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Physiognomic development of *Pseudotsuga* forests in relation to initial structure and disturbance intensity

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Halpern, Charles B.^{1*} & Franklin, Jerry F.²

¹Department of Forest Science, Oregon State University, Corvallis, OR 97331-5705 USA; ²College of Forest Resources, University of Washington, Seattle, WA 98195 USA; *Tel. +1 503 7507331; Fax +1 503 7371393; E-mail HALPERNC%CCMAIL@UCS.ORST.EDU

Abstract. Physiognomic patterns may vary significantly during succession despite a tendency for larger-growth forms to gradually replace smaller ones. Development of understory structure was observed for 25 yr after harvest of *Pseudotsuga* forests on two sites in the western Cascade Range, Oregon. We examine the influences of disturbance intensity and initial vegetation structure on the origin, direction, and rate of physiognomic change.

Broad-scale changes in vegetation structure differed between sites. On Watershed 1, herbs dominated for 11 yr, after which shrubs became co-dominant. In contrast, Watershed 3 never exhibited a distinct, transitional shrub phase - herbs dominated for 18 yr, after which trees assumed co-dominance.

The pattern and rate of physiognomic succession also varied among pre-disturbance plant communities and with disturbance intensity. Differences among communities largely corresponded with initial vegetation structure, reflecting the disturbance tolerance of forest herbs and shrubs. Canopy closure occurred most rapidly in the initially depauperate, but tree-dominated *Coptis* community. Along the disturbance gradient, shifts from herb to shrub dominance occurred earlier on burned than on unburned sites due to rapid development of invading shrubs, whose germination and establishment were stimulated by fire. However, subsequent transitions to tree dominance showed no clear relationship with disturbance intensity.

These long-term trends suggest that pre-disturbance community structure and disturbance intensity are major determinants of physiognomic succession, but that their effects may be modified by historical or stochastic factors such as limited seed availability or local fluctuations in weather.

Keywords: Clearcut logging; Community structure; Forest understory; Growth-form; Seral origin; Slash burning; Succession. Nomenclature: Hitchcock & Cronquist (1973).

Introduction

Changes in vegetation physiognomy during succession represent the most prominent and ubiquitous responses of plant communities to disturbance. Traditional models of physiognomic change describe the sequential replacement of growth-forms of increasing stature (e.g. Clements 1916). Low growing herbs dominate early in succession, are supplanted by taller shrubs which in turn, are overtopped by trees. Despite the generality of this pattern, there are numerous instances in which physiognomic stages during succession are absent or delayed. In some forests, for example, dominance by lower growthforms may simply not occur; trees survive disturbance, resprout, and rapidly restore pre-disturbance community. structure (e.g. Trabaud & Lepart 1980). In other forests, herbs dominate early in succession, but a transitional shrub phase is precluded by rapid closure of the tree canopy (e.g. Corns & LaRoy 1976). Still elsewhere, growth-form progression may be arrested for decades by the inhibitory effect of dense shrub canopies on tree growth (e.g. Niering et al. 1986).

We have observed similar physiognomic variation in long-term studies of succession following harvest of *Pseudotsuga* forests. The timing of transition from herb to shrub dominance may vary by a decade, and in some instances, early canopy closure may supplant intermediate shrub dominance. Whether or not physiognomic changes in these forests parallel the classical model, the underlying process is nevertheless complex - different mechanisms may give rise to similar or divergent patterns. In this paper, we explore the nature of this variation.

In *Pseudotsuga* forests, as in other communities that experience catastrophic disturbance, two principal seral groups comprise the post-disturbance vegetation, residuals (members of the original forest community) and

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invaders (non-forest species that colonize after disturbance). The differential growth and longevity of these groups produce the sequential pattern of growth-form dominance that constitutes physiognomic succession. In turn, the establishment and long-term development of residuals and invaders are particularly sensitive to two factors, initial understory structure (e.g. through the legacy of surviving growth-forms), and disturbance intensity (e.g. through disturbance-dependent recruitment of colonizers). In this paper, we compare the dynamics of seral groups in a series of permanent forest plots that span both a range of initial structural conditions (i.e. herb-, shrub-, or tree-dominated understories) and a gradient in soil disturbance (i. e. from relatively undisturbed to heavily burned soils). We examine how these factors affect the contributions of invaders and residuals to growth-form sequences and thereby elucidate some of the mechanisms that generate variation in physiognomic succession.

