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Abstract

PLANT SPECIES DIVERSITY IN NATURAL AND MANAGED FORESTS OF THE PACIFIC NORTHWEST1,2

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. With the exception of the tropics, nowhere has the relationship between resource management and conservation of biological diversity been more controversial than in the Pacific Northwest region of the United States. Widespread loss and fragmentation of old-growth ecosystems have stimulated critical review and revision of existing forest management policies. However, studies of the consequences of forest management for plant species diversity are sorely lacking. We present data from permanent-plot and chronose- quence studies in managed and unmanaged forests of western Oregon and Washington to describe the early responses of understory communities to forest harvest, and to suggest how post-harvest practices that alternatural successional processes may influence long-term patterns of diversity and species occurrence.

Permanent-plot studies of early succession in old-growth *Pseudotsuga* forests suggest that changes in understory diversity are fairly short-lived following clear-cut logging and slash burning. Populations of most vascular plant species recover to original levels prior to canopy closure. However, diversity may remain depressed for more than two decades on severely burned sites, and some species may experience local extinction. Evidence of the effects of post-harvest practices on vascular plant diversity is limited by an absence of community-level studies in older, managed forests.

Chronosequence studies of natural forest stands indicate that, following canopy closure, vascular plant species diversity tends to increase with time, peaking in old growth. Few understory species are restricted to, or absent from, any stage of stand development (i.e., young, mature, or old growth). However, many species differ significantly in their abundance among stages. A majority of these showed greatest abundance in old growth. Changes in levels of resources (increased shade), changes in the spatial variability of resources and environments (increased horizontal and vertical heterogeneity), and species' sensitivity to fire and slow rates of reestablishment/growth may drive these trends during natural stand development.

Silvicultural prescriptions that maintain or foster spatial and temporal diversity of re- sources and environments will be most effective in maintaining plant species diversity. Practices associated with intensive, short-rotation plantation forestry, that preclude or delay the development of old-growth attributes, may result in long-term loss of diversity. Ulti- mately, it may be necessary to manage some stands on long rotations (150-300 yr) to maintain understory species that require long periods to recover from disturbance.

Key words: disturbance; diversity; forest management; forest structure; logging; old growth; overstory; Pseudotsuga menziesii; *species heterogeneity; species richness; succession; understory.*

INTRODUCTION

The correlates and causes of species diversity have long intrigued naturalists and ecologists (e.g., Darwin 1859, Clements 1916, Hutchinson 1959, Huston 1979, May 1988). Countless studies have considered patterns of diversity at spatial scales ranging from metre-square plots to latitudinal gradients, and at temporal scales ranging from seasonal changes to geologic or evolu- tionary time. Numerous conceptual models have been developed that offer mechanistic explanations for the pattern and maintenance of diversity (e.g., MacArthur and Wilson 1963, Grubb 1977, Connell 1978, Huston 1979, Menge and Sutherland 1987).

In recent years, motivated in large part by wide- spread loss of species and natural habitats, ecological research has focused increasingly on the consequences of exploitive and long-term management activities for species diversity. Consideration of biological diversity has also guided the design, implementation, and cri- tique of existing policy on natural resource manage- ment (Harris 1984, Salwasser 1990, Westman 1990, Lubchenco et al. 1991, Kessler et al. 1992).

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2For reprints of this 67-page group of papers on plant diversity in managed forests, see footnote 1, page 911.

tionship between natural resource use and conservation biodiversity been more controversial than in the Pa- cific Northwest region of the United States (Swanson and Franklin 1992, 1993, Lippke and Oliver 1993). Stimulated by societal and scientific concern over the loss and fragmentation of old-growth ecosystems, USDA (United States Department of Agriculture) For- est Service management practices and policies-both explicit and perceived-are undergoing critical review (Forest Ecosystem Management Assessment Team 1993, Thomas et al. 1993).

