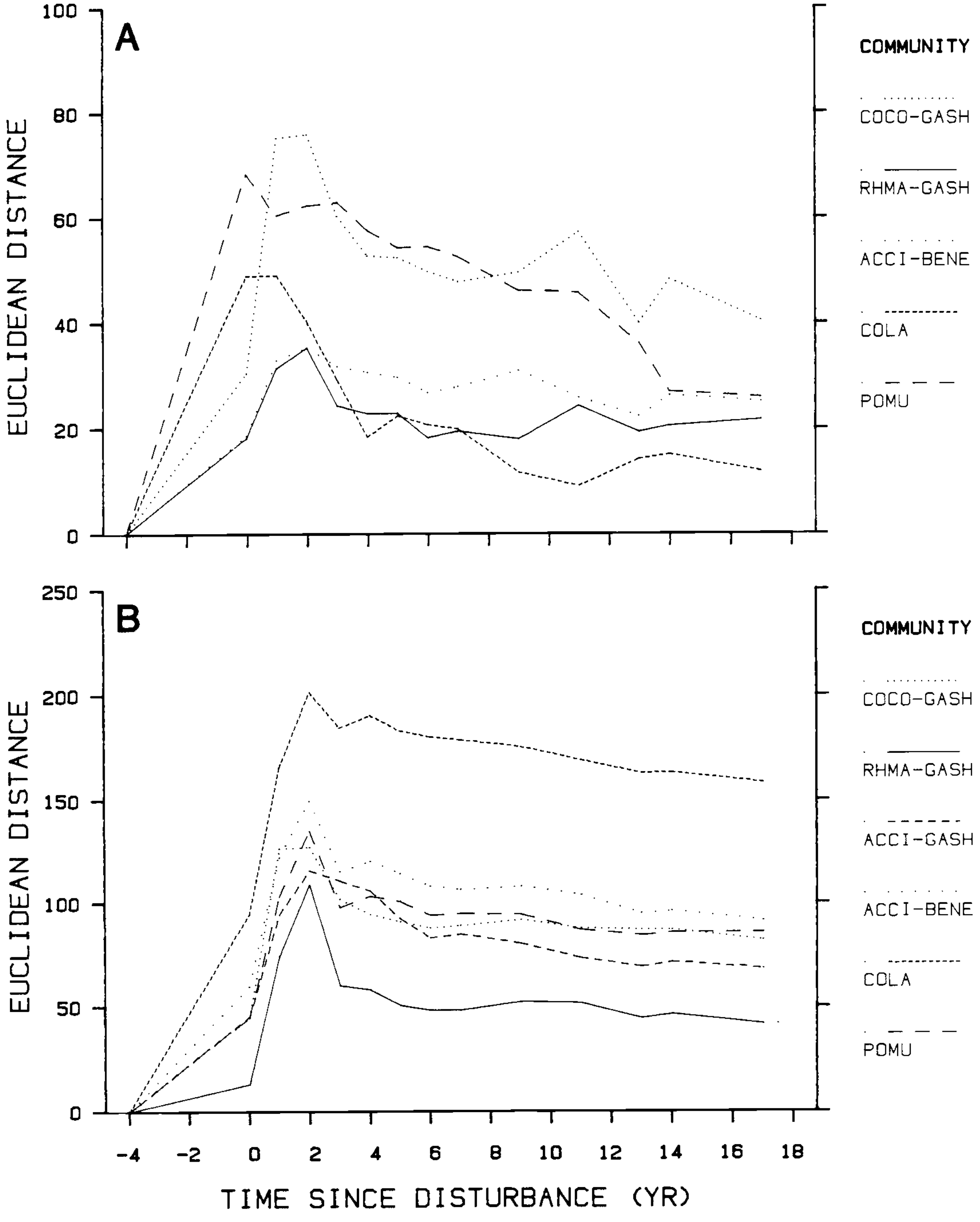
Figure IV-8. Changes in Euclidean distance with time for the initial plant communities of Watershed 1. Community abbreviations: COCO-GASH = Corylus-Gaultheria, RHMA-GASH = Rhododendron-Gaultheria, ACCI-GASH = Acer-Gaultheria, ACCI-BENE = Acer-Berberis, COLA = Coptis, POMU = Polystichum. See text for details.

