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Plant succession in areas of scorched and blown-down forest after the 1980 eruption of Mount St. Helens, Washington

Charles B. Halpern
Department of Forest Science
Oregon State University
Corvallis, OR 97331, USA

Peter M. Frenzen
Mount St. Helens National Volcanic Monument
Amboy, WA 98601, USA

Joseph E. Means
Pacific Northwest Research Station
United States Department of Agriculture Forest Service
Corvallis, OR 97331, USA

and

Jerry F. Franklin
College of Forest Resources
University of Washington
Seattle, WA 98195, USA

Address all correspondence to: Charles B. Halpern, Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA. Telephone: 503-757-4436.

Keywords: Detrended correspondence analysis, Life-form development, Plant recovery, Species diversity, Tephra, Volcanic disturbance.

Abstract

Patterns of plant succession were studied in areas of scorched and blown-down forest resulting from the 1980 eruption of Mount St. Helens, Washington. Changes in plant abundance were observed for a 7 yr period in permanent sample plots representing four types of post-disturbance habitats, or site types. A large proportion of the post-eruption vegetation derived from plants that persisted through disturbance. Survival and subsequent recovery of understory species were greatest in forests that supported a snowpack at the time of eruption. Gradually, however, species composition on previously forested plots converged toward that of formerly clearcut sites, due to widespread recruitment and clonal expansion of early seral forbs.

Trends in plant cover, species diversity, and community composition were highly variable among sample plots, suggesting that numerous factors, interacting at a variety of spatial scales, have influenced plant recovery and reestablishment. Despite this variation, plant cover and species richness increased with time among all site types, while species evenness declined. The abundance of life-forms such as low/sub-shrubs and tall shrubs was correlated with depth of burial by tephra and with the amount and type of large, woody debris. We predict that, although the rate and direction of future successional change will vary among site types, recovery of initial community composition and structure will be much slower than after other types of catastrophic disturbance such as clearcut logging or wildfire.

Nomenclature of vascular plants follows: Hitchcock, C. L. and Cronquist, A. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, WA.

Introduction

Large-scale disturbances profoundly alter the composition and structure of plant communities, yet they are rarely uniform in their influence on vegetation. Volcanic eruptions, in particular, are characterized by strong gradients in disturbance intensity and vegetation damage that correspond with distance and direction from the point of disturbance initiation (e.g., Griggs 1919a, Eggler 1948, Smathers & Mueller-Dombois 1974). In addition to such gradients, patterns of plant survival and community recovery may be influenced by numerous other factors (both abiotic and biotic) acting prior to, during, and after an eruption. Early observations of the 1980 eruption of Mount St. Helens, Washington, revealed that, in addition to distance from the crater, other variables such as local wind patterns, landform and topography, snow cover, and early erosional activity interacted to produce a complex mosaic of disturbance effects, post-disturbance environments, and residual plant populations (Rosenfeld 1980, Lipman & Mullineaux 1981, Franklin et al. 1985, 1988, Bilderback 1987).

Patterns of early plant recovery have been described for a variety of habitats at Mount St. Helens: intact and disturbed subalpine vegetation (Wood & del Moral 1987, 1988, del Moral & Wood 1988); debris avalanche surfaces (Dale 1986, Adams et al. 1987); riparian corridors in and adjacent to the blast zone (Kiilsgaard et al. 1986, Kiilsgaard 1987); and more distant, intact forests receiving shallow deposits of tephra (Antos & Zobel 1985a, 1986, Zobel & Antos 1986). In this paper, we examine patterns and mechanisms of plant recovery in areas of blown-down and scorched forest northeast of the volcano--the most extensive of the habitats in the devastated zone. Here, trees killed by the heat of the eruption were either flattened by the force of the blast or left standing, but stripped of foliage and/or fine branches. In addition, air-fall tephra (volcanic ejecta comprised of ash and pumice) from the initial and subsequent eruptions formed deposits 10 to 60 cm deep (Waitt & Dzurisin 1981). Within this zone of devastation, physical and biological conditions varied widely with changes in topography, depth and texture of tephra, distribution of organic material, and survival of understory plant and animal populations. Our data are based on 7 yr of observation of permanent sample plots established immediately after the eruption. Vegetation patterns during the first growing season (1980) indicated that characteristics of disturbance, as well as of pre- and post-eruption site conditions were important in plant survival and initial recovery (Means et al. 1982, Franklin et al. 1985, McKee et al. 1987). In this paper, we assess how disturbance characteristics and site conditions have affected longer-term changes in community composition and structure. In particular, we examine how trends in plant cover, species diversity, and community composition have been influenced by: (1) type and intensity of disturbance, (2) seral status of the pre-existing vegetation, (3) site conditions at the time of disturbance (e.g., the presence of snow cover), and (4) physical characteristics of the post-eruption environment (e.g., topographic features, depth of tephra, and type and abundance of large woody debris).

Study area

Permanent study sites lie within the northeastern portion of the devastated area of Mount St. Helens, Washington (lat. 46 16 N, long. 122 09 W). Sample plots are located between 710 and 1250 m elevation, encompassing both the Tsuga heterophylla and Abies amabilis Zones (Franklin & Dyrness 1973). At the time of the eruption, this area supported a mosaic of recently clearcut and planted sites interspersed with natural and old-growth forests up to 600 years-of-age. At lower elevations, the most common tree species included Pseudotsuga menziesii, Tsuga heterophylla, and Thuja plicata and at higher elevations, Abies amabilis, A. procera, *Pinus contorta*, and *Tsuga mertensiana* (Franklin & Dyrness 1973, Franklin *et al*. 1985, 1988, McKee *et al*. 1987). In mature forests, basal areas ranged from 60 to 110 m^2/ha; the dominant trees exceeded 1 m in diameter at breast height and 50 m in height (McKee *et al*. 1987). The composition and structure of forest understories prior to the eruption were probably similar to those reported in earlier descriptions of regional vegetation (Franklin & Dyrness 1973, Brockway *et al*. 1983).

The climate is maritime, with cool wet winters and warm, dry summers, as evident from pre-disturbance weather records (Spirit Lake Ranger Station, 987 m elevation). Temperatures range from mean monthly minima of $-4.2^{o}C$ in January and $7.3^{o}C$ in August to mean monthly maxima of $0.5^{o}C$ in January and $22.2^{o}C$ in July (Climatological Handbook Columbia Basin States 1969). Annual precipitation averages 2373 mm, yet only 7% falls between June and August. At higher elevations deep winter snowpacks accumulate and may persist through July.

Methods

Plot establishment and sampling

During the summer of 1980, 35 permanently staked transects 100 m in length were established in four major post-disturbance habitats, or site types (Fig. 1 and Table 1), within the devastated area (Means *et al*. 1982, Franklin *et al*. 1985, 1988, McKee *et al*. 1987):

(1) Blown-down forests (BD): These previously forested sites occupy large portions of the devastated area. Here, the force of the eruption was strong enough to uproot or break off mature trees within 10 m of the ground. Within the understory, nearly all above-ground plant parts were destroyed.

(2) Blown-down forests with snow (BDS): These sites, which typically occur at higher elevations in the devastated area (Table 1), also had trees uprooted or

snapped off by the blast. However, much of the understory vegetation survived, buried beneath a snowpack at the time of the eruption.

(3) Scorched forests (S): These sites occupy a narrow band at the edge of the zone of blown-down forest where the magnitude of the blast was less extreme. Most trees were killed by the eruption but remained standing. Although mortality of understory species was high, some above-ground plant parts persisted.

(4) Clearcuts (CC): These previously logged and burned sites were common in the area where forests were blown-down and scorched. At the time of the eruption they supported young planted stands dominated by perennial herbs and shrubs.

During the first growing season (1980), vegetation sampling was conducted within 5 circular subplots (250 m^2) evenly spaced along each of the 35 original transects. However, because annual remeasurements of all transects and subplots were not possible, we only present data for the 15 transects in which the same three subplots were sampled on all remeasurement dates.

Annually from 1980 to 1984, and again in 1986, visual estimates of percent canopy cover were made for all vascular plant species and for bryophytes as a group. During initial sampling (1980), physical features such as slope, aspect, and average depth of tephra were measured for each subplot and averaged for each transect (Table 1). Other site characteristics such as elevation and distance from the crater were determined from topographic maps. Average percent cover of logs was estimated along an intercept line spanning the diameter of each subplot. In blown-down forests, intercept lines were placed perpendicular to the direction of tree-fall; in clearcut and scorched forests, lines were placed perpendicular to the transect. During 1981, percent cover of tree rootwads and rills (narrow erosional channels), as well as logs, was visually estimated.

Analyses

Origin of the vegetation

To examine the origin of post-disturbance vegetation, all taxa were assigned to one of two groups: (1) colonizing species, those either typically absent from the above-ground vegetation of undisturbed forests or restricted to locally disturbed microsites and (2) original forest species, those characterizing the above-ground vegetation of undisturbed forest communities. Species assignments were based on previous regional descriptions of forest understory composition (Franklin & Dyrness 1973, Brockway et al. 1983) and on observations of adjacent, relatively undisturbed forest. Relatively uncommon species that could not easily be assigned to either group were excluded from these comparisons.

Life-form development

To assess changes in vegetation structure, we assigned each plant species to one of nine life-form groups--bryophyte, sedge or rush, grass, fern, annual or biennial forb, perennial forb, low or sub-shrub, tall shrub, or tree (Appendix 1). Relationships between the cover of each life-form at each sampling date and site characteristics were examined with multiple linear regressions. In each regression model the independent variables included general physical features (i.e., distance from the crater, slope, aspect, average tephra depth, and elevation [Table 1]), as well as ground surface features (i.e., cover of logs, rills, and rootwads). To test for changes in the cover of life-forms with time, we examined simple linear regressions of cover versus time for each site type. All regression analyses were performed with the MGLH procedure of SYSTAT©. The assumptions of the model were met for a majority of, but not for all, life-form--by--sampling date or life-form--by--site type permutations. Differences in life-form cover between pairs of site types at each sampling date were tested with the Games and Howell method (Sokal & Rohlf 1981) which assumes heterogeneous variance. All statistical analyses of life-form cover were based on log-transformed data.

