

Response of Forest Vegetation to Varying Levels and Patterns of Green-tree Retention: An Overview of a Long-term Experiment

Abstract

Timber harvest with retention of live ("green") trees, snags, and logs is now a standard practice on federal "matrix" lands within the range of the northern spotted owl. Although specific guidelines have been adopted for the levels and spatial configurations of retained structures, neither the ecological assumptions that underlie these recommendations nor the outcomes of these practices have been rigorously tested. The Demonstration of Ecosystem Management Options (DEMO) study examines the responses of forest ecosystems in the Pacific Northwest to varying levels (percentage of basal area) and patterns (dispersed versus aggregated) of green-tree retention. In this paper we describe vegetation studies that form the foundation of this long-term, interdisciplinary experiment. We review the results of retrospective analyses and simulation models which suggest that even minimal levels of retention may have important effects on forest development. We describe the characteristics of the DEMO sites, the experimental design, and the principal variables of interest (stand structure, tree regeneration and growth, and understory composition and diversity). We speculate about the silvicultural and ecological responses of forests to varying levels and patterns of retention and focus in particular on the dynamics of the forest understory. We anticipate strong contrasts among treatments in the establishment of early-seral, open-site species, and in the persistence of shade-tolerant plants associated with older forests or forest-interior environments. Short-term responses are likely to be driven by variation in the distribution and intensity of harvest disturbance. Longer-term trends are expected to reflect the effects of contrasting patterns of canopy retention. We conclude by discussing some of the scientific challenges faced in designing and implementing large-scale, interdisciplinary experiments.

Introduction

Traditionally, management of federal forests in western Oregon and Washington has focused on the production, utilization, and regeneration of timber resources. Until fairly recently (late 1980s), clearcut logging and broadcast burning were standard practices. Clearcut units were dispersed in space and time, logging slash was burned to reduce fire hazard and/or competition from non-crop species, and trees were planted with uniform spacing at high densities. It has become increasingly apparent, however, that these harvest practices do not produce the same complexity of pattern as arises through natural disturbance—a complexity that is thought to underlie the recovery of forest ecosystems following large-scale disturbance (e.g., Franklin et al. 1995, Perry and Amaranthus 1997). For example, historic wild-fires in the western Cascade Range were episodic, varying in size, frequency, and intensity with elevation, topography, and local climate (Teensma 1987, Morrison and Swanson 1990, Agee 1993). Even where natural fires were catastrophic, individual trees or groups of trees often survived and

large amounts of woody debris remained as logs and snags. It has also become apparent that the structural and compositional attributes that develop through conventional management practices differ markedly from those shaped by natural successional processes (Spies et al. 1988, Hansen et al. 1991, Spies and Franklin 1991, Halpern and Spies 1995, Tappeiner et al. 1997).

Federal forest management policies and practices have changed significantly in the last decade in response to growing concerns that traditional approaches have led to widespread loss and fragmentation of old-growth ecosystems and to attendant declines in biological diversity (FEMAT 1993, Thomas et al. 1993, Tuchmann et al. 1996). A new framework is emerging, characterized by a shift in emphasis from management of a single commodity resource to a broader consideration of ecosystem components and functions. Loosely defined as "ecosystem management," this approach seeks to incorporate ecological knowledge into forest management to sustain biological diversity, as well as timber production (Kessler et al. 1992, Grumbine 1994, Christensen et al. 1996).

Consequently, forest managers have begun to implement silvicultural prescriptions that are intended to more closely mimic the processes and outcomes of natural disturbance and succession by retaining structural characteristics of the former forest—in particular, large live trees (“green trees”), snags, and logs (Franklin 1989, Hopwood 1991, Franklin et al. 1997).

Green-tree or structural retention is now a standard component of harvest prescriptions for federal “matrix” lands within the range of the northern spotted owl (*Strix occidentalis caurina*). Although specific guidelines have been adopted for the levels and spatial configurations of retained structures (USDA and USDI 1994), neither the ecological assumptions that underlie these recommendations nor the outcomes of these practices have been tested. The Demonstration of Ecosystem Management Options (DEMO) study is among the first in the Pacific Northwest to systematically examine the responses of diverse groups of forest organisms and processes to experimental variation in the amount and pattern of live trees retained through harvest (Aubry et al. 1998). In this paper we provide an overview of vegetation studies that form a foundation of this long-term, interdisciplinary research. Our studies have two fundamental objectives: (1) to elucidate the effects of the level and pattern of retention on key elements of forest structure and composition, and to suggest possible mechanisms for these effects; and (2) to provide information on changes in forest structure and composition necessary to interpret the responses of the organisms and processes under investigation in companion studies (see Aubry et al. 1999 and other papers in this volume). A goal of this paper—indeed a major goal of this entire volume—is to encourage additional research participation in the DEMO study. There are numerous opportunities to take advantage of the current experimental design and the comprehensive set of baseline vegetation data.