disturbance. Among the individual soil disturbance classes, however, community responses varied dramatically. This heterogeneity reflects changes in the response of principal residual and invading species along the disturbance gradient. On undisturbed sites, for example, resistance of the *Coptis* community was intermediate and its resilience high (Fig. IV-9A). Invading species (e.g., *Senecio sylvaticus*, *Epilobium paniculatum*, and *Rubus parviflorus*) were relatively uncommon. The most common species within an initially depauperate understory (e.g., *Berberis nervosa*, *Coptis laciniata*, and *Tsuga heterophylla*) persisted through overstory removal and showed gradual expansion. Undisturbed *Coptis* sites were local refugia for *T. heterophylla*; an abundance of survivors subsequently reestablished a dense understory tree canopy.

In contrast, both resistance and resilience were significantly low for the lightly burned sites in *Coptis* communities (Fig. IV-9B). Characteristic forest species recovered minimally. Seral communities were dominated by invading species displaying enhanced establishment on burned soils, and by initially uncommon residuals that were released from competition. Without an initially dominant, residual herb and shrub flora, long-term recovery on these sites may require canopy closure to eliminate invaders. However, reestablishment of the *Tsuga heterophylla* sub-canopy will be slower than on undisturbed sites, as reproduction must be from seed.

Figure IV-9. Changes in Euclidean distance with time for the initial plant communities of Watershed 1 within two disturbance regimes. **A)** the undisturbed soil class, **B)** the lightly burned soil class. Community abbreviations: COCO-GASH = *Corylus-Gaultheria*, RHMA-GASH = *Rhododendron-Gaultheria*, ACCI-GASH = *Acer-Gaultheria*, ACCI-BENE = *Acer-Berberis*, COLA = *Coptis*, POMU = *Polystichum*. See text for details.

Figure IV-9.


A
EUCLIDEAN DISTANCE
0
20
40
60
80
100
COMMUNITY
COCO-GASH
RHMA-GASH
ACCI-BENE
COLA
POMU
B
EUCLIDEAN DISTANCE
0
50
100
150
200
250
COMMUNITY
COCO-GASH
RHMA-GASH
ACCI-GASH
ACCI-BENE
COLA
POMU
-4
-2
0
2
4
6
8
10
12
14
16
18
TIME SINCE DISTURBANCE (YR)

GENERAL CONCLUSIONS

Alternate Paths of Succession

Multiple paths of succession were observed following logging and slash burning of old-growth *Pseudotsuga* forests. Understory communities arrayed along a complex gradient of available moisture showed convergent, as well as discrete successional sequences. Early convergence of seral communities within mesic and dry sites, reflected the compositional similarity of pre-disturbance communities and the broad distributional range of colonizing species. However, the vegetative recovery of a forest flora moderately resistant to fire, resulted in subsequent sorting of seral communities, and a general return toward initial composition. Successional pathways within moist communities were discrete in comparison. Unique developmental sequences reflected distinct residual and invading floras.

Alternate successional sequences were also initiated when disturbance varied in intensity. Rates and directions of compositional change reflected a corresponding gradient in the response to disturbance of dominant residual and invading species. However, the nature of the response gradient varied. For example, on WS1, the abundance and persistence of colonizers increased, whereas the recovery of residuals decreased, with disturbance. Results from WS3, however, suggest that long-term recovery is not necessarily a function of disturbance intensity. Here, the suite of dominant invading herbs were equally abundant among the disturbed and burned sites, although the distributions of individual species differed with disturbance intensity and with time. Moreover, the dominant residual component reestablished across the entire disturbance gradient.

