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UNDERSTORY DEVELOPMENT IN PSEUDOTSUGA FORESTS: MULTIPLE PATHS OF SUCCESSION

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ABSTRACT: Vegetation changes after catastrophic disturbance commonly follow multiple pathways, reflecting variation in initial community composition, intensity of disturbance, or availability of propagules. In this paper we examine patterns of understory development during 21 yr of succession in logged and burned Pseudotsuga forests in the western Cascade Range, Oregon. We use detrended correspondence analysis ordination to assess the successional pathways of six forest communities exposed to a gradient in disturbance. We then use Euclidean distances between pre- and post-disturbance samples in ordination space to evaluate the resistance and resilience of communities. DCA ordination reveals multiple paths of succession characterized by 1) initially rapid floristic change away from pre-disturbance composition, followed by gradual return and 2) increasing compositional change with disturbance intensity. Community resistance and resilience reflect interactions between disturbance intensity and the life history traits of dominant residual and invading species.

INTRODUCTION

Catastrophic disturbances such as clearcut logging or wildfire profoundly influence the composition of vegetation. Species comprising a post-disturbance community derive from a variety of sources--wind dispersed seed, on-site or buried propagules, and resprouting survivors. Their ultimate contribution to the seral flora reflects a complex interaction of initial abundance, disturbance intensity, propagule availability, and chance. Thus, in ecosystems subject to large-scale, heterogeneous disturbance, succession commonly follows multiple pathways (e.g., Cattelino and others 1979, Noble and Slatyer 1980). Further, the ability of component species to resist disturbance determines the relative change in community composition; reestablishment from seed or vegetative propagules determines the rate and extent to which initial composition is restored.

In this paper, we examine the response of Pseudotsuga forest communities to clearcut logging and slash burning. The data presented derive from 22 yr of observation of permanent plots in the western Cascade Range of Oregon. We first describe how successional pathways vary with initial community composition and with disturbance intensity. We then discuss how these factors influence community resistance to disturbance and long-term recovery, or resilience.

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STUDY AREA

The study area, Watershed 1 of the H. J. Andrews Experimental Forest, lies along the western slope of the central Cascade Range, 80 km east of Eugene, Oregon. Elevations range from 442-1013 m and slopes average 50-60%. Soils are derived from tuffs and breccias and are primarily loam textured, moderately stony, and porous (Dyrness 1969). The climate is maritime with mild, wet winters and warm, dry summers. Annual precipitation averages 2302 mm, yet only 6% falls from June to August. Average minimum temperatures range from -5.5°C in January to 11.9°C in August; average maxima range from 5.5°C in January to 23.3°C in July (Bierlmaier and McKee in press).

Vegetation on Watershed 1 (WS1) is representative of the Tsuga heterophylla zone (Franklin and Dyrness 1973). Prior to logging, forest canopies were dominated by mature and old-growth Pseudotsuga menziesii (125 and 300-500 years-of-age, respectively), with Tsuga heterophylla in a variety of age classes. Understory vegetation was composed of six plant communities arrayed along a gradient of available moisture (Table 1).

Table 1.--Characteristics of the six forest understory communities of Watershed 1. Communities are arranged in order of increasing available moisture

Plant Community	Topographic Position	Dominant Species
Corylus cornuta - Gaultheria shallon	ridgetops; S-facing, upper slopes	Corylus cornuta, Acer circinatum, Berberis nervosa
Rhododendron macrophyllum - Gaultheria shallon	ridgetops; mid-slope benches	Rhododendron macrophyllum, Gaultheria shallon
Acer circinatum - Gaultheria shallon	mid- to upper, S-facing slopes	Acer circinatum, Gaultheria shallon
Acer circinatum - Berberis nervosa	mid- to lower-slopes	Acer circinatum
Coptis laciniata	mid- to lower-slopes	Tsuga heterophylla
Polystichum munitum	bottom- and steep, N- to E-facing slopes; seeps	Polystichum munitum, Acer circinatum

METHODS

During 1962, prior to logging of WS1, 134 permanent plots (2 X 2 m) were established, sampled, and assigned to one of six understory communities (Table 1). Within each plot, visual estimates of projected canopy cover (%) were made for all species less than 6 m tall. WS1 was clearcut over a 4 yr period (fall 1962-summer 1966). After logging, plots were resampled (summer 1966), slash was burned (October 1966), and plots were assigned to soil disturbance classes:

1. Undisturbed. Soil surface similar to that of the original forest--little mixing of soil and litter and no evidence of fire.
2. Disturbed - Unburned. Litter removed or mixed with mineral soil, but no evidence of fire.
3. Lightly burned. Surface litter charred by fire.
4. Heavily burned. Surface litter entirely consumed by intense fire.