Species diversity

Trends in species diversity among post-disturbance habitats were compared at three scales. First, we estimated local species richness as the mean number of species per 250 m^2 subplot. Second, for transects representing each site type, three diversity indices (Hill 1973) were calculated:

(1) Species richness, N_0, the mean number of species per transect.

(2) Species heterogeneity, N_2, the reciprocal of Simpson's index ($1/\sum_i p_i{}^2$, where p_i is the proportional abundance of the i-th species in the sample). N_2 integrates the number and relative abundance of taxa and may be expressed as the number of equally common species required to produce the same heterogeneity as that in the observed sample (Peet 1974).

(3) Mean species evenness, R_1, the ratio of N_1 (the exponent of Shannon's information measure, $\exp\text{-}[\sum_i p_i \log_e p_i]$, and N_2). R_1 reflects the relative equitability of species' distributions.

Finally, at the habitat level, we constructed dominance-diversity curves through time for each site type, based on the relative mean cover of species within all subplots.

All measures of subplot and transect diversity were calculated with PRHILL (B. G. Smith, unpublished program), a FORTRAN program that generates complete sets of Hill diversity indices and ratios (Hill 1973) for defined sets of samples.

To test for changes in diversity with time, simple linear regressions of richness, heterogeneity, and evenness versus time were examined using the MGLH procedure of SYSTAT© Annual differences in diversity between pairs of site types were tested using the Games and Howell method (Sokal & Rohlf 1981) where variances were heterogeneous. Where variances were homogeneous, the Tukey-Kramer procedure (Sokal & Rohlf 1981) was employed.

Relationships between subplot and transect diversity (i.e., subplot richness, N_0, N_2, and R_1) and site characteristics were examined with multiple linear regressions using the MGLH procedure of SYSTAT© The independent variables used in these models were the same as those used in the multiple linear regressions of life-form cover.

Compositional changes

Compositional changes among post-disturbance habitats were assessed in three ways. First, constancy and mean cover of all vascular plant species were calculated for each transect and site type during each sampling year. Taxa that were indistinguishable as distinct species during various stages of their life histories (e.g., *Cirsium arvense* and *C. vulgare*, *Lolium multiflorum* and *L. perenne*, or *Vaccinium alaskense* and *V. ovalifolium*) were grouped at the genus-level (Appendix 1).

Second, compositional changes were examined with ordination analysis. Composite, or average, samples, used as input for these analyses, were formed for each site type for each sampling year. Ordinations were performed with DECORANA, a FORTRAN program for detrended correspondence analysis (DCA) (Hill 1979, Hill & Gauch 1980) which simultaneously orders samples and species. Within the samples ordination, points representing the same composite sample, or site type, in successive years were connected sequentially to portray compositional change through time. The technique has been applied to permanent plot data from a diversity of ecosystems (van der Maarel 1969, Austin 1977, Malanson & Trabaud 1987, Halpern 1988). Because ordinations based on species cover differed little from those based on constancy, we only present results derived from the latter, more conservative measure of abundance.

Finally, changes in floristic similarity (percent similarity) both within and between site types were estimated with Sorensen's Index, a measure based on the degree to which species co-occur among pairs of samples. Sorensen's Index is computed as: $SI = 2c/(a+b)$, where c is the number of species common to both samples and a and b are the total number of species in each sample. For each sampling date, within and between site type similarity were calculated with the FORTRAN program, DISTAN (B. G. Smith, unpublished program), and represent the mean similarity of all pairs of subplots within or between site types, respectively.

Results

Origin of the vegetation

Total plant cover during the first growing season after the eruption (1980) was generally low on all site types (Fig. 2). Among the three previously forested habitats, first year plant cover was comprised solely of original understory species reemerging from the tephra (Fig. 3). However, on previously clearcut sites, plant cover was dominated by emergent shoots of perennial colonizing herbs (e.g., Epilobium angustifolium) that were prominent prior to the eruption. During 1981, rapid establishment of alien grasses in blown-down and scorched forests dramatically reduced the proportion of total cover contributed by original understory species (Fig. 3). Subsequently on these sites, plant cover was dominated by perennial colonizers that established from wind-dispersed seed (e.g., E. angustifolium and Anaphalis margaritacea). In blown-down forests with snow, survival and recovery of understory plants were greatest and invasion of fugitive species was minimal; consequently, original forest species dominated plant cover throughout the study period (Fig. 3).

Life-form development

Temporal trends

Mean total plant cover increased significantly with time in all post-disturbance habitats (Fig. 2 and Table 2a). Although these increases were, for the most part, gradual, mean cover peaked early (1981) in scorched forest (Fig. 2) due to temporary, but dramatic, establishment of grasses (primarily artificially seeded Lolium spp.) on one of three transects. Among the life-forms with greatest abundance, canopy cover of perennial forbs increased significantly ($p < .01$) with time in all habitats and cover of tall shrubs, within all but clearcut sites (Table 2a). Among the other life-forms, significant increases in cover were less widespread among habitats.

There were no significant differences in total plant cover among the post-disturbance habitats throughout the study period (Table 3a). However, the relative contributions of individual life-forms to total plant cover varied among site types. For 2 to 3 growing seasons after the eruption (1980 to 1982), artificially seeded grasses (primarily Lolium spp.) dominated blown-down and scorched forests but were largely absent from blown-down forests with snow (Fig. 2). Instead, tall shrubs (e.g., Vaccinium spp. and Menziesia ferruginea) and surviving understory trees (e.g., Abies amabilis) were prominent on these sites. Between years 4 and 7 (1983 and 1986), perennial forbs (primarily Epilobium angustifolium and Anaphalis margaritacea) dominated blown-down, scorched, and clearcut forests, whereas a diversity of life-forms (e.g., perennial forbs, low/sub-shrubs, tall shrubs, and understory trees) were abundant in blown-down forests with snow. Nevertheless, cover of the most widely abundant life-forms (i.e., perennial forbs and tall shrubs) rarely differed significantly between pairs of site types (Table 3a). In contrast, cover of bryophytes, sedges and rushes, and annual or biennial forbs often differed significantly ($p < .05$) among post-disturbance habitats (Table 3a).

Relationships with environmental factors

Canopy cover of most life-form groups was poorly correlated with general site characteristics (Table 4a). For several life-forms--fern, annual or biennial forb, perennial forb, and tree--there was no relationship between cover and the environmental variables tested. In contrast, for 3 to 6 growing seasons, cover of low/sub-shrubs and tall shrubs was negatively correlated with tephra depth and/or positively correlated with cover of rootwads. For the remaining groups--bryophytes, sedges/rushes, and grasses--canopy cover was briefly (1 to 2 yr) correlated with aspect, elevation, tephra depth, and cover of logs, rills, or rootwads.

Species diversity

Overall floristics

A diverse vascular flora characterized the post-eruption vegetation (Appendix 1). A total of 117 species representing 29 families and 86 genera was observed within the 15 permanent transects (45 subplots). The five families with the greatest number of species were the Gramineae (16 species), Compositae (12), Ericaceae (12), Rosaceae (11), and Polypodiaceae (7).

Temporal trends in richness and heterogeneity

Within all habitats, the mean number of species per subplot (Fig. 4) and transect (N_0, Fig. 5a) increased significantly ($p < .01$) with time (Table 2b). Although the greatest values were found in blown-down forests with snow, there were no significant differences in mean subplot or transect richness between site types during the sampling period (Table 3b). Within all habitats, herbs and low-shrubs accounted for the greatest number of species, particularly after the second growing season (Fig. 4). In blown-down forests with snow, tall shrub species were also common (Fig. 4b).

Within most post-disturbance habitats, mean species heterogeneity (N_2) changed little during the study period (Fig. 5b). However, in blown-down forests with snow, N_2 was significantly greater ($p < .05$) than in all other habitats in 1981 and 1982 and in all but scorched forests in 1986 (Table 3b). Mean species evenness, R_1 (Fig. 5c), declined significantly with time in all habitats except for blown-down forests with snow (Table 3b). The most rapid changes occurred between years 1 and 3. There were few significant differences in evenness between site types during the study period (Table 3b).

Dominance-diversity curves for all post-disturbance habitats changed gradually with time from linear in shape with relatively few species to log-normal in shape with increasing numbers of relatively rare species (Fig. 6). Thus, similar to the average diversity patterns on transects (Fig. 5), the overall richness of the four post-eruption habitats increased with time while the equitability of species' abundances declined.

Relationships with environmental factors

In general, species richness and evenness were poorly correlated with general site characteristics (Table 4b). However, for much of the study period, heterogeneity (integrating the number and relative abundance of species) was negatively correlated with tephra depth and positively correlated with cover of tree rootwads.

Compositional changes

The four post-disturbance habitats maintained fairly distinct floristic composition through time, as indicated by their discrete successional trajectories within the ordination field (Fig. 7a). These separate pathways reflected differences in the forest flora persisting through disturbance. Blown-down forests with snow (BDS, Fig. 7a), with high scores along DCA Axis 1, were most distinct. A diversity of species, representing an array of life-forms, survived on these sites, including herbaceous taxa (e.g., *Gymnocarpium dryopteris* [Gd], *Luzula parviflora* [Lp], *Smilacina racemosa* [Sr], and *Valeriana sitchensis* [Vs], Fig. 7b); sub-shrubs (e.g., *Rubus lasiococcus* [Rl] and *R. pedatus* [Re], Fig. 7c); tall shrubs (e.g., *Alnus sinuata* [As], *Menziesia ferruginea* [Mf], and *Sorbus sitchensis* [So], Fig. 7c); and understory trees (e.g., *Abies amabilis* [Aa] and *Tsuga mertensiana* [Tm], Fig. 7c) (see also Appendix 1). Scorched forests (S, Fig. 7a), with generally high scores along Axis 2, supported a different suite of surviving forbs (e.g., *Pyrola picta* [Pp] and *Cornus canadensis* [Cc], Fig. 7b) and woody taxa (e.g., *Chimaphila umbellata* [Cu] and *Acer circinatum* [Ac], Fig. 7c) (see also Appendix 1). Although few forest understory species were restricted to clearcut sites (CC, Fig. 7a) early seral perennials such as *Anaphalis margaritacea*, *Epilobium angustifolium* (Am and Ea, Fig. 7b), and *Rubus parviflorus* (Rp, Fig. 7c) showed greatest development here. Initial survival and subsequent recovery of understory herbs and shrubs were poorest in blown-down forests (BD, Fig. 7a) and few species showed strong site fidelity. As a consequence, blown-down forests occur in the center of both ordination axes.