Alternate paths of community succession may derive from temporal, as well as spatial characteristics of disturbance. For example, the local prominence of Epilobium angustifolium in undisturbed Polystichum plots of WS1 largely reflected the timing of disturbance within these sites. In particular, undisturbed plots experienced a prolonged period of recovery prior to slash burning because they were principally logged during the first of 4 yr of staggered harvesting (Halpern 1987). During this period, individuals that established from seed showed vigorous rhizomatous expansion. Further, as burning disturbance was virtually absent from undisturbed sites, succession was effectively initiated 1-3 yr earlier on undisturbed sites than on disturbed or burned sites.

The time-courses for Pseudotsuga communities illustrate the importance of initial composition and disturbance intensity in seral forest development. Successional paths were largely a consequence of the differential response of original forest species and available colonizers to the gradient in disturbance. However, historical factors such as variation in seed bank distribution (Halpern 1987) or random events such as timing of disturbance or fluctuations in weather (Halpern 1987) may influence the long-term dynamics of developing communities. The results of this study lend support to the growing number of models incorporating both deterministic factors and chance in explaining alternate paths of community succession (Lyon and Stickney 1976, Noble and Slatyer 1977, 1980, Cattelino et al. 1979, MacMahon 1981, Horn 1981, Morgan and Neuenschwander 1985, Steinhorst 1985).

Community Resistance and Resilience

Within the range of disturbance intensities studied, Pseudotsuga communities on WS1 exhibited an inherent tendency to return toward the initial state. Early deviation following disturbance reflected temporary, but dramatic, loss of forest dominants, with concomitant establishment of colonizers and release of forest subordinates. The long-term recovery of characteristic species, however, generally resulted in an understory composition resembling that of the original community. Other authors have referred to this tendency as stability (May 1973, Holling 1973, Orians 1975), adjustment stability (Sutherland 1981, Connell and Sousa 1983), resilience (Westman 1978, 1985, Pimm 1984, Keeley 1986, Westman and O'Leary 1986), or elasticity (Cairns and Dickson 1977). Recovery of understory composition and structure in Pseudotsuga forest communities is founded in the moderate tolerance of initial forest dominants to disturbances such as soil churning or fire, and in their ability to perennate from subterranean structures. Although rates of recovery may vary depending on the disturbance regime and on the life history of the dominant species, community resilience is widespread in terrestrial ecosystems subject to fire (e.g, Hanes 1971, Naveh 1975, Black and Bliss 1978, Ohmann and Grigal 1979, Viereck and Dyrness 1979, Trabaud and Lepart 1980, Gill 1981, Mallik and Gimingham 1983, Christensen 1985, Keeley 1986, Westman and O'Leary 1986).

Both resistance and resilience were similar among all but the most structurally and compositionally distinct communities, reflecting a common pattern of initial decline, colonization, release, and recovery among broadly distributed groups of invading and residual species. Contrasting patterns between depauperate _Coptis_ and well-developed _Polystichum_ communities suggest that differences in initial community structure and composition may result in corresponding differences in the immediate and long-term response to disturbance. Low resistance and resilience in the _Coptis_ community illustrated the continuous preemption of abundant bare ground by opportunist species (e.g., annual and perennial colonizers and initially sub-dominant herbs) within a community poor in dominant residuals. Higher resistance and resilience in the _Polystichum_ community may have derived from the greater overall survival of dominants, as well as from their earlier and more continuous preemption of space by vegetative expansion.

Resistance and resilience measures among the disturbance classes of WS1 suggest that both the magnitude of initial compositional displacement and the degree of recovery were directly related to the intensity of disturbance. These trends were largely a consequence of the differential response of residual and invading species to the gradient in disturbance. Original community dominants generally showed poorer initial survival and slower recovery with increasing disturbance. In contrast, invading annuals and woody perennials showed increased rates of establishment and development with intensity of disturbance. Initially subordinate herbs and sub-shrubs exhibited an array of regenerative strategies, however, resulting in a broad distribution across the disturbance gradient (e.g., species reproducing by vegetative means on unburned sites and those by seed on burned sites).