We begin with a review of the literature on the responses of forest communities to retention of green trees: the results of previous experiments, retrospective analyses, and modeling efforts have been useful in designing the current work and have stimulated some of the hypotheses we pose. Second, we describe the range of environments, forest types, and disturbance histories represented by the DEMO sites. Third, we provide a brief overview of the experimental design, discuss the

primary variables of interest, and outline our long-term sampling approaches. Fourth, we present a series of hypotheses that focus on the responses of forest understory communities to varying levels and patterns of retention. We discuss the ecological bases of our hypotheses and describe the analytical approaches used to test them. We conclude by discussing some of the scientific challenges faced in designing and implementing large-scale, interdisciplinary studies that must balance ecological interests, experimental rigor, and relevance for forest management.

Vegetation Response to Green-tree Retention: A Review of the Literature

The conceptual basis for green-tree retention lies in the strong functional links among forest structure, biological diversity, and ecological process observed in natural forest ecosystems (Franklin et al. 1981, 1987; Harmon et al. 1986; Maser et al. 1988; Schowalter 1989; Ruggiero et al. 1991; Spies and Franklin 1991; North 1993). There is strong circumstantial evidence that the maintenance and/or recovery of forest organisms and processes following disturbance are enhanced by the persistence of remnant forest structures (e.g., Perry et al. 1989, Franklin et al. 1995, Perry and Amaranthus 1997). Franklin et al. (1997) review the history of development, diversity of goals and approaches, and resulting expectations of silvicultural systems that employ structural retention. Emphasizing the maintenance of biological diversity, they attribute an array of ecological functions to retained structures. For example, residual trees may ameliorate extremes in microclimate (Chen et al. 1993, 1995), provide energy subsidies for heterotrophic organisms (Perry 1994), serve as habitat for arboreal species (Berg et al. 1994, Carey and Johnson 1995, Peck and McCune 1997), serve as sources for recolonization of organisms associated with original stand structures (Busing et al. 1995), or enhance connectivity by facilitating movement of organisms within the matrix of managed forest (Franklin et al. 1997).

Retention of green trees should contribute in similar fashion to the persistence and recovery of forest understory communities, yet, to date, few studies have explicitly addressed this question. We are aware of only a single, short-term study that has evaluated the consequences of dispersed retention for forest understory communities. North et al. (1996) found that, 16 mo after

harvest, the species composition of a dispersed retention unit (27 trees/ha) resembled that of an adjacent clearcut to a greater degree than that of an adjacent, intact forest (reflecting abundant establishment of early successional species). However, shade-tolerant forest species were more diverse and abundant in the dispersed unit than in the clearcut, suggesting that forest understory taxa may benefit from the increased shading and/or reduced disturbance afforded by retained trees. Unfortunately, these short-term, unreplicated observations afford only a limited view of the possible effects of green-tree retention.

Studies of understory responses to thinning in younger forests may offer additional insights. It has been found that thinning generally leads to greater plant species diversity (in large part due to the establishment of invasive or exotic species) and to increased plant cover (Witler 1975, Alaback and Herman 1988, Bailey 1996), although the nature of these responses may vary with the vegetation, environment, or intensity of thinning. For example, where thinning leads to increased dominance by clonal shrubs (e.g., Tappeiner et al. 1991, Huffman et al. 1994), there may be a resultant decline in species diversity (Alaback and Herman 1988). There has been little consideration of the effects of thinning on plant species that are associated with late-seral environments or that are sensitive to logging disturbance (but see Bailey [1996]).