Despite their separation in ordination space, successional trajectories of previously forested sites (i.e., BD, BDS, and S, Fig. 7a) are directed toward clearcut sites, indicating a floristic convergence with time among post-disturbance habitats toward an early seral composition (see also Table 5a). Floristic similarity (percent similarity) within site types increased concurrently (Table 5b), indicating a parallel convergence in composition among subplots comprising each habitat. Floristic changes were rapid for 1 to 3 yr after disturbance (1980 to 1982), but were slow thereafter. Total compositional change during the study period was greatest in blown-down and scorched forests and lowest in clearcut sites (Fig. 7a and Table 5b).

Overall convergence on the floristic composition of post-eruption clearcuts, largely corresponds with the continuous, widespread recruitment of wind-dispersed perennial forbs characteristic of early successional sites (e.g., Anaphalis margaritacea [Am], Cirsium spp. [Ci], Epilobium angustifolium [Ea], E. watsonii [Ew], Hieracium albiflorum [Ha], and Hypochaeris radicata [Hr], Fig. 7b and Appendix 1). However, early increases in floristic similarity among habitats were also a consequence of brief, but widespread, establishment of Lolium multiflorum and L. perenne (Lo, Fig. 7b and Appendix 1) following aerial seeding of grass-legume mixtures within portions of the devastated area (see Franklin et al. 1988 and references therein).

Discussion

Patterns and mechanisms of recovery

Our observations within the devastated area indicate that plant recovery and reestablishment have been driven by a combination of primary and secondary successional processes reflecting a diversity of historical, environmental, and disturbance-related phenomena. Early post-eruption patterns were largely determined by pre-disturbance conditions--by the initial composition of the vegetation and by the presence or absence of protective snow cover at the time of the eruption. Subsequent changes, however, have reflected a balance between species recovery and invasion as influenced by initial patterns of survival, modes and rates of reproduction, and post-disturbance site conditions.

Although plants recovered quickly on some sites, most sites have remained fairly barren. On average, revegetation of the devastated area has been slow; 7 growing seasons after the eruption, mean total plant cover was < 10% among the major post-disturbance habitats. Although these rates of recovery are similar to those in scorched forests buried by pumice from the 1959 eruption of Kilauea Iki, Hawaii

(Smathers & Mueller-Dombois 1974), they are markedly slower than for other types of catastrophic disturbance in the Pacific Northwest. For example, average plant cover on recent landslide surfaces, may exceed 25% within the same time period (Miles & Swanson 1986); on clearcut and burned sites it may exceed 100% (Dyrness 1973, Halpern 1987, in press, Schoonmaker & McKee 1988). Under these latter conditions, plant survival is typically greater, seed sources are more abundant, and soil characteristics are more conducive to seedling establishment and growth.

A large proportion of the post-eruption vegetation derived from surviving individuals, as has been found in an array of other ecosystems buried by volcanic ejecta (Eggler 1959, 1963, Griggs 1918, 1922, Hendrix 1981, Tsuyuzaki 1987). Although persistence through volcanic burial may be less likely than through other types of catastrophic disturbance, many herb and shrub species have the potential to move perennating buds into or through tephra or to initiate adventitious roots from stems, while retaining rooting structures in older buried soils (Eggler 1948, Griggs 1918, 1919b, Smathers & Mueller-Dombois 1974, Antos & Zobel 1985b,c, 1987, Adams *et al*. 1987). During the first growing season after the eruption, taxa such as *Vaccinium* spp. and *Acer circinatum* resprouted in blown-down and scorched forests, while shoots of *Epilobium angustifolium* and *Anaphalis margaritacea* emerged on clearcut sites (Means *et al*. 1982, Adams *et al*. 1987, Hemstrom & Emmingham 1987, McKee *et al*. 1987, Stevens *et al*. 1987, Veirs 1987). For many characteristic forest species, emergence or extrication due to erosion were delayed for one or more growing seasons (e.g., *Chimaphila umbellata*, *Clintonia uniflora*, *Erythronium* sp., and *Menziesia ferruginea* [Appendix 1]). Such gradual reappearance of buried plants accounted for a large percentage of early increases in species richness. In nearby intact forests, Zobel & Antos (1986) documented survival of buried understory plants for > 3 growing seasons. Griggs (1919a,b) observed similar patterns of survival among plants buried by tephra at Kodiak Island, Alaska.

In this study, both persistence through disturbance and subsequent recovery were greatest in blown-down forests with snow. Plants buried by snowpack were better protected from the heat of the eruption than were exposed understory plants (Means et al. 1982, Franklin et al. 1985, McKee et al. 1987). Moreover, the cracking and slumping of tephra that accompanied snowmelt enhanced the ability of plants to emerge through deep deposits. Snowpack was particularly important for local persistence of understory trees (Fig. 2); coniferous species (e.g., Abies amabilis, Tsuga heterophylla, and T. mertensiana), incapable of sprouting, would otherwise have been eliminated from the devastated area (Franklin et al. 1988). The ameliorating influence of snow in blown-down forests contrasted sharply with its effect in intact stands; here, plant recovery was reduced where snowpacks were present (Antos & Zobel 1982). Yet unlike sites in the blast zone, plants in these forests were not affected directly by the eruption, but by subsequent burial.

Despite the early prominence of survivors, species establishing from seeds or spores became increasingly abundant with time. For example, within 2 to 3 growing seasons after the eruption, numerous wind-dispersed forbs in the families Compositae (Anaphalis margaritacea, Cirsium spp., Gnaphalium microcephalum, Hieracium albiflorum, Hypochaeris radicata, and Senecio sylvaticus) and Onagraceae (Epilobium angustifolium and E. watsonii) colonized widely on forested sites (Appendix 1). Furthermore, colonizing perennials such as A. margaritacea and E. angustifolium showed vigorous, clonal expansion, attaining widespread dominance with time. Populations of E. angustifolium typically expand vegetatively, rather than by continuous recruitment of seedlings (van Andel 1975, Haeussler & Coates 1986, Halpern in press). Through these processes, despite initial floristic differences among post-disturbance habitats, species composition in the devastated area converged toward that of formerly clearcut sites. Early compositional convergence among seral forest communities has also been observed after logging and slash burning, but these patterns reflect the ubiquitous establishment of winter annual, as well as perennial, forbs (Halpern 1988).

Recruitment of annual and biennial life-forms contributed surprisingly little to overall revegetation of the devastated area (see also Adams et al. 1987, Stevens et al. 1987, Veirs 1987). In contrast, winter annuals such as Senecio sylvaticus and Epilobium paniculatum are frequently abundant after other types of catastrophic disturbance in the region (West & Chilcote 1968, Dyrness 1973, Halpern 1988, in press). Recruitment of annual and biennial life-forms was probably limited by dispersal distances of several kilometers to seed sources outside the devastated area. Seedling establishment for many species may also be inhibited by nitrogen deficient tephra (Eggler 1959, Griggs 1919b, but see del Moral & Clampitt 1985, Wood & del Moral 1987) or by moisture or temperature stress on tephra surfaces. These latter factors influence establishment by seed in subalpine environments at Mount St. Helens (del Moral & Clampitt 1985, Braatne & Chapin 1986, Wood & del Moral 1987). However, on our sites, the abundant recruitment of Epilobium angustifolium and Anaphalis margaritacea--possessing seed morphologies similar to the winter annuals--suggests that: 1) these factors do not have an overriding influence on our sites and that 2) dispersal distances may be the principal factor limiting establishment. Local seed sources for these perennial forbs were provided by flowering populations that resprouted vigorously on formerly clearcut sites throughout the study area.

Early physiognomic changes within the four post-disturbance habitats, as expressed by sequences of life-form development, differed from the classical pattern as described by Clements (1916). Bryophytes, as well as annual and biennial herbs, played relatively minor pioneering roles, while perennial herbs and woody life-forms developed concurrently. In blown-down forests with snow, shrubs developed more rapidly than did perennial forbs. Such ostensibly anomalous life-form sequences are not unusual following volcanic disturbance (e.g., Griggs 1918, Smathers & Mueller-Dombois 1974). They illustrate that where post-disturbance vegetation largely derives from surviving individuals, physiognomic trends may depend more on differences among life-forms in their tolerance of disturbance than in their modes of dispersal or rates of growth.

Relationships with post-disturbance habitat, environment, and microsite characteristics

Despite differences among site types in the composition of pre-disturbance vegetation, post-eruption site conditions, and the proportions of surviving versus colonizing plants, there were no significant differences in total plant cover during the study period. Moreover, significant differences in life-form cover between site types were restricted to those groups that had low overall abundance and were completely absent in one or more habitats (e.g., sedges/rushes and ferns). This lack of significant differences among habitats in total plant cover or in the cover of major life-forms, in part, can be attributed to large variances among the relatively few transects sampled. This variability suggests that factors other than those correlated with site type may determine trends in plant establishment and growth and that chance survival or recruitment may play a major role in recovery. For example, tephra depth varies greatly with site type (Table 1) but is negatively correlated with cover of low/sub-shrubs and tall shrubs and with mean species heterogeneity (N_2). Similar relationships between plant survival and depth of burial or extent of erosion have been observed in intact forests further from the crater (Antos & Zobel 1985a) and in other volcanically disturbed vegetation (Griggs 1918, 1919b, Taylor 1957, Eggler 1959, 1963, Smathers & Mueller-Dombois 1974, Beard 1976, Hendrix 1981).