Post-burning remeasurements were annual for 7 yr and, thereafter, were generally biennial.

Successional pathways were examined by ordinating composite samples through time using DECORANA, a FORTRAN program for detrended correspondence analysis (DCA) (Hill 1979). Composites represent the average cover of each species within each 1) plant community, 2) soil disturbance class, or 3) combination of community and disturbance class for each sampling year. Within each ordination field (e.g., Fig. 1) points representing the same composite sample in successive years were connected sequentially to form successional trajectories.
Measures of community resistance to disturbance and long-term recovery, or resilience, were derived from Euclidean distances between composite samples in ordination space. Resistance was defined as inversely proportional to the maximum Euclidean distance between pre- (time 0) and post-disturbance (time x) composite samples. Resilience was defined as inversely proportional to the Euclidean distance between pre-disturbance and final samples (17 yr).

RESULTS AND DISCUSSION

Multiple Pathways

Plant Communities--Ordination of community samples through time reveals a series of distinct successional trajectories (Fig. 1). Communities are aligned initially along Axis 2, generally corresponding with the moisture gradient. Following disturbance, rapid floristic change away from initial composition is followed by slow, unidirectional return. In addition, successional trajectories remain aligned along the initial moisture gradient.

Early post-disturbance patterns reflect the temporary loss of community dominants (e.g., *Acer circinatum* or *Berberis nervosa*) and the establishment of fugitive annuals (e.g., *Senecio sylvaticus* or *Epilobium paniculatum*). Subsequent compositional changes are less dramatic, reflecting gradual shifts in the abundance of rather persistent invading and residual species, with varying recovery to initial community composition (Halpern 1987).

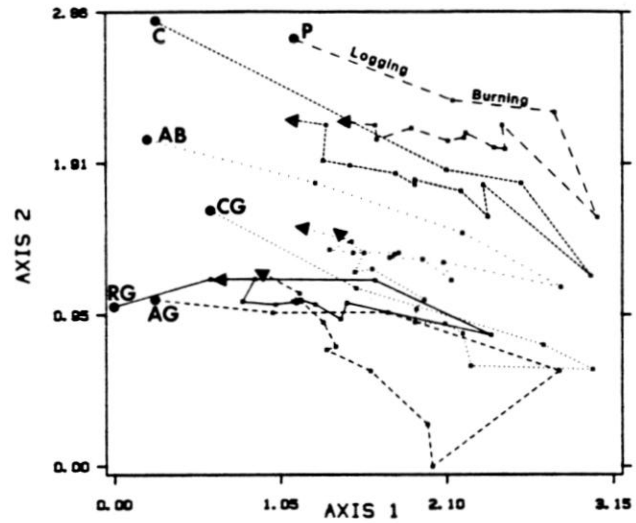

Figure 1.--DCA ordination through time of composite samples representing initial communities. Lines connect the same sample in subsequent years. Closed circles represent initial communities; second and third points represent post-logging and post-burning samples, respectively; arrows coincide with final samples (year 17) and indicate the direction of change through time. Community codes: CG = *Corylus-Gaultheria*, RG = *Rhododendron-Gaultheria*, AG = *Acer-Gaultheria*, AB = *Acer-Berberis*, C = *Coptis*, P = *Polystichum*.

Intensity of Soil Disturbance--The intensity of soil disturbance profoundly influenced the magnitude and direction of vegetation change. Ordinations through time of composite samples representing soil disturbance classes reveal increasing compositional change with disturbance intensity (Axis 1, Fig. 2). For example, composition on undisturbed sites (A, Fig. 2) changed relatively little after burning because initial dominants

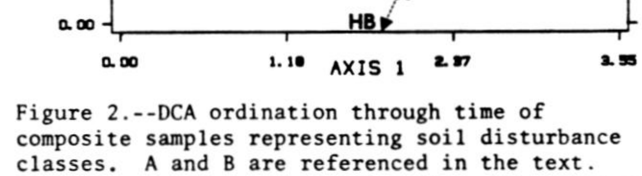

Figure 2.--DCA ordination through time of composite samples representing soil disturbance classes. A and B are referenced in the text. Disturbance codes: U = Undisturbed, DU = Disturbed-Unburned, LB = Lightly burned, HB = Heavily burned. See Figure 1 caption for details.

persisted. On lightly and heavily burned sites, in contrast, major changes in composition occurred; sample positions after 2 yr (B, Fig. 2), coincide with the maximum abundance of annual colonizers (e.g., Senecio sylvaticus and Epilobium paniculatum). Local prominence of these species reflected copious seed production, the interaction of a winter annual life cycle with fall burning, and an affinity for the high soil fertility associated with recent burns (West and Chilcote 1968).