Methods

The study sites, Watersheds 1 and 3 (WS1 and WS3) of the H. J. Andrews Experimental Forest, Oregon, lie along the western slope of the central Cascade Range (44° 15' N, 122° 10' W). Pre-disturbance forests were dominated by mature (125-yr-old) and old-growth (300to 500-yr-old) Pseudotsuga menziesii and by Tsuga heterophylla in a range of size and age classes. Six plant communities, arrayed along a gradient of available soil moisture, were identified prior to harvest (Rothacher, Dyrness & Fredriksen 1967; Dyrness 1973). The entire 96 ha of WS1 were clearcut logged between fall 1962 and spring 1966 and broadcast burned in fall 1966. On WS3, three smaller areas totaling 25 ha were harvested during winter 1962-63 and burned in fall 1964. Subsequently, Pseudotsuga menziesii was aerially seeded and/ or planted on both sites. Histories of disturbance and seeding/planting are described more fully in Dyrness (1973) and Halpern (1987, 1989).

A total of 192 2 m \times 2 m permanent understory sample plots were established prior to harvest - 131 on WS1, 61 on WS3. To assess the influence of initial vegetation structure on physiognomic succession, each plot was assigned to one of the six initially defined plant communities. To assess the effect of disturbance intensity on structural changes, each plot was assigned to one of four soil disturbance classes (Dyrness 1973);

(1) Undisturbed: Minimal mixing of soil and litter; no evidence of fire.

(2) Disturbed-unburned: Litter removed or mixed with mineral soil; little evidence of fire.

(3) Lightly burned: Litter potentially removed or mixed

with mineral soil; surface litter charred by fire.

(4) Heavily burned: Litter potentially removed or mixed with mineral soil; surface litter completely consumed by fire. J

Loss of total plant cover increased from undisturbed through heavily burned plots (Halpern 1987). Thus, despite potential qualitative differences, these disturbance classes represent a gradient in intensity of soil disturbance.

Each vascular plant species was assigned to one of three physiognomic classes, or vegetation layers - herb. shrub, or regenerating tree - based on its growth-form and potential height at maturity (Dyrness 1973; Halpern 1987). Herbs included forbs, ferns, graminoids, and low woody species < 0.6 m tall at maturity. Shrubs included woody species > 0.6 m tall at maturity, but absent from the forest canopy or sub-canopy. Trees included original canopy or sub-canopy species, as well as colonizers with potentially similar stature. To trace the seral origins of each growth-form, each species was classified as an invader or residual (Dyrness 1973; Halpern 1987). Invaders were defined as species either absent from the above-ground vegetation in undisturbed forest or locally restricted to disturbed microsites. Residuals were defined as species characteristic of the undisturbed forest. [See Halpern (1987) for a complete classification of species.]

Within each plot, visual estimates of percent canopy cover were made for each vascular plant species < 6 m tall. Plots were sampled prior to harvest, after logging and after slash burning, and periodically through 1987. For each sampling date, canopy cover was summed for all species in each growth-form or seral group, potentially resulting in 100 % cover during any year. For comparative purposes, we define the growth-form (or seral group) with the greatest cover as dominant; groups with > 50% cover or with cover at least 75\% that of the dominant are defined as co-dominant. Because timing of logging and burning differed between watersheds, we express time as 'time since disturbance' (see Fig. 1). Thus, times '-4' and '-1' represent pre-disturbance samples for WS1 and WS3, respectively. For both sites, times '0' and '1' represent the growing seasons after logging and slash burning, respectively.