Organic substrates were also important for the survival and recovery of life-forms such as low/sub-shrubs (including *Chimaphila umbellata*, *Rubus lasiococcus*, and *R. ursinus*). Following tephra deposition, rootwads and logs may serve as local refugia for understory plants (see review in Antos & Zobel 1987). Plants rooted on these elevated microsites are more likely to receive thinner deposits or to be exposed more rapidly than those on adjacent, level surfaces. Furthermore, the exposed mineral soil of rootwads provides greater potential sources of nutrients and mycorrhizal associates than does tephra. On mudflow surfaces near Mount St. Helens, rootwads similarly appeared to enhance survival of previously established plants and recolonization by seed (Halpern & Harmon 1983). Logs should also serve as plant refugia, but in our study, relationships between log cover and life-form abundance were masked by the recent nature of much of the downed wood in these systems. Although we did not find statistically significant correlations between subplot log cover and life-form abundance, we observed striking instances of such relationships at a smaller scale. For example, where trees fallen by the blast prevented deep tephra accumulation, lush shrub growth often emerged. In addition, detailed microsite observations suggest that survival of bryophytes and perennial forbs was greater on logs than on adjacent tephra surfaces (P. M. Frenzen, unpublished data) as has been noted outside the devastated area (Antos & Zobel 1985, 1987). Logs may eventually provide major germination sites in blown-down and scorched forests because they contain potentially significant sources of water, nutrients, and microbial resources (Harmon *et al*. 1986). Logs should also influence plant recovery indirectly by ameliorating micro-environmental conditions for seedling establishment on adjacent tephra surfaces. Snags and logs have served this function on recent mudflows at Mount Rainier, Washington (Frenzen *et al*. 1988) and on volcanic substrates at Kilauea Iki, Hawaii (Smathers & Mueller-Dombois 1974).

The general absence of correlations of larger-scale environmental features with life-form abundance or species diversity (Table 4) suggests that, within these forest zones, site characteristics (e.g., slope, aspect, and elevation) typically associated with variation in community composition and structure have little influence on early patterns of recovery after volcanic disturbance. Instead, primary and secondary successional processes interacting at a variety of spatial scales determine patterns of community development.

Future trends

Trends in total plant cover indicate that, among most post-disturbance habitats in the devastated area, community recovery has accelerated with time (Fig. 2). Vegetative spread should continue to dominate future increases in plant cover. However, long-term patterns of diversity suggest that, although invasion rates have declined, rare and uncommon species (both ruderal and late seral) may continue to colonize (cf. Eggler 1963, Rejmanek *et al*. 1982, del Moral & Wood 1988). Common fugitive annuals such as *Senecio sylvaticus* and *Epilobium paniculatum* may gradually increase in abundance as recruitment and reproduction within dispersed populations provide local sources of seed (cf. Wood & del Moral 1988). Physical factors (e.g., surface temperatures, soil moisture, or nutrient availability) or the absence of mycorrhizal symbionts may be inhibiting invasion or recovery of species on many sites. However, as plant cover and structural diversity increase, biotic factors (e.g., dispersal of seeds and fungal spores by animals, plant competition, and herbivory), will become increasingly important influences in community development.

It may take decades for plant cover to reach pre-eruption levels on sites that were forested in 1980. Compositional trends suggest that seral forbs (e.g., *Epilobium angustifolium* and *Anaphalis margaritacea*) currently dominating many sites will continue to expand clonally. Populations of residual forest taxa, spreading by rhizomes, stolons, or newly established individuals, will eventually replace them. Yet, because both primary and secondary successional processes are contributing to revegetation of the tephra, overall recovery will undoubtedly occur more slowly than after other types of large-scale disturbance such as clearcut logging or fire (Halpern 1987, in press, Schoonmaker & McKee 1988). Furthermore, rates of replacement will probably vary markedly among post-eruption habitats. Transitions to dominance by typical forest species should be relatively slow in clearcuts, where seral forb populations were well-developed prior to eruption and in blown-down forests, where initial understory survival was poor. Decline of seral forbs should occur relatively rapidly in blown-down forests with snow; here, initial invasion was low and early recovery of understory plants was high. Moreover, canopy closure should be greatly enhanced by advanced regeneration of Abies amabilis and Tsuga spp. As a consequence, we expect the composition of post-disturbance habitats to begin to diverge, a contrast with patterns to date. On some sites, closure of the tree canopy may take as long as a century. Overall recovery of pre-eruption species composition and understory structure will occur more slowly. Among individual stands, however, it is likely that local composition and structure have been permanently altered by catastrophic disturbance.

Acknowledgements

Many people contributed to this study. M. A. Hemstrom and A. McKee collaborated in the initial design and establishment of the sample plots. We gratefully acknowledge the numerous individuals who assisted with field sampling and data entry. We thank J. A. Antos, A. M. Olson, B. G. Smith, F. J. Swanson, and D. B. Zobel for critical reviews of earlier versions of the manuscript. B. G. Smith developed computer programs used in the analysis. This research was supported by the Pacific Northwest Research Station, USDA Forest Service; Oregon State University; and the National Science Foundation (grants DEB 7925939, DEB 8012162, DEB 8024471, and BSR 8300370).

Appendix 1. The constancy class (C) and year of first observation (Yr) of all vascular plant taxa observed between 1980 and 1986. Constancy classes: C = common (> 50% constancy among subplots during any growing season), u = uncommon (15-49% constancy during any growing season), r = rare (consistently < 15% constancy), blank = absent. Year of first observation is coded as growing seasons since the eruption: 1 = 1980, 2 = 1981, 3 = 1982, 4 = 1983, 5 = 1984, 7 = 1986.

Life-form /	Blown-down forest		Blown-down forest with snow		Scorched forest		Clearcut	
Taxon	C	Yr	C	Yr	C	Yr	C	Yr
Sedge and rush species								
Carex mertensii							r	3
Carex pachystachya			r	7			r	7
Carex rossii			u	5				
Carex spectabilis							u	7
Carex sp.	u	5	u	4	u	7	u	1
Juncus sp.							r	2
Luzula parviflora	r	7	C	3			r	1
Grass species								
Agrostis alba							r	7
Agrostis exarata	u	5			u	7	u	5
Agrostis scabra							r	5
Agrostis sp.	r	7	u	5			r	4
Bromus sp.	r	5						

Appendix 1.--Continued.

Life-form / Taxon	Blown-down forest		Blown-down forest with snow		Scorched forest		Clearcut	
	C	Yr	C	Yr	C	Yr	C	Yr
Grass species (continued)								
Cinna latifolia			r	7				
Dactylis glomerata	u	3			u	3	u	2
Festuca occidentalis			r	7				
Festuca rubra	u	5					r	4
Festuca spp. (*F. arundinacea* and *F. pratensis*)					u	2	u	4
Holcus spp. (*H. lanatus* and *H. mollis*)	u	3			u	4		
Lolium spp. (*L. perenne* and *L. multiflorum*[a])	C	2			C	2	C	2
Phleum pratense							r	4
Poa interior	r	7						
Fern species								
Athyrium filix-femina	u	3	u	1	u	7		
Blechnum spicant	r	7	r	7				
Cystopteris fragilis	u	7	u	7	u	5		
Gymnocarpium dryopteris	r	5	u	1				
Polypodium sp.	u	3	C	2	r	4	r	7

Appendix 1.--Continued.

Life-form / Taxon	Blown-down forest		Blown-down forest with snow		Scorched forest		Clearcut	
	C	Yr	C	Yr	C	Yr	C	Yr
Fern species (continued)								
Polystichum munitum	u	5	u	7	u	5	r	4
Pteridium aquilinum	r	7	u	3	u	2		
Annual or biennial forb species								
Epilobium minutum	r	4	r	7			r	2
Epilobium paniculatum	u	7			u	7	u	5
Lactuca muralis					r	5		
Lotus purshianus							r	7
Polygonum minimum	r	5						
Senecio sylvaticus	C	2	u	4	C	3	C	2
Verbascum sp.	r	2						
Perennial forb species								
Achillea millefolium	r	7						
Achlys triphylla	u	1	u	2			r	3
Adenocaulon bicolor					r	3		
Agoseris spp.	r	4			r	4		
Anaphalis margaritaceae	C	2	C	3	C	2	C	1
Anemone deltoidea							r	3
Apocynum androsaemifolium							r	3

Appendix 1.--Continued.

Life-form / Taxon	Blown-down forest		Blown-down forest with snow		Scorched forest		Clearcut	
	C	Yr	C	Yr	C	Yr	C	Yr
Perennial forb species (continued)								
Aruncus sylvester			u	2	r	7		
Campanula scouleri	u	5	r	4	r	1	u	4
Cirsium spp. (*C. arvense* and *C. vulgare*[a])	C	2	u	3	C	2	u	1
Clintonia uniflora	u	3	r	1	u	2		
Cornus canadensis	u	1			u	1	r	1
Epilobium angustifolium	C	2	C	2	C	2	C	1
Epilobium watsonii	C	3	u	3	C	4	u	3
Erythronium sp.			u	2				
Fragaria vesca							r	4
Gnaphalium microcephalum	u	3	r	5	r	4	u	3
Heuchera micrantha	r	4						
Hieracium albiflorum	C	3	C	3	C	1	C	1
Hieracium sp.					r	1		
Hypochaeris radicata	u	4	u	3	C	3	u	4
Hypopitys monotropa					r	2		
Lactuca sp.[b]	r	7	r	7	r	7		
Lupinus latifolius	u	3	r	4	u	3	u	1
Lupinus lepidus							r	7

Appendix 1.--Continued.

Life-form / Taxon	Blown-down forest		Blown-down forest with snow		Scorched forest		Clearcut	
	C	Yr	C	Yr	C	Yr	C	Yr
Perennial forb species (continued)								
Maianthemum dilatatum					r	3		
Mitella breweri			u	7				
Nothochelone nemorosa	r	7	r	7				
Penstemon cardwellii	r	7	r	7				
Penstemon sp.	r	3					r	7
Petasites frigidus							r	5
Polygonum sp.[b]							r	3
Pyrola asarifolia	r	5						
Pyrola picta	u	7			u	2	r	5
Pyrola secunda			r	2	u	2		
Rumex acetosella			r	3			r	7
Saxifraga sp.	r	7					u	7
Smilacina racemosa	r	2	u	1				
Smilacina stellata			r	1				
Spergularia rubra							r	5
Stellaria crispa			r	7				
Streptopus sp.			u	2				
Tiarella trifoliata	u	1	C	2	u	3	r	2
Trautvetteria caroliniensis							r	3

Appendix 1.--Continued.