Knowledge from recent ecological studies of natural and managed systems has helped to assess and redesign forest management policies in the Pacific Northwest (Franklin et al. 1981, Harris 1984, Spies et al. 1988, Spies and Franklin 1991, Swanson and Franklin 1992). However, research that focuses on the consequences of management activities for biological diversity has been biased heavily toward the needs and responses of wild- life (e.g., Ruggiero et al. 1991, Orians 1992:papers therein, Hansen et al. 1993, McComb et al. 1993). De- spite a long history of silvicultural research in the re- gion, community-oriented studies that consider plant species diversity are rare (but see Long 1977, Halpern 1987, Schoonmaker and McKee 1988, Halpern et al. 1992b). Given that the understory layer directly or in- directly supports much of the floristic and faunistic diversity of Pacific Northwest forests, and given the scale and intensity with which we have manipulated these systems, it is surprising that little ecological re- search has explicitly addressed the effects of manage- ment on plant species diversity.

Our objective in this paper is to fill, in part, this broad gap in understanding through a synthesis of com- munity-level research in managed and unmanaged for- ests of the region. Using permanent-plot and chrono- sequence studies of logged and natural forests in west- ern Oregon and Washington, we describe some of the early responses of vegetation to clear-cutting and slash burning, and suggest how post-harvest practices that alter or circumvent natural successional processes in- fluence long-term patterns of vascular-plant species di- versity. We consider two broad classes of management effects: (1) initial effects of disturbances (e.g., clear- cut logging, slash burning, and physical soil distur- bance) on existing plant populations, and (2) longer- term effects of management activities (e.g., control of competing vegetation, planting, thinning, or rotation length) on recovering plant populations. To illustrate some of the early effects of forest harvest on plant species diversity, we present data from three long-term, permanent-plot studies of succession in and adjacent to the Andrews Experimental Forest, Oregon. Empir- ical evidence for the longer-term effects of post-harvest practices is limited by a lack of community-based stud- ies in oIder, managed stands *(>50* yr). We approach the problem indirectly instead, by examining trends in a chronosequence of natural stands representing young,

mature, and old-growth forests of western Oregon and southwestern Washington. We describe changes in spe- cies diversity and occurrence through natural stand de- velopment; propose a set of successional mechanisms to explain these trends; and, based on species' life his- tories and presence in natural stands, identify a set of conditions that appear critical in maintaining plant spe- cies diversity within managed-forest landscapes. We conclude with a discussion of priorities for future re- search.

ECOLOGICAL AND HISTORICAL SETTING

We limit our discussion to the low- to mid-elevation, Pseudotsuga menziesii-dominated forests that charac- terize much of the region west of the Cascade crest in Oregon and Washington. Prior to the turn of the century these forests encompassed an area of >11.3 X l06 ha (Harris 1984), occupying a broad set of landforms and environments from British Columbia to the coastal and Klamath Mountains of northern California. Most stands originated after catastrophic wildfire of varying size (Hemstrom and Franklin 1982, Agee 1991), although periodic, low-intensity underburns were also common in places (Teensma 1987, Morrison and Swanson 1990). Prior to human suppression of fire, natural fire return intervals ranged from <50 yr along the crest of the Coast Range in southern Oregon to as many as 750 yr in moist, coastal forests of the northern Oregon Coast Range, the Olympics, and the Washington Cascades (Agee 1991). Windstorms, in the form of large cata- strophic events and smaller chronic disturbances (Ruth and Yoder 1953, Lynott and Cramer 1966), and, to a lesser extent, pathogens (Childs 1970, Gedney 198 1), also initiated and shaped the development of these for- ests.

Typically, young and mature forests in this region are dominated by Pseudotsuga, and occasionally by Tsuga heterophylla or Alnus rubra. Within 200 yr, stands begin to exhibit many of the compositional and structural characteristics associated with old growth (Franklin et al. 1981, Spies et al. 1988, Spies and Franklin 1991): codominance of Tsuga in the overstory, presence of large numbers of snags, accumulations of downed woody debris, and a vertically and horizontally complex structure created by a multi-tiered canopy. Forest structure, productivity, and understory compo- sition vary among environments, but appear closely related to available moisture (Dyrness et al. 1974, Zo- be1 et al. 1976, Hemstrom et al. 1987). Repeatedly within the latitudinal range of these forests, drier, less productive sites are dominated by an understory of the low shrub Gaultheria shallon, and moister, more pro- ductive sites, by the fern Polystichum muniturn.

Within less than a century, natural-disturbance re- gimes have been severely altered by human activities. Wildfire, windstorms, and insect outbreaks of varying size, frequency, and intensity have been replaced by short-rotation timber harvest and prescribed burning-