Results

Watershed-level patterns

Physiognomic changes on Watersheds 1 and 3 were characterized by gradual shifts in dominance among growth-forms of increasing stature (Fig. 1a, b). On both sites, long-term herb dominance - 11 yr on WS1 and 18

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Fig. 1. Changes in total canopy cover with time for the growth-forms (a and b) and seral groups (c-f) of Watersheds 1 and 3. Vertical bars represent ± 1 SE.

yr on WS3 - was due to early expansion of invading herbs (Fig. 1c, d), persistent release of residual herbs (Fig. 1e, f), and comparatively slower development of invading (Fig. 1c, d) and residual shrubs (Fig. 1e, f). Subsequent dominance by shrubs was either of short duration (WS1, Fig. 1a) or absent (WS3, Fig. 1b), depending on the long-term dynamics of invading shrubs (Fig. 1c, d). Specifically, on WS1 invading shrubs exhibited continuous expansion for 17 yr, then declined abruptly. On WS3, however, cover of invaders increased for only 9 yr, limiting the importance of shrubs prior to initiation of canopy closure.

Transitions to tree dominance occurred late in the study - after 20 yr on both sites (Fig. 1a, b). Nevertheless, understory tree cover surpassed pre-disturbance levels within 11-13 yr. Tree canopies were largely dominated by residual species - *Pseudotsuga menziesii* and to a lesser extent, *Tsuga heterophylla* - but the relative contributions of planted and naturally regenerating *P. menziesii* are unknown.

Patterns among soil disturbance classes

Intensity of soil disturbance strongly influenced longterm physiognomic trends. On WS1, transitions from herb to shrub dominance occurred earlier on burned (11-12 yr) than on unburned plots (15 yr) (Fig. 2a). Moreover on WS3, an intermediate shrub phase (18-19 yr) occurred only on burned plots (Fig. 2b). Variation in the rate of physiognomic succession along the disturbance gradient was closely linked to the long-term dynamics of residual herbs and invading shrubs. For example, on undisturbed plots, residual herbs expanded dramatically, maintaining high cover through final sampling (Fig. 3b). In contrast, invading shrubs displayed relatively poor development (Fig. 3a). Although residual shrubs recovered or expanded beyond pre-disturbance levels (Fig. 3b), greater release of residual herbs maintained herb dominance through initiation of canopy closure. On burned plots, however, residual herbs regenerated relatively slowly (Fig. 3f, h) whereas invading shrubs expanded rapidly (Figs. 3e, g), promoting earlier transition to shrub dominance.

Subsequent transitions to tree-dominance were not related to disturbance intensity. Tree cover (primarily residuals such as *Pseudotsuga menziesii* and *Tsuga heterophylla*) developed most rapidly on heavily burned plots on WS1 (Fig. 2a), but on disturbed-unburned plots on WS3 (Fig. 2b). Invading species contributed minimally to canopy development along the entire disturbance gradient (Fig. 3).

Patterns among plant communities

Physiognomic changes differed markedly among the six forest understory communities (Fig. 4). Rates of succession did not parallel the principal environmental gradient of available soil moisture along which pre-

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Fig. 3. Changes in total cover of invading and residual herbs, shrubs, and trees among the four soil disturbance classes of Watershed 1.

disturbance forest communities were arrayed. Instead, patterns of dominance and rates of growth-form transition corresponded with pre-disturbance physiognomy.

For example on WS1, in forest communities with

well-developed shrub layers (i. e. Corylus-Gaultheria, Rhododendron-Gaultheria, Acer-Gaultheria, and Acer-Berberis), shrubs became co-dominant earlier than in herb-rich types (i. e. Polystichum) (Fig. 4a). Similarly,

Fig. 4. Changes in dominance of the principal growth-forms among the six plant communities of (a) Watershed 1 and (b) Watershed 3. See Fig. 2 for other details.



in shrub-dominated communities on WS3 (i.e. *Rhododendron-Gaultheria* and *Acer-Berberis*), herb dominance was relatively brief (Fig. 4b).