Insights into the potential long-term consequences of green-tree retention for understory communities may be aided by retrospective analyses of natural, two-tiered (two-aged) stands. These young-to-mature forests support an emergent canopy of older, scattered residual trees and have been described as the natural analogues of forests that may develop following retention harvest (e.g., Rose and Muir 1996, Peck and McCune 1997, Zenner et al. 1998). Traut (1994) described differences in understory species composition in plots with and without natural, residual trees and attributed these differences, in part, to the effects of residual trees on the density and composition of the regenerating tree layer. Unfortunately, causal mechanisms cannot be deduced through retrospective analysis, nor is it possible to distinguish direct effects (e.g., shading by residual trees) from indirect ones (e.g., species interactions or local variation in disturbance history, initial composition, or other site features). Replicated, pre-treat-

ment measurements in the DEMO study will provide a basis for separating the potential effects of retained trees from initial species composition and other site-level variation.

Considerably more attention has been devoted to the effects of residual trees on forest stand development and tree growth. For example, through analysis of annual growth rings North et al. (1996) observed that for 6 yr after dispersed retention harvest, the basal area increment of retained Douglas-fir (*Pseudotsuga menziesii*) was 15% lower than that in an adjacent, uncut forest. This is not the response typically observed in younger, thinned stands (reviews in Barrett [1980], Bailey [1996], North et al. [1996]); it may reflect a "thinning shock" in which resources are differentially allocated to roots (Oliver and Larson 1990). Long-term measurements of tree growth among replicate DEMO blocks may suggest whether these are local or general phenomena, and whether they represent short-term or more persistent effects.

Retrospective studies of natural, two-tiered stands also provide insights into the long-term effects of dispersed retention on forest development and tree growth. Regional comparisons of 70- to 110-yr-old stands with and without older (>200 yr) residual trees suggest that above a threshold density (ca. 15 trees/ha), residuals can affect the composition of younger cohorts and reduce their basal area growth (Rose and Muir 1996). Negative effects on basal area growth have also been reported from paired-plot studies in western Oregon. Here, however, the strongest effect per unit basal area of residual trees occurred at the lowest levels of residual tree density (5 trees/ha; Zenner et al. 1998) or basal area (5-10 m²/ha; Acker et al. 1998).

Stand responses to green-tree retention may also include increased mortality due to windthrow of isolated residual trees. Removal of 30-60% of the initial volume of mature and old-growth forests in northwestern British Columbia resulted in rates of windthrow of 0.3 to 8.2% of trees within 2 yr after harvest (Coates 1997). However, mortality can vary markedly from site to site, reflecting variation in the level of retention, initial stand density and composition, stand age, local weather conditions, and landform. For example, among 44 green-tree retention sites in western Oregon, rates of windthrow-related mortality ranged from 0 to nearly 60% (mean of 16%), with the greatest losses observed soon after harvest (Adler [1994]

and Hunter [1995] cited in Franklin et al. [1997]). By comparison, annual rates of mortality in unmanaged mature and old-growth forests of western Oregon and Washington average <1% (Franklin et al. 1987). The randomized block design of the DEMO study will permit separation of treatment effects (level or pattern of retention) on mortality from effects associated with site-specific factors (e.g., topography, soils).

Forest gap and stand-level growth and yield models have also been used to explore the possible effects of varying levels of dispersed retention on forest stand development and wood production. Some of the predictions of these models are intuitive (indeed some are predetermined by growth equations, McKenzie 1994). For example, the degree to which models simulate the development of old-growth stand characteristics (e.g., tree size-class structure) improves with the number of trees retained through harvest (Hansen et al. 1995), and relative to clearcut logging, cumulative basal area and volume growth are reduced when live trees are retained (Birch and Johnson 1992, Hansen et al. 1995). Other simulation results, although less intuitive, are supported by retrospective analyses of natural stands. In particular, reductions in stand basal area growth per residual tree are predicted to be strongest at the lowest levels of retention (5 trees/ha; Hansen et al. 1995). Still other simulation results are quite surprising and seem to contradict empirical observations. For example, under low levels of dispersed retention (as few as 5 trees/ha) and given sufficient time (240 yr), naturally establishing, shade-tolerant species such as western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) can outcompete planted Douglas-fir (Hansen et al. 1995). To what extent the spatial configuration of residual trees may influence stand development has not been examined empirically or through simulation, despite the fact that aggregated retention is now a standard practice on federal matrix lands in the region (USDA and USDI 1994). Comparisons of aggregated and dispersed retention in the DEMO design explicitly test for such effects.