Subsequently, composition changed gradually from herb- to shrub-dominated understories (Axis 2, Fig. 2). Differences in the distribution of residuals and invaders account for the increase in trajectory length with disturbance intensity. For example, undisturbed sites were reoccupied by resprouting dominants (e.g., Acer circinatum), whereas disturbed and burned sites were dominated by invading shrubs--Rubus parviflorus on disturbed-unburned sites and Ceanothus velutinus and C. sanguineus on lightly and heavily burned sites.

Interaction of Initial Composition and Disturbance Intensity--Multiple successional paths may reflect the combined influence of initial composition and disturbance intensity. For example, where soil was undisturbed, communities generally maintained their initial floristic character through time (Fig. 3A). Successional trajectories are variously directed, occupying small discrete zones within the ordination field. Distances encompassing each trajectory are consistently shorter than those separating them. Two trends account for these patterns: 1) invaders played a minor role on undisturbed sites and 2) original community dominants persisted through disturbance and generally recovered to initial abundance.

In contrast, where soil was lightly burned, communities changed profoundly in response to fire (Fig. 3B). Pre-disturbance samples are aligned along Axis 2, roughly coinciding with the moisture gradient. After burning, however, community trajectories briefly converge due to widespread establishment of invading annuals and temporary loss of forest residuals. Trajectories subsequently diverge as communities display distinct patterns of development (Halpern 1987). Additionally, recovery of original community composition is poorer on lightly burned (Fig. 3B) than on undisturbed sites (Fig. 3A), as indicated by distances separa ting initial and final samples.

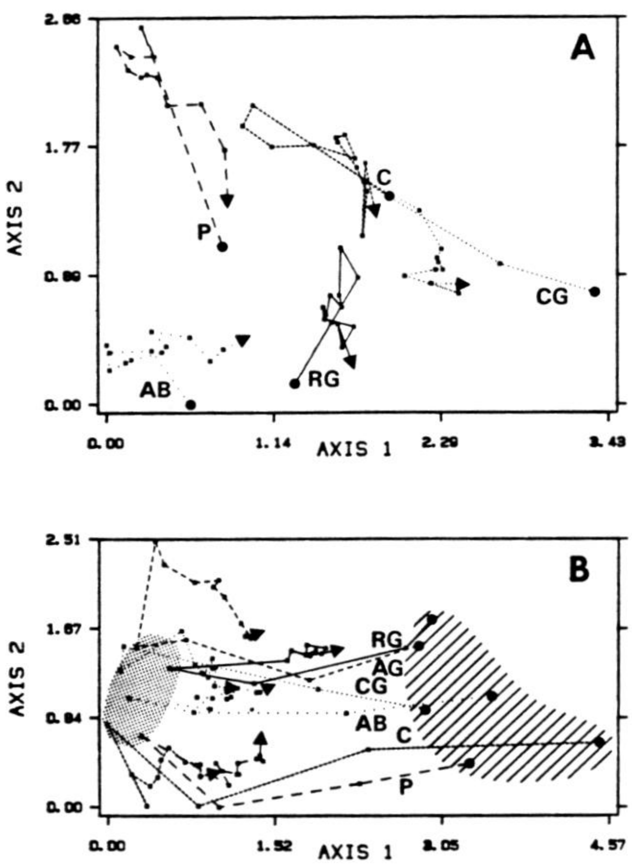

Figure 3.--DCA ordination through time of composite samples representing initial communities on A) undisturbed and B) lightly burned sites. Hatched and stippled areas illustrate convergence from initial (hatched) to post-burning (stippled) composition. See Figure 1 caption for details.

Measures of Resistance and Resilience

Resistance and resilience are measures of the immediate and long-term response of communities to disturbance, respectively. Resistance to disturbance reflects both the persistence of initial species' canopies and the exclusion of invaders. Community resilience derives from the recovery of initial dominants and the elimination of invaders.