Pre-disturbance community structure also influenced physiognomic trends in herb- and tree-dominated forest types. For example, in herb-rich sites on WS3 (i. e. *Acer-Gaultheria* and *Polystichum* types), a transitional shrub phase was absent as herbs dominated for most of the study period (Fig. 4b). In the tree-dominated, but otherwise depauperate *Coptis* community, shrubs displayed minimal importance. Transitions to tree dominance were rapid (Fig. 4a, b) and at final sampling, tree cover (dominated by residuals) averaged 81 % on WS1 and 114 % on WS3 (Fig. 5h).

Differences in the duration of herb layer dominance among communities may be attributed to the long-term responses of residual herbs. Their recovery and expansion, in turn, corresponded with their pre-disturbance abundance (Fig. 5). Differences in shrub layer development among communities were also correlated with the pre-disturbance abundance of shrubs (Fig. 5). However, because residual shrubs were subordinate to invaders for most of the period prior to canopy closure, transitions to shrub dominance were largely tied to the relative growth of invading shrubs. In an extreme example on WS1, unusually high establishment and expansion of invaders in the Acer-Gaultheria type (> 100 % cover) promoted very rapid transition to shrub dominance (Fig. 4a).

Discussion

Watershed-level changes in physiognomy: patterns and mechanisms

On WS1, gradual transitions from herb to shrub to tree dominance clearly support the traditional view (e.g. Clements 1916) of physiognomic succession. However, in this study, the mechanisms underlying growth-form replacement differ from those upon which the classical model is based - that is, upon progressive invasions or floristic relays (Egler 1954) during which earlier stages promote establishment of subsequent stages [i. e. the facilitation model of Connell & Slatyer (1977)]. Instead, seral groups established concurrently and longterm changes in dominance were attributed to differences in initial abundance, growth rate, and longevity. These characteristics have been associated with the concept of initial floristic composition (Egler 1954) and with the successional mechanisms of tolerance and inhibition (Connell & Slatyer 1977). The importance of differential establishment and survival for long-term physiognomic development was particularly evident on WS3, where poor recruitment and early senescence of



Fig. 5. Changes in total cover of invading and residual herbs, shrubs, and trees among the five community types of Watershed 3.

invading shrubs resulted in direct transition from herbto tree-dominance.

Changes in understory structure largely reflected the rate and magnitude of development of three seral groups - residual herbs, invading shrubs, and residual trees. Although invading herbs dominated early succession, their importance was relatively short-lived. In contrast, residual herbs, exhibiting a diversity of reproductive strategies and responses to disturbance (Halpern 1989), gained prominence 4 - 5 yr after burning and maintained it through initiation of canopy closure. In particular, forest canopy removal and soil disturbance stimulated the recruitment or vegetative release of many subordinate herbs (e.g. Hieracium albiflorum and Trientalis latifolia) and sub-shrubs (e.g. Whipplea modesta, Linnaea borealis, and Rubus ursinus) (Halpern 1989). In addition, dominant understory taxa such as Berberis nervosa, Gaultheria shallon, and Polystichum munitum regenerated continuously from surviving rhizomes or stem bases (Halpern 1989). However, their poorer overall recovery on WS1 may reflect watershed-level differences in disturbance intensity, competition, or site environment. First, proportionally more plots were burned on WS1 than on WS3 (61 % vs. 50 %, Halpern 1987). Second, both the magnitude and duration of competition from invading herbs and tall shrubs were probably greater on WS1 than on WS3 (cf. Fig. 1c, d). Finally, environmental conditions (e.g. temperature and moisture) were undoubtedly harsher on WS1 than on WS3 due to the greater area of disturbance relative to forest perimeter. Nevertheless, most herb layer dominants on both sites regained or surpassed their predisturbance canopy cover by final sampling (Halpern 1987, 1989).

Physiognomic succession from herb to shrub dominance was closely tied to the performance of invading . .

shrubs (largely Ceanothus spp.). Originating from buried seeds, Ceanothus spp. typically develop more quickly than do residual shrubs, despite the ability of residuals to resprout from root crowns. Thus, relatively rapid growth of invaders on WS1 resulted in a shift from herb to shrub dominance 14 yr after burning. On WS3 in contrast, a discrete shrub phase was absent due to poor establishment of Ceanothus sanguineus and to early, frost-induced senescence of evergreen C. velutinus, the dominant woody invader (Halpern 1987, 1989). These watershed-level differences - stemming from variation in available seed and local weather conditions - illustrate that historical or stochastic phenomena, affecting the establishment or longevity of key seral taxa, may indirectly determine the duration or existence of a shrub phase.