Life-form / Taxon	Blown-down forest		Blown-down forest with snow		Scorched forest		Clearcut	
	C	Yr	C	Yr	C	Yr	C	Yr
Perennial forb species (continued)								
Trifolium repens							r	3
Trillium ovatum	r	2	u	1	r	2		
Valeriana sitchensis			u	2			r	2
Vancouveria hexandra							r	2
Vicia sp.[b]	r	2						
Vicia villosa							r	2
Low or sub-shrub species								
Berberis nervosa			r	2				
Chimaphila menziesii	r	1			r	2		
Chimaphila umbellata	u	2	r	2	C	2		
Gaultheria shallon	r	3			r	7		
Linnaea borealis					r	1		
Pachistima myrsinites					r	7	r	7
Rubus lasiococcus	u	1	C	1	r	3	r	2
Rubus pedatus			u	1	r	1	r	3
Rubus ursinus	r	4			u	2	u	1

Appendix 1.--Continued.

Life-form / Taxon	Blown-down forest		Blown-down forest with snow		Scorched forest		Clearcut	
	C	Yr	C	Yr	C	Yr	C	Yr
Tall shrub species								
Acer circinatum	u	1	r	4	C	1	r	4
Acer glabrum	r	7			u	1		
Alnus sinuata			u	1				
Amelanchier alnifolia					r	7		
Menziesia ferruginea	r	3	C	1				
Oplopanax horridum			u	1			r	3
Ribes bracteosum			u	2				
Rosa gymnocarpa	r	2			r	1		
Rubus leucodermis							r	4
Rubus parviflorus	u	3	u	3	r	7	u	1
Rubus spectabilis	r	7	C	1	u	5	u	2
Salix lasiandra	r	7					r	4
Salix sitchensis	u	7	r	5	r	7	u	3
Salix sp.	r	5					r	3
Sambucus sp.			u	3	r	7	u	7
Sorbus sitchensis			u	1				
Vaccinium membranaceum	C	1	C	1	C	1	u	1
Vaccinium parvifolium	r	5	C	4	u	3	u	4
Vaccinium spp. (V. alaskense and V. ovalifolium)	C	1	C	1	C	1	u	1

Appendix 1.--Continued.

Life-form / Taxon	Blown-down forest		Blown-down forest with snow		Scorched forest		Clearcut	
	C	Yr	C	Yr	C	Yr	C	Yr
Regenerating tree species								
Abies amabilis			C	1			u	4
Abies sp.	u	4	r	7	r	4		
Alnus rubra			u	2				
Populus trichocarpa							r	7
Pseudotsuga menziesii	u	2	u	4	C	3	u	2
Thuja plicata					r	5		
Tsuga heterophylla	u	4	u	2	C	4	r	5
Tsuga mertensiana			u	1			r	4

[a] = annual species.

[b] = annual, biennial, or perennial species.

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Table 1. Site and environmental characteristics of the 15 permanent transects grouped by post-disturbance site type. Transect values represent the means of three 250m^2 subplots.

	Site and environmental characteristics				
Site type / Transect	Distance from crater (km)	Slope (%)	Aspect (degrees)	Tephra depth (cm)	Elevation (m)
Blown-down forest					
Commonwealth Mine	15.3	63	226	12	1100
Middle Clearwater Creek	15.8	4	234	25	710
Upper Bean Creek	12.4	49	117	36	1150
Upper Clearwater Bridge	14.8	7	56	25	750
Mean	14.6	31	171	24	928
Blown-down forest with snow					
Meta Lake (north)	13.6	32	180	9	1100
Meta Lake (south)	13.6	32	14	16	1100
Cedar Creek	11.4	40	90	33	1250
Mean	12.9	35	91	19	1150
Scorched forest					
Polar Star Mine	7.9	0	---	13	850
Commonwealth Mine	5.3	60	220	12	1100
Middle Clearwater Creek	5.8	8	249	20	710
Mean	6.3	23	235	15	887

Table 1.--Continued.

	Site and environmental characteristics				
Site type / Transect	Distance from crater (km)	Slope (%)	Aspect (degrees)	Tephra depth (cm)	Elevation (m)
Clearcut					
Commonwealth Mine	5.3	50	234	16	1100
Middle Clearwater Creek	5.8	3	198	21	710
Upper Bean Creek	2.4	46	91	24	1150
Upper Clearwater Bridge	4.8	25	39	15	750
Cedar Creek	1.4	5	90	46	1250
Mean	13.9	26	117	24	992

Table 2. Slopes (and standard errors) for linear regressions of (a) life-form cover and (b) species diversity versus time for the four site types. Slopes significantly different from zero are indicated by *, p < .05, or **, p < .01. All regressions are based on transect means. Regressions of life-form cover are based on log-transformed data.

	Slope of linear regression			
Life-form cover / Species diversity	Blown-down forest	Blown-down forest with snow	Scorched forest	Clearcut
(a) Life-form cover				
Total species	0.134 ** (0.031)	0.103 * (0.046)	0.132 * (0.050)	0.081 * (0.033)
Bryophyte	0.000 (0.000)	0.002 ** (0.001)	0.000 (0.000)	0.001 (0.001)
Sedge/rush	0.019 ** (0.005)	0.024 ** (0.008)	0.022 (0.013)	0.008 * (0.003)
Grass	-0.009 (0.030)	0.000 (0.000)	-0.035 (0.058)	0.005 (0.021)
Fern	0.001 ** (0.000)	-0.006 (0.013)	0.007 (0.004)	0.000 (0.000)
Annual/biennial forb	0.002 (0.004)	0.000 (0.000)	0.010 (0.006)	0.006 (0.004)
Perennial forb	0.160 ** (0.024)	0.088 ** (0.018)	0.154 ** (0.024)	0.086 ** (0.024)
Low/sub-shrub	0.001 (0.001)	0.064 (0.039)	0.020 * (0.009)	0.012 (0.022)
Tall shrub	0.025 ** (0.007)	0.091 ** (0.026)	0.064 * (0.027)	0.034 (0.019)
Tree	0.000 (0.000)	-0.018 (0.039)	0.001 (0.001)	0.000 (0.000)

Table 2.--Continued.

Life-form cover / Species diversity	Slope of linear regression: Blown-down forest	Blown-down forest with snow	Scorched forest	Clearcut
(b) Species diversity				
Mean number of species/subplot	1.990 ** (0.238)	2.179 ** (0.700)	2.198 ** (0.329)	1.382 ** (0.230)
Richness (N_0)	3.393 ** (0.343)	3.505 ** (0.956)	3.548 ** (0.454)	2.289 ** (0.393)
Heterogeneity (N_2)	0.098 (0.124)	0.337 (0.229)	0.022 (0.169)	0.269 * (0.115)
Evenness (R_1)	-0.042 ** (0.010)	-0.016 (0.013)	-0.044 ** (0.011)	-0.023 ** (0.008)

Table 3. Pairwise comparisons of (a) life-form cover and (b) species diversity among site types indicating directions (>) of significant differences. Site type codes: BD = Blown-down forest; BDS = Blown-down forest with snow; S = Scorched forest; CC = Clearcut. --- indicates no significant differences among all pairs of site types. = indicates no significant difference between the pair of site types designated. If site type code is not listed there was no significant difference with any other site type. All regressions are based on transect means. Regressions of life-form cover are based on log-transformed data. Significance, p < .05, is based on Games and Howell method for life-form cover, Tukey-Kramer method for species diversity.

Life-form cover/	Year					
Species diversity	1980	1981	1982	1983	1984	1986
(a) Life-form cover						
Total species	---	---	---	---	---	---
Bryophyte	---	BD>BDS= CC	BD>BDS> CC	BDS>BD> CC>S	BD>CC	S>CC
Sedge/rush	---	CC>BD= BDS=S	CC>BDS> BD=S	BDS>CC> BD=S	BDS>CC> BD=S	BDS>CC> BD>S
Grass	---	---	---	---	---	---
Fern	---	---	S>BD= CC	S>BD>CC	BD>CC	BD>CC
Annual/biennial forb	CC>BD= BDS=S	BD>CC> BDS>S	---	S>BDS	BD>BDS	BD>BDS
Perennial forb	BD>S	S>BD	---	---	---	---
Low/sub-shrub	---	S>BD	---	---	---	---
Tall shrub	---	---	---	---	---	---
Tree	---	---	CC>BD= S	S>BD= CC	S>BD= CC	CC>S> BD

Table 3.--Continued.

Life-form cover/ Species diversity	Year 1980	 1981	 1982	 1983	 1984	 1986
(b) Species diversity						
Mean number of species/subplot	---	---	---	---	---	---
Richness (N_0)	---	---	---	---	---	---
Heterogeneity (N_2)	---	BDS>BD S=CC	BDS>BD= S=CC	---	---	BDS>BD= CC
Evenness (R_1)	---	---	---	---	CC>S= BD	---

Table 4. Site and environmental variables with coefficients significantly ($p < .05$) different from zero for multiple linear regressions of (a) life-form cover and (b) species diversity for each sampling year. Numbers indicate sampling dates (coded as growing seasons since the eruption) where coefficients are significantly different from zero. Codes for sampling dates: 1 = 1980, 2 = 1981, 3 = 1982, 4 = 1983, 5 = 1984, 7 = 1986. --- indicates coefficient not significantly different from zero. - indicates a negative correlation. All regressions are based on transect means. Regressions of life-form cover are based on log-transformed data.

	Site characteristics								
Life-form cover/ Species diversity	Distance from crater	Slope	Aspect	Tephra depth	Elevation	Log cover		Rill cover	Rootwad cover
						1980	1981	1981	1981
(a) Life-form cover									
Total species	---	---	---	---	---	---	1^{-}	---	1
Bryophyte	---	---	---	4^{-}	$4^{-},5^{-}$	4^{-}	---	4,5	---
Sedge/rush	---	---	4	---	---	---	4^{-}	---	4
Grass	---	---	---	---	$3^{-},7^{-}$	---	---	---	---
Fern	---	---	---	---	---	---	---	---	---
Annual/biennial forb	---	---	---	---	---	---	---	---	---
Perennial forb	---	---	---	---	---	---	---	---	---
Low/sub-shrub	---	---	---	$(1\text{-}4,7)^{-}$	---	---	1^{-}	2	1-5,7
Tall shrub	---	---	---	$(4,5,7)^{-}$	---	---	---	---	---
Tree	---	---	---	---	---	---	---	---	---

Table 4.--Continued.