Intensity of Disturbance--Both resistance and resilience varied inversely with the intensity of disturbance (Fig. 4). For example, undisturbed

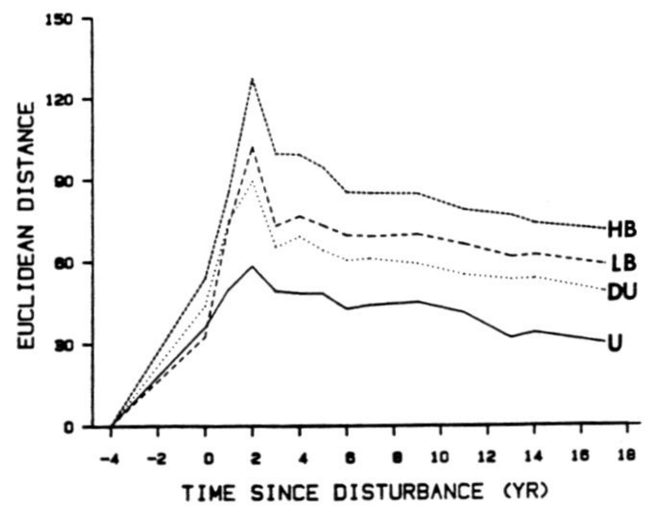

Figure 4.--Changes in Euclidean distance with time between pre- and post-disturbance composite samples representing soil disturbance classes. Times "-4", "0", and "1" represent initial forest, post-logging, and post-burning samples, respectively. See Figure 2 caption for disturbance class codes.

sites displayed high resistance (i.e., small maximum Euclidean distance) relative to disturbed and burned sites. In this system, loss of above-ground structures appears directly related to fire severity. The establishment of invading annuals is also directly related to disturbance intensity. For example, invaders such as Senecio sylvaticus may respond to the increased availability of germination sites and of soil nitrogen on burned sites (West and Chilcote 1968).

The resilience of undisturbed sites was also greatest (i.e., smallest Euclidean distance at final sampling). Understory recovery in Pseudotsuga forests typically depends on vegetative expansion of survivors, as reproduction from seed appears poor (Haeussler and Coates 1986; Russel 1974). Nevertheless, initial dominants recover more slowly on burned sites than on unburned sites (Haeussler and Coates 1986; Kraemer 1977; Steen 1966), despite an ability to sprout after severe fire. Furthermore, both the magnitude and duration of dominance of the principal invading shrubs, Ceanothus sanguineus and C. velutinus, increase with disturbance intensity. Because elevated temperatures stimulate germination of its buried seed, Ceanothus typically increases in abundance with burning intensity (references cited in Conard and others 1985). Its greater persistence on burned sites may reflect reduced competition from residual shrubs, as well as differences in its establishment.

Plant Communities--Plant communities generally were similar both in their resistance and resilience (Fig. 5). However, the contrast was greatest between Coptis and Polystichum communities. The Coptis type--associated with dense sub-canopies of Tsuga heterophylla--is extremely depauperate. Invading species dominated the post-disturbance flora and a paucity of residuals resulted in poor long-term recovery. In contrast, the Polystichum type is typically well-developed. Although invaders were briefly dominant, surviving residuals served as centers for vegetative expansion, promoting relatively rapid community recovery.

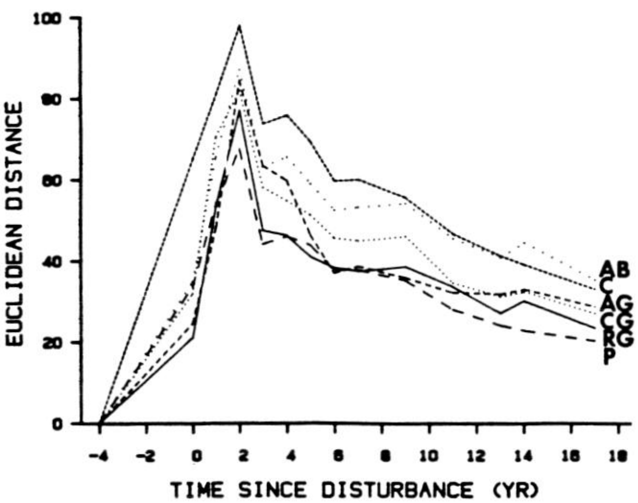

Figure 5.--Changes in Euclidean distance with time for the initial communities. See Figure 4 caption for details and Figure 1 caption for community codes.