The overall development of tree cover on Watersheds 1 and 3 was surprisingly parallel, despite different histories of seeding and planting. These similarities are difficult to explain mechanistically because the relative contributions of artificially and naturally regenerating Pseudotsuga menziesii, the dominant tree species, are unknown. On the other hand, greater development of Tsuga heterophylla on WS3 is easier to interpret because it either survived disturbance or reestablished naturally. Its greater survival on WS3 may reflect a lower incidence of burning on that site (Halpern 1987). Denser recruitment may derive from heavier seed rain and a more benign environment - both a function of the proportionally greater forest perimeter of the smaller clearcut areas. The parallel development of total cover, but differential success of P. menziesii and T. heterophylla between sites illustrate that a common pattern of canopy closure may have multiple origins.

Effects of disturbance intensity and initial vegetation structure

In Pseudotsuga forests, increasing intensity of disturbance accelerates physiognomic succession by two mechanisms. First, it shifts early dominance of the herb layer from long-lived, residual forest herbs that are released by canopy removal (e.g. Linnaea borealis and Whipplea modesta) to short-lived colonizers (e.g. Senecio sylvaticus and Epilobium paniculatum) whose establishment is promoted by exposed soil, enhanced nutrient levels, and reduced competition from surviving vegetation. Increasing intensity of soil disturbance also accelerates physiognomic succession by stimulating the germination of invading shrubs while reducing the survival of residual herbs. Establishment of invading Ceanothus generally varies directly with burn severity (Biswell 1961; Orme & Leege 1976; Conard et al. 1985; Halpern 1989) whereas recovery of residual Berberis nervosa.

Gaultheria shallon, or Polystichum munitum declines with disturbance intensity (Halpern 1989). However, our observations also suggest that patterns of shrub dominance may be determined ultimately by historical factors, such as seed availability, or chance events, such as local frost.

In Pseudotsuga forests, pre-disturbance community structure also plays a major role in long-term development of community physiognomy. In this study, initially herb-rich communities maintained herb dominance through initiation of canopy closure; shrub-dominated types generally regained shrub dominance after an initial herb phase; and tree-dominated sites progressed most rapidly toward canopy closure. Interestingly, rates of succession and growth-form recovery were not related to available soil moisture - the principal environmental gradient along which initial forest communities were arrayed. Recovery of understory dominants was comparable among relatively xeric (e.g. Corylus-Gaultheria), mesic (e.g. Acer-Gaultheria and Acer-Berberis) and moist (Polystichum) communities. This structural stability stems from the capacity for most forest species to persist through disturbance, to resprout from root collars or rhizomes, and to spread vegetatively, despite markedly altered environmental conditions (Haeussler & Coates 1986; Halpern 1988, 1989).

Unlike their residual counterparts, invading herbs showed little fidelity to initial forest communities; they appeared more sensitive to timing or intensity of disturbance (Halpern 1987). The responses of invading shrubs were more complex, particularly on WS3, where greatest development was on initially shrub-dominated, mesicto dry-sites. Although the dominant, *Ceanothus velutinus*, may possess an affinity for mesic sites, disturbance history and environment interact in determining its distribution and abundance [Conard et al. (1985) and references therein].