	Site characteristics								
Life-form cover/ Species diversity	Distance from crater	Slope	Aspect	Tephra depth	Eleva- tion	Log cover 1980	Log cover 1981	Rill cover 1981	Rootwad cover 1981
(b) Species diversity									
Mean number of species/subplot	---	---	---	---	---	---	---	---	---
Richness (N_0)	---	---	---	---	---	---	---	---	1
Heterogeneity (N_2)	---	---	---	$(2,3,5,7)^-$	7^-	---	$5^-,7^-$	7	2,3,5,7
Evenness (R_1)	---	---	---	2	---	---	---	---	---

Table 5. Changes in percent similarity (Sorensen's Index) through time (a) between site types and (b) within site types. Values represent the means of all pairwise comparisons among subplots.

	Percent similarity					
	1980	1981	1982	1983	1984	1986
(a) Between site types						
Blown-down forest and blown-down forest with snow	23	16	26	32	33	35
Blown-down forest and scorched forest	16	24	31	43	45	41
Blown-down forest and clearcut	12	16	35	41	42	37
Blown-down forest with snow and scorched forest	14	17	24	29	29	32
Blown-down forest with snow and clearcut	6	7	19	28	29	30
Scorched forest and clearcut	2	9	24	30	35	34

Table 5.--Continued.

	Percent similarity					
	1980	1981	1982	1983	1984	1986
(b) Within site types						
Blown-down forest						
1980	24					
1981	12	27				
1982	6	19	42			
1983	6	20	47	52		
1984	4	18	44	51	48	
1986	4	15	39	45	45	43
Blown-down forest with snow						
1980	28					
1981	28	38				
1982	25	41	47			
1983	20	33	43	44		
1984	16	33	43	41	47	
1986	17	29	39	39	45	46

Table 5.--Continued.

	Percent similarity					
	1980	1981	1982	1983	1984	1986
(b) Within site types (continued)						
Scorched forest						
1980	26					
1981	27	29				
1982	15	23	32			
1983	17	26	38	44		
1984	13	22	35	47	48	
1986	10	19	31	41	45	41
Clearcut						
1980	20					
1981	18	23				
1982	18	25	35			
1983	18	30	37	40		
1984	16	28	37	41	38	
1986	15	22	32	34	37	37

Figure Captions

Fig. 1. The four types of post-eruption habitats, or site types. (a) Blown-down forest (Commonwealth Mine transect, 1980); (b) Blown-down forest with snow (note surviving understory trees) (Meta Lake south transect, 1983); (c) Scorched forest (Commonwealth Mine transect, 1983); and (d) Clearcut (Commonwealth Mine transect, 1981).

Fig. 2. Changes in mean total (additive) cover of life-forms within each site type. Only life-forms with > 0.5% total cover during at least one growing season are presented. Life-form codes: B = bryophytes, G = grasses, PF = perennial forbs, LS = low/sub-shrubs, TS = tall shrubs, UT = understory trees, OL = total cover of all other life-forms.

Fig. 3. Changes in the proportion of total plant cover contributed by forest species within each site type.

Fig. 4. Changes in the mean number of species (by major growth-form) within the 250 m^2 subplots representing each site type. Graminoids include grasses, sedges, and rushes; herbs and low shrubs include annual/biennial forbs, perennial forbs, and low/sub-shrubs.

Fig. 5. Changes in the mean species richness (N_0), heterogeneity (N_2), and evenness (R_1) of transects representing each site type.

Fig. 6. Dominance-diversity curves based on the relative mean cover of species in all subplots comprising each site type. n = number of subplots.

Figure Captions (Continued)

Fig. 7. (a) Detrended correspondence analysis (DCA) ordination through time of composite samples representing each post-disturbance site type. Lines connect the same composite sample in subsequent years. Large solid circles represent the first growing season after the eruption (1980); arrowheads coincide with the most recent sample (1986) and indicate the direction of change through time. Site type codes: BD = Blown-down forest, BDS = Blown-down forest with snow, S = Scorched forest, CC = Clearcut. For clarity, the corresponding species ordination is partitioned into two broad groups: (b) herbaceous taxa and (c) woody or semi-woody taxa. Only taxa with > 30% constancy are presented. Codes for herbaceous species: Af - Athyrium filix-femina, Am - Anaphalis margaritacea, Cc - Cornus canadensis, Ci - Cirsium arvense and C. vulgare, Ea - Epilobium angustifolium, Ew - Epilobium watsonii, Fe - Festuca arundinacea and F. pratensis, Gd - Gymnocarpium dryopteris, Gm - Gnaphalium microcephalum, Ha - Hieracium albiflorum, Hr - Hypochaeris radicata, Lo - Lolium multiflorum and L. perenne, Lp - Luzula parviflora, Pa - Pteridium aquilinum, Pm - Polystichum munitum, Po - Polypodium sp., Pp - Pyrola picta, Ss - Senecio sylvaticus, Sr - Smilacina racemosa, To - Trillium ovatum, Tt - Tiarella trifoliata, Vs - Valeriana sitchensis. Codes for woody species: Aa - Abies amabilis, Ac - Acer circinatum, As - Alnus sinuata, Cu - Chimaphila umbellata, Mf - Menziesia ferruginea, Ps - Pseudotsuga menziesii, Re - Rubus pedatus, Rl - Rubus lasiococcus, Rp - Rubus parviflorus, Rs - Rubus spectabilis, Ru - Rubus ursinus, So - Sorbus sitchensis, Th - Tsuga heterophylla, Tm - Tsuga mertensiana, Va - Vaccinium alaskense and V. ovalifolium, Vm - Vaccinium membranaceum, Vp - Vaccinium parvifolium.

Halpern, Franzen, Means & Franklin

Fig 1

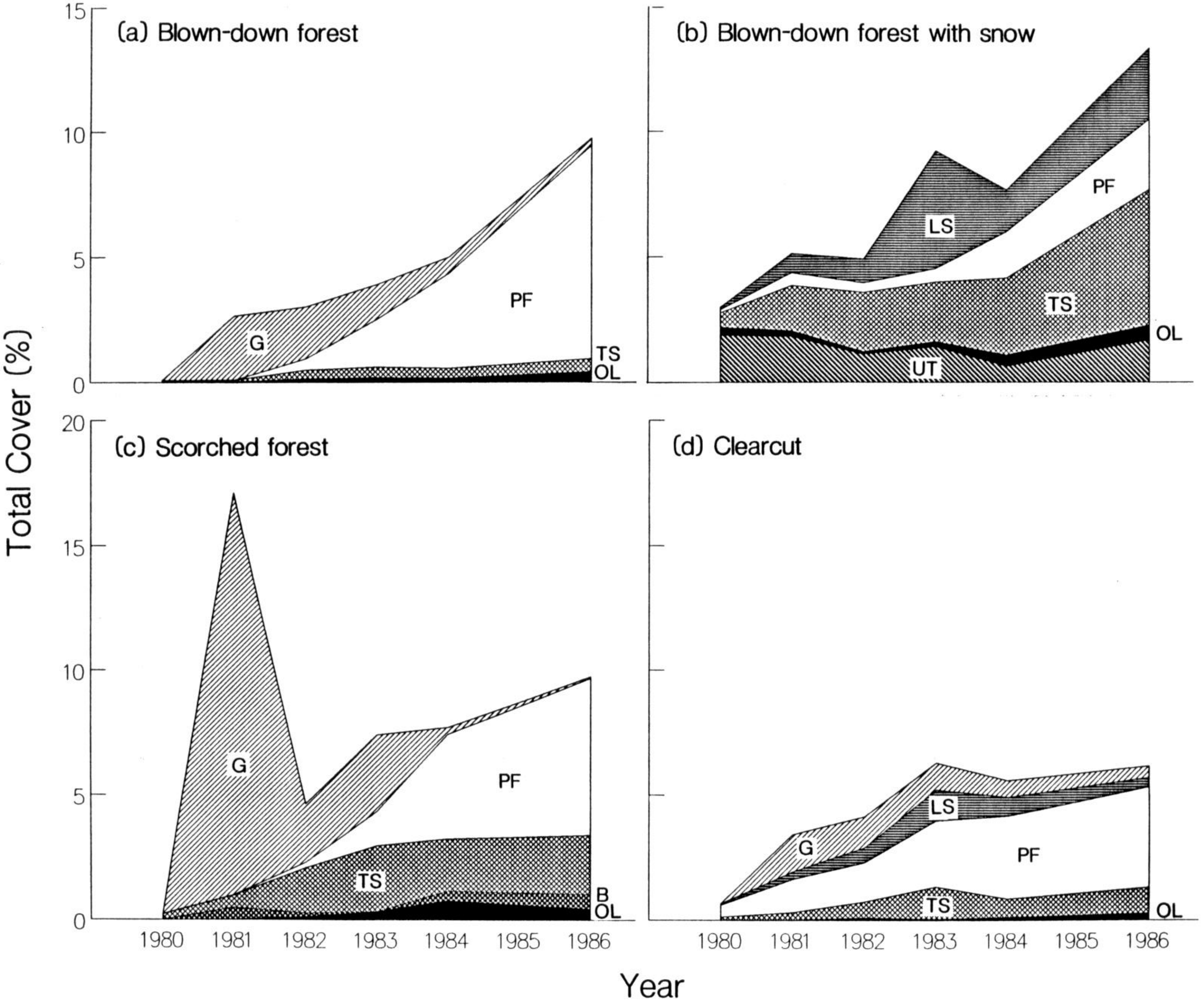

(a) Blown-down forest
(b) Blown-down forest with snow
(c) Scorched forest
(d) Clearcut
Total Cover (%)
0
5
10
15
20
1980
1981
1982
1983
1984
1985
1986
Year
G
PF
TS
OL
LS
UT
B

Fig2

Fig 3.