Interaction of Initial Composition and Disturbance Intensity--Among disturbance classes, community responses varied dramatically. For example, on undisturbed sites, resistance of the depauperate Coptis community was intermediate and resilience was high (Fig. 6A). Surviving Tsuga heterophylla reestablished a dense understory tree canopy, largely preempting invaders. In contrast, resistance and resilience were relatively low for lightly burned Coptis sites (Fig. 6B). Seral communities were dominated by invaders and by initially uncommon residuals released from competition. Without a well-developed residual flora, long-term recovery after light burning may require canopy closure to eliminate these species. However, formation of a dense Tsuga heterophylla sub-canopy will be slower than on undisturbed sites, as re-establishment must be from seed.

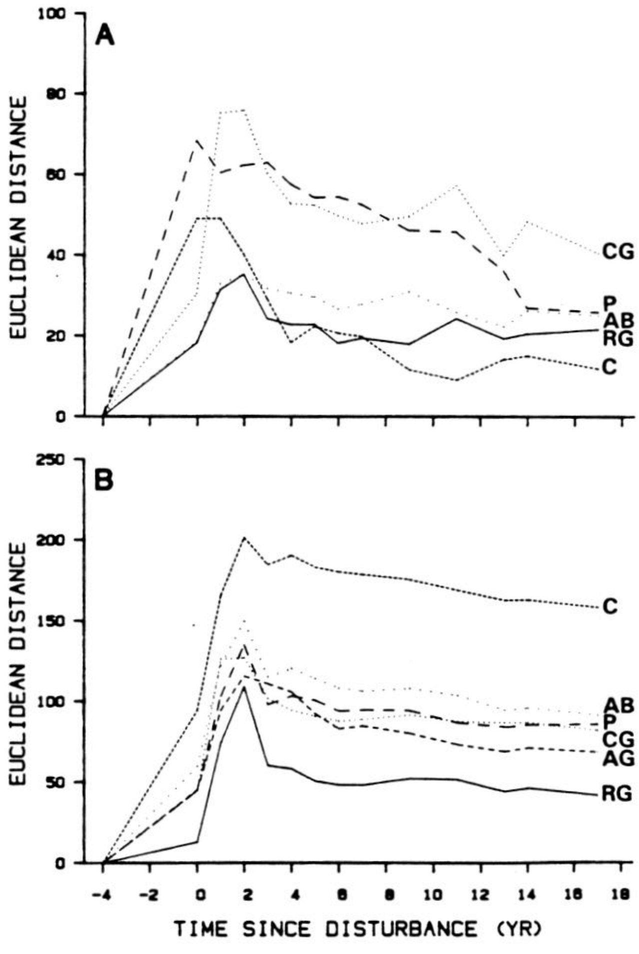

Figure 6.--Changes in Euclidean distance with time for the initial communities on A) undisturbed sites and B) lightly burned sites. See Figure 4 caption for details and Figure 1 caption for community codes.

CONCLUSIONS

Multiple Paths of Succession

Multiple paths of succession were observed after logging and burning of *Pseudotsuga* forests. Alternate pathways illustrate the importance of initial composition and disturbance intensity in understory development. Community trajectories were rather distinct, characterized by maintenance of the initial moisture gradient and by a gradual return toward initial composition. Alternate paths of succession also resulted from differences in disturbance intensity. The magnitude and direction of compositional change reflected variation in the response of dominant residual and invading species to a gradient in disturbance.

Community Resistance and Resilience

Within the range of disturbance intensities studied, *Pseudotsuga* communities exhibited an inherent tendency to return toward initial composition. Other authors have termed this trend stability (e.g., May 1973), adjustment stability (e.g., Sutherland 1981), or resilience (e.g., Westman 1978). Recovery from catastrophic disturbance in our system is founded in the moderate resistance of community dominants to logging and burning, and in their ability to subsequently perennate from subterranean structures.

Disturbance intensity largely determined the magnitude of compositional change and the degree of recovery. Initial composition and structure also influenced the resistance and resilience of communities (e.g., depauperate *Coptis* and well-developed *Polystichum* types). The interaction of disturbance intensity and initial composition further contributed to variation in the immediate and long-term response of communities to catastrophic disturbance.

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