Stochastic effects and local species patterns are also potentially important in shaping the response of communities to disturbance. For many communities in this study, the estimates of resistance and resilience within particular disturbance regimes were based on limited numbers of sample plots. For example, the two plots representing undisturbed *Polystichum* sites displayed relatively low resistance, reflecting the local loss of dominant shrub and tree species (e.g., *Acer circinatum* and *Tsuga heterophylla*). Because both species were minimally reduced on undisturbed sites of adjacent communities, the effect appears to be local and stochastic (attributed to the vagaries of logging). Similarly, within the single plot representing undisturbed *Corylus* - *Gaultheria* sites, the principal shrub and tree species (e.g., *Corylus cornuta* and *Taxus brevifolia*) were dramatically reduced. In fact, *C. cornuta* was reduced more on undisturbed than on lightly burned sites. Although the canopy of *C. cornuta* completely regenerated within the sampling period, community recovery was precluded by the local persistence of initially uncommon understory species (e.g., Linnaea borealis and Rubus parviflorus). Thus, the local recovery of communities may be altered by random events and small-scale variation in species response, manifested in local extinction or atypical expansion of species. A clearer understanding of the overall importance of these factors would be revealed by a balanced experimental design. Nevertheless, the results emphasize the potential modifying influence of local variation and of stochastic effects on community properties which are largely shaped by the life histories of the initial species and by disturbance intensity.

Chapter 5

SUMMARY

Long-term successional patterns following clearcut logging and slash burning of two Pseudotsuga watersheds were diverse, varying with initial composition, intensity of disturbance, and logging and burning history.

A majority of forest species persisted through disturbance or reemerged within 1-2 yr. Invading species primarily established within 2-3 growing season following burning, although new species were recruited throughout the sampling period. Long-term changes in composition, however, were characterized by the differential expansion and decline of dominant residual and invading species, rather than by sequential recruitment and replacement.

The stature of seral understory vegetation generally increased with time. Average watershed patterns indicated that herbs and low shrubs peaked in abundance within 2-6 yr following burning and tall shrubs assumed co-dominance within 10-18 yr. However, changes in physiognomy and composition varied widely among initial plant communities and along the gradient of disturbance intensity.

Invading species generally displayed greater abundance on disturbed or burned than on undisturbed sites, reflecting life histories directly dependent on fire or on the site conditions characterizing disturbed or burned soils. Their patterns of abundance reflected the origin of propagules, life cycle phenology, potential for vegetative reproduction, longevity, variation in the timing of disturbance, and spatial variation in disturbance intensity.

Residual species generally displayed greater development on undisturbed than on disturbed or burned sites. Their patterns of abundance reflected initial distributions, resistance to disturbance, mode of post-disturbance reproduction, morphological characteristics, and spatial variation in disturbance intensity.

Although long-term changes in vegetation physiognomy and composition could largely be explained by the differential response of these species to disturbance, other trends illustrated the importance of historical and stochastic factors in understory development. Variation in the availability of propagules, in weather conditions, and in the timing of logging and burning may influence long-term successional patterns.

Detrended correspondence analysis of successional community data suggests that early, but transient compositional convergence is common among seral forest communities on mesic to dry sites, due to the similarity of initial community floras and to the broad distribution of colonizing species. These analyses also indicate that compositional change increases with intensity of disturbance.

Measures of resistance and resilience, derived from Euclidean distances in ordination space, suggest that maximum compositional displacement and long-term community recovery are largely determined by the intensity of disturbance and by the life history traits of dominant residual and invading species. Within the range of disturbance intensities studied, Pseudotsuga communities display an inherent tendency to return toward pre-disturbance composition. The resilience of these communities derives from the ability of initial forest dominants to repsrout following burning.

Chapter 6

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