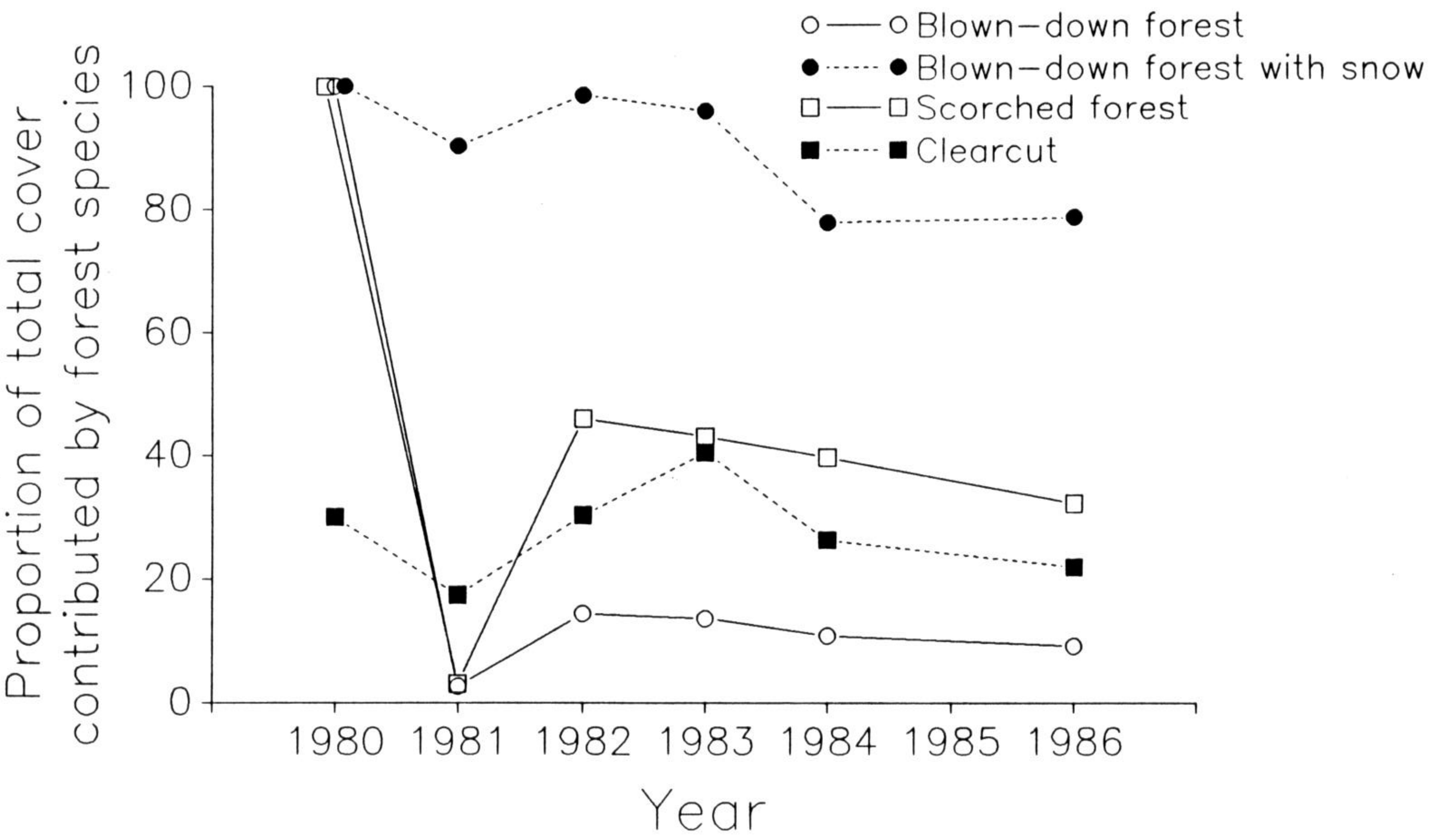

Blown–down forest
Blown–down forest with snow
Scorched forest
Clearcut
Proportion of total cover contributed by forest species
100
80
60
40
20
0
1980
1981
1982
1983
1984
1985
1986
Year

Fig 4.

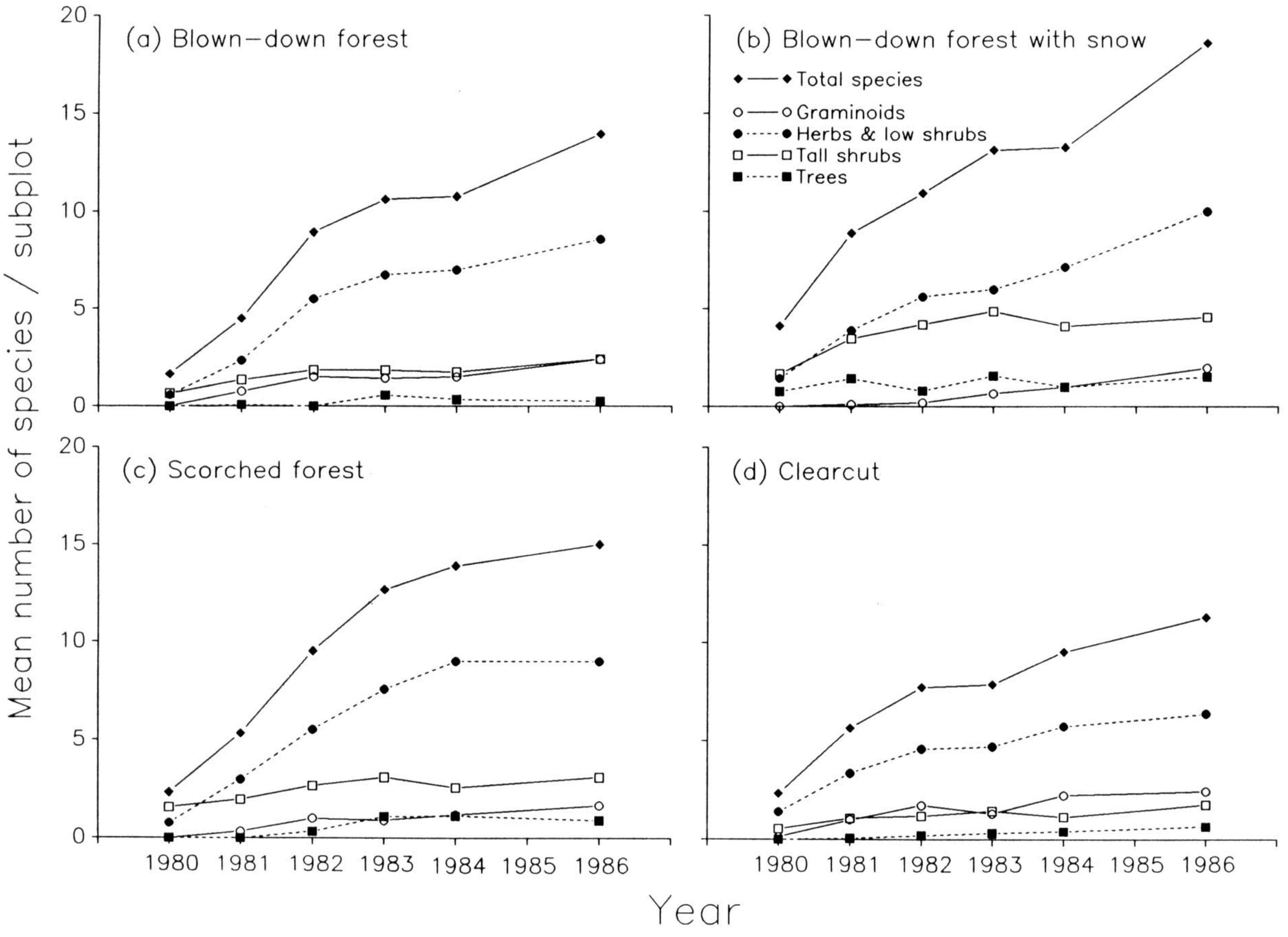
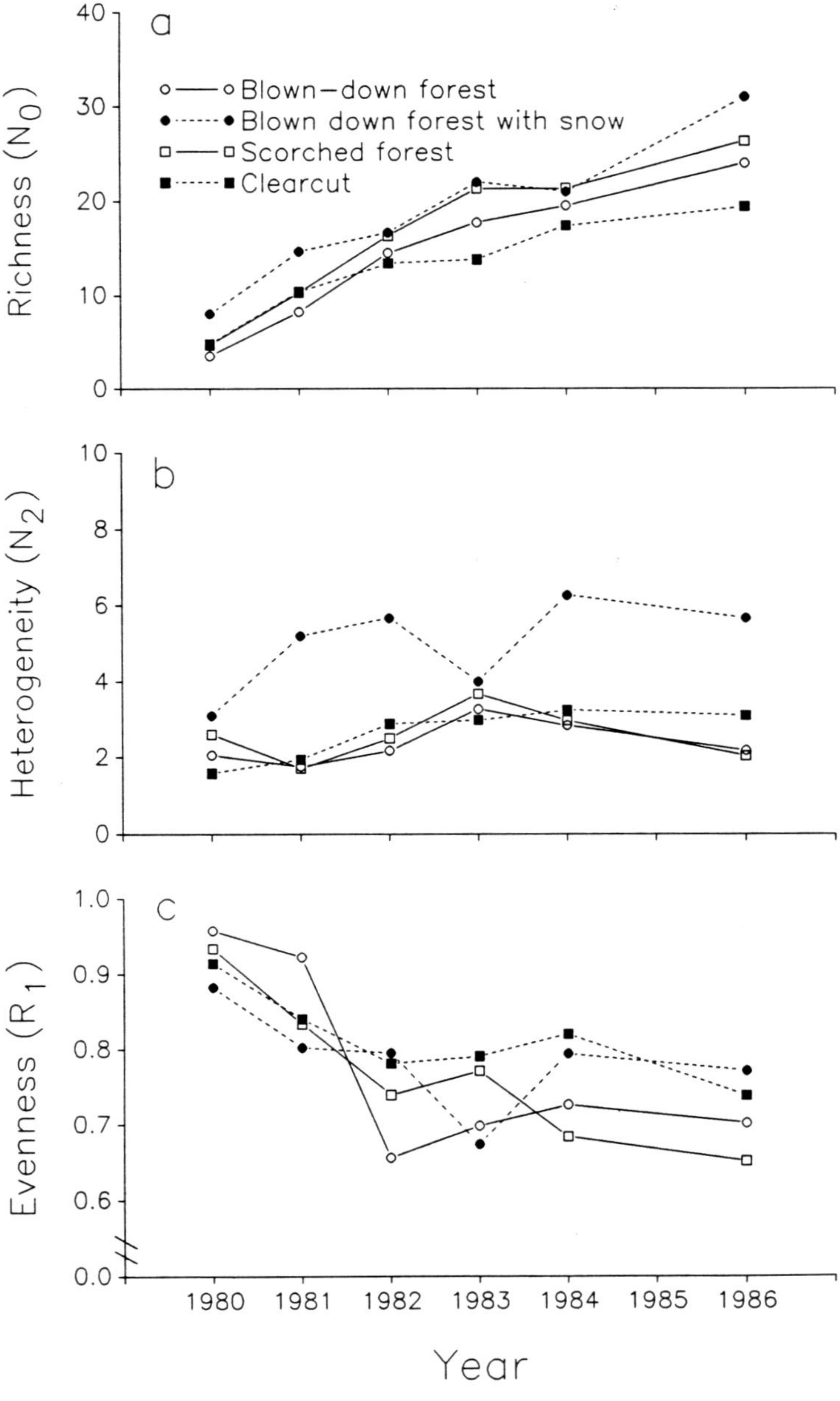