Disturbance may significantly modify the degree to which initial forest structure is expressed during succession. For example, although the dominant shrubs in these forests, Acer circinatum and Rhododendron macrophyllum, are moderately resistant to fire (Halpern 1989), their post-disturbance regeneration is slower than that of invading shrubs. Consequently, except for initially shrub-dominated sites that escape physical disturbance or fire, residual shrubs contribute minimally to physiognomic changes during early succession. Nevertheless, positive correlations between pre- and post-disturbance vegetation structure result from disturbance-related phenomena. For example, although the Polystichum community on WS3 was typified by a lush herbaceous flora, the unusually rapid recovery of the herb layer (Fig. 5) reflected dramatic release of subordinate, rather than dominant, forest herbs in

response to low levels of disturbance (73 % unburned plots, Halpern 1987). Similarly, rapid shifts to shrub dominance in communities with initially well-developed shrub layers [e.g. Acer-Gaultheria (WS1) and Rhododendron-Gaultheria and Acer-Berberis (WS3), (Fig. 4)], were attributed not to residual shrubs, but to invaders (i. e. Ceanothus spp.) that responded to locally severe disturbance [(65-83 % burned plots Halpern (1987)]. As a consequence, ostensibly similar changes in seral understory structure may come about through significantly different mechanisms.

In most terrestrial ecosystems there is an overall correspondence between plant size, longevity, and slow growth. Thus, there is a tendency for larger growthforms to gradually replace smaller ones with time. The results of this study suggest that similar relationships drive physiognomic succession in Pseudotsuga forests, although multiple mechanisms (e.g. different seral origins) may be responsible for a single pattern. On the other hand, disturbance intensity and pre-disturbance community structure - factors that affect the availability, survival, and/or recruitment of seral plant groups - may determine the manner and degree to which growth-form sequences diverge from the classical form. Historical factors or chance events that reduce the availability or longevity of potentially dominant groups may further modify the pattern and process of physiognomic succession.

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References

- Bierlmaier, F. A. & McKee, A. 1989. Climatic summaries and documentation for the primary meteorological station, H. J. Andrews Experimental Forest, 1972 to 1984. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-242.
- Biswell, H. H. 1961. Manipulation of chamise brush for deer range improvement. Calif. Fish Game 47: 125-144.

- Clements, F. E. 1916. Plant succession. Carnegie Institution of Washington Publication 242, Washington, DC.
- Conard, S. G., Jaramillo, A. E., Cromack Jr., K. & Rose, S. (eds.) 1985. The role of the genus *Ceanothus* in western forest ecosystems. USDA For. Serv. Gen. Tech. Rep. PNW-182.
- Connell, J. H. & Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144.
- Corns, I. G. W. & LaRoi, G. H. 1976. A comparison of mature with recently clearcut and scarified lodgepole pine forests in the Lower Foothills of Alberta. Can. J. For. Res. 6: 20-32.
- Dyrness, C. T. 1973. Early stages of plant succession following logging and slash burning in the western Cascades of Oregon. Ecology 54: 57-68.
- Egler, F. E. 1954. Vegetation science concepts. 1. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412-417.
- Haeussler, S. & Coates, D. 1986. Autecological characteristics of selected species that compete with conifers in British Columbia: a literature review. B. C. Ministry Forest Land Management, Rep. No. 33.
- Halpern, C. B. 1987. Twenty-one years of secondary succession in *Pseudotsuga* forests of the western Cascade Range, Oregon. Ph.D. dissertation, Oregon State University, Corvallis, OR.
- Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69: 1703-1715.
- Halpern, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70: 704-720.
- Hitchcock, C. L. & Cronquist, A. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle, WA.
- Niering, W. A., Dreyer, G. D., Egler, F. E. & Anderson Jr., J. P. 1986. Stability of a Viburnum lentago shrub community after 30 years. Bull. Torr. Bot. Club 113: 23-27.
- Orme, M. L. & Leege, T. A. 1976. Emergence and survival of redstem (*Ceanothus sanguineus*) following prescribed burning. Tall Timb. Fire Ecol. Conf. 14: 391-420.
- Rothacher, J., Dyrness, C. T. & Fredriksen, R. L. 1967. Hydrologic and related characteristics of three small watersheds in the Oregon Cascades. USDA For. Serv. PNW For. and Range Exp. Sta., Portland, OR.
- Trabaud, L. & Lepart, J. 1980. Diversity and stability in garrigue ecosystems after fire. Vegetatio 43: 49-57.

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