(a) Blown−down forest
(b) Blown−down forest with snow
Total species
Graminoids
Herbs & low shrubs
Tall shrubs
Trees
(c) Scorched forest
(d) Clearcut
Mean number of species / subplot
0
5
10
15
20
1980
1981
1982
1983
1984
1985
1986
Year

Fig 5.



a
Richness (N_0)
○—○ Blown-down forest
●----● Blown down forest with snow
□—□ Scorched forest
■----■ Clearcut
0
10
20
30
40
b
Heterogeneity (N_2)
0
2
4
6
8
10
c
Evenness (R_1)
0.0
0.6
0.7
0.8
0.9
1.0
1980
1981
1982
1983
1984
1985
1986
Year

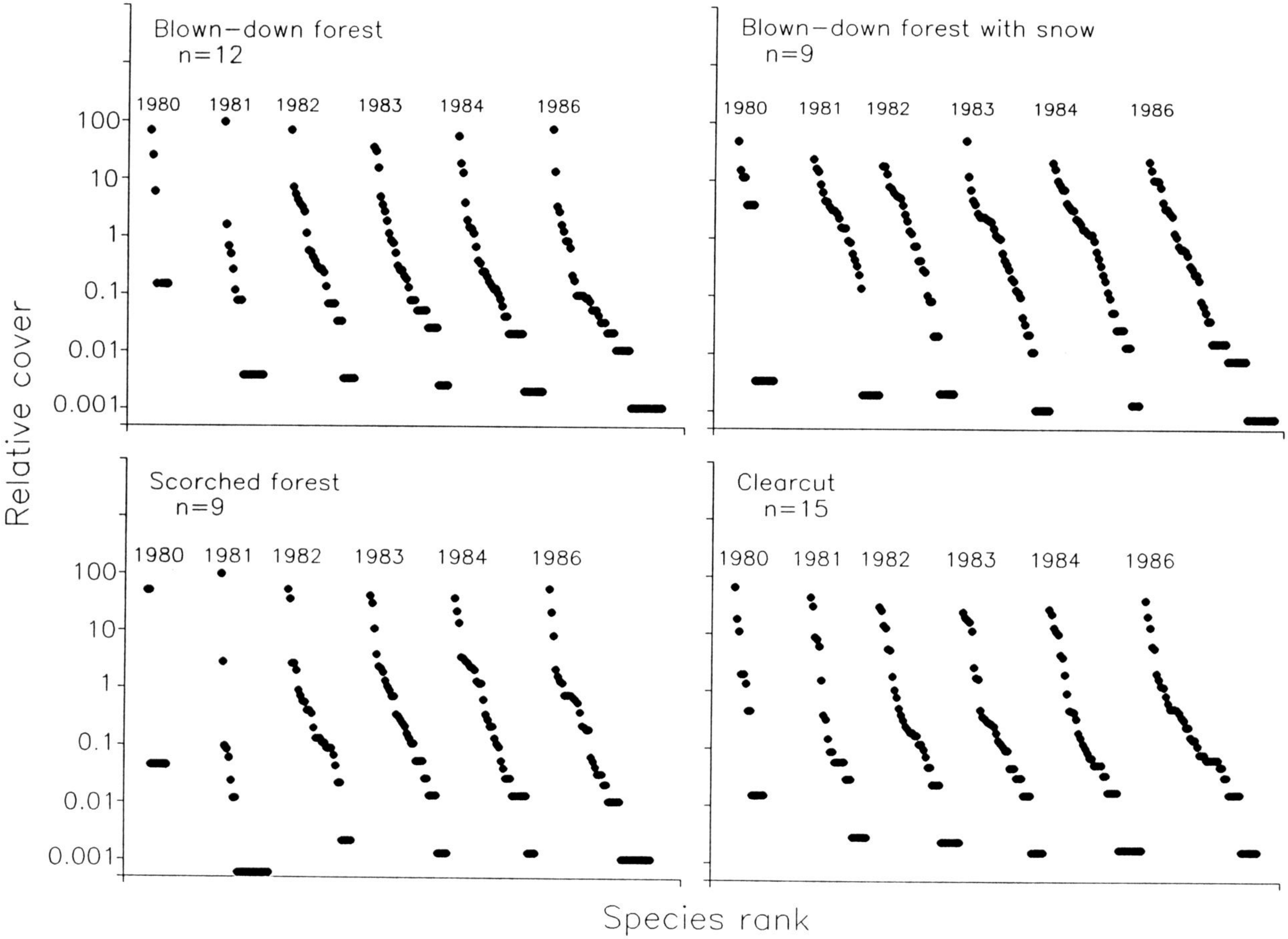

Blown-down forest
n=12
Blown-down forest with snow
n=9
Scorched forest
n=9
Clearcut
n=15
1980
1981
1982
1983
1984
1986
100
10
1
0.1
0.01
0.001
Relative cover
Species rank

Fig 6

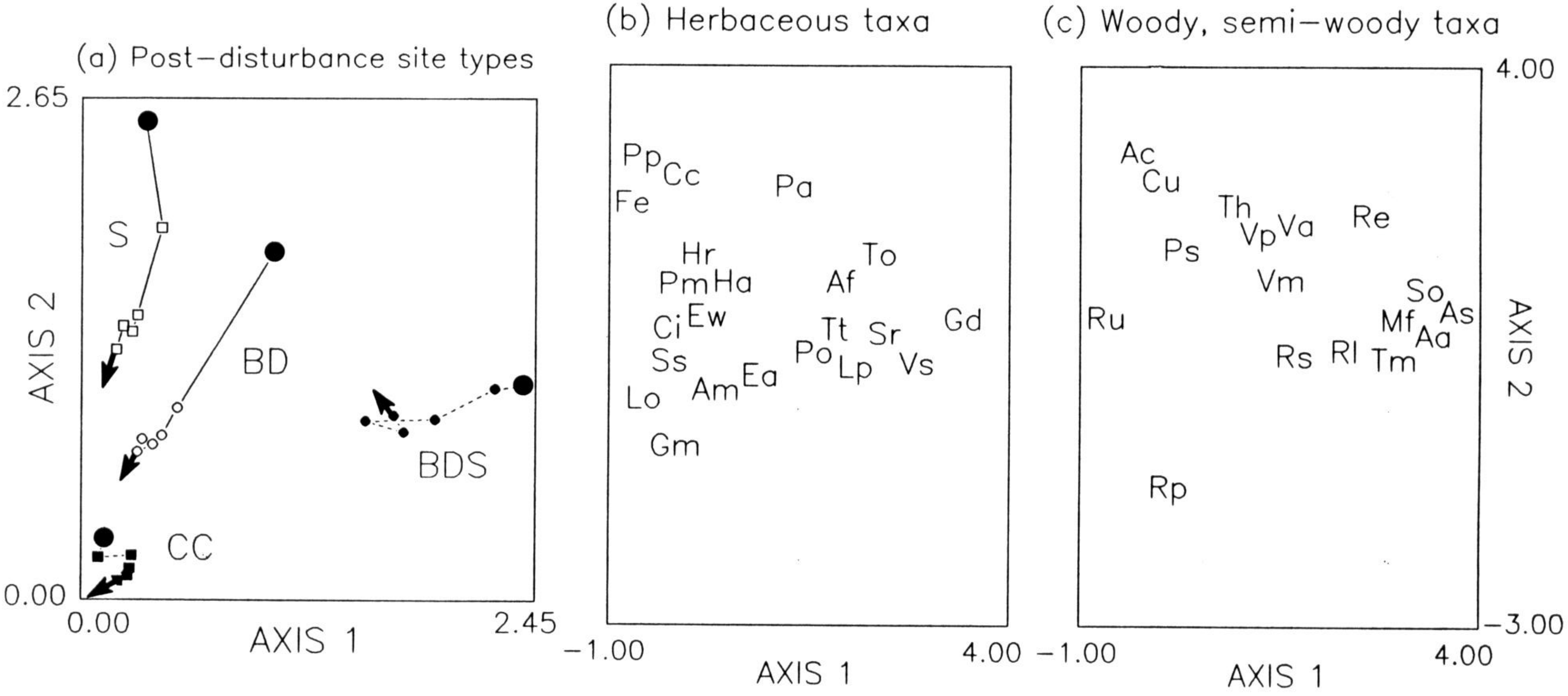

(a) Post–disturbance site types
2.65
0.00
AXIS 2
0.00
2.45
AXIS 1
S
BD
BDS
CC
(b) Herbaceous taxa
Pp
Cc
Fe
Pa
Hr
Pm
Ha
To
Af
Ci
Ew
Ss
Tt
Sr
Gd
Po
Lp
Vs
Lo
Am
Ea
Gm
−1.00
4.00
AXIS 1
(c) Woody, semi–woody taxa
Ac
Cu
Th
Vp
Va
Re
Ps
Vm
Ru
So
As
Mf
Aa
Rs
Rl
Tm
Rp
−1.00
4.00
AXIS 1
4.00
−3.00
AXIS 2

Fig 7.