Methods

Study Areas

To establish a broad geographic and ecological base of inference, eight study blocks were selected

to represent a diversity of forest types in western Oregon (Umpqua N. F.) and Washington (Gifford Pinchot N. F. and Washington DNR) (see Aubry et al. 1999). Blocks encompass markedly different physical environments, stand ages, and forest structures (Table 1). Sites were chosen to minimize the variation in environment and vegetation among treatment units within each block, within the constraints imposed by current landscape configurations and past management activities (Aubry et al. 1999). To varying degrees this goal was achieved (but see a discussion of this issue in the Challenges section, below).

Across blocks, elevations range from ca. 200-1700 m, slopes vary from gentle to steep, and nearly all aspects are represented (Table 1). Most sites lie within the western hemlock (*Tsuga heterophylla*) forest zone (Franklin and Dyrness 1973). Two blocks, Little White Salmon and Dog Prairie are located in the more easterly grand fir (*Abies grandis*) and white fir (*Abies concolor*) zones, respectively, and a third, Paradise Hills, occupies the colder, wetter, silver fir (*Abies amabilis*) zone. *Pseudotsuga menziesii* dominates all sites but associated tree species vary from block to block (Table 1).

Forest structure varies among blocks, reflecting differences in stand age (e.g., Little River vs. Layng Creek), regeneration and disturbance history, and physical environment (Table 1). Forest understory composition also varies: some blocks have depauperate ground layers (e.g., Dog Prairie) while others support dense herb and shrub communities (e.g., Layng Creek, Little White Salmon). Despite this heterogeneity, many blocks share the same dominant taxa (e.g., vine maple [*Acer circinatum*], Oregon grape [*Berberis nervosa*], salal [*Gaultheria shallon*], and huckleberry [*Vaccinium* spp.]; Table 1). Differences in stand structure and composition among treatment units within each block are generally small compared to differences among blocks (Table 1; but see Challenges section and Table 4).

Sites have had varying histories of recent disturbance (Aubry et al. 1999). For example, Layng Creek and Capitol Forest are second-rotation stands (i.e., clearcut but regenerated naturally) and all four blocks on the Umpqua N. F. have been thinned or salvage logged. In contrast, the three blocks on the Gifford Pinchot N. F. support mature, undisturbed forest.

TABLE 1. General environmental features and pre-harvest structural and compositional characteristics of the eight study blocks. Ranges are based on mean values for each of the six treatment units within each block.

Location/ Block	Elevation (m)	Slope (deg)	Aspect	Stand age (yr)	Tree density (no./ha) ^a	Basal area (m ² /ha)	Douglas- fir site index (m at 50 yr)	Major (minor) overstory species ^b	Major understory species ^c
Oregon: Umpqua National Forest									
Watson Falls	945-1310	4-7	flat	110-130	310-500	36-52	40-43	Psme (Abco, Tshe, Pipo, Pimo)	Abco, Psme, Amal, Libo2, Symo, Bene, Smst
Little River	1220-1400	14-40	varied	200-520 ^d	255-473	82-127	29	Psme (Tshe, Abco)	Tshe, Acci, Bene, Oxor, Actr
Laying Creek	490-790	20-41	SE	60-80	227-331	32-46	34-40	Psme (Acma, Cacth)	Acci, Cococ, Gash, Bene, Pomu
Dog Prairie	1460-1710	34-62	SW	165	258-475	72-106	30	Psme (Abco, Abmas, Cade)	Abco
Washington: Gifford Pinchot National Forest									
Butte	975-1280	40-53	E-SE	70-80	759-1781	48-65	27-32	Psme (Tshe, Thpl)	Tshe, Thpl, Acci, Vame, Vapa, Bene, Ptaq
Little White Salmon	825-975	40-66	NW-NE	140-170	182-335	61-77	30	Psme (Abgr, Conu)	Conu, Acci, Acgld, Cococ, Actr, Smst, Bene
Paradise Hills	850-1035	9-33	varied	110-140	512-1005	59-87	26-33	Psme (Tshe, Thpl, Abam)	Tshe, Abam, Acci, Vame, Vapa, Gash, Xete, Coca
Washington: Department of Natural Resources									
Capitol Forest	210-275	28-52	varied	65	221-562	54-73	37-41	Psme (Tshe, Thpl, Alru)	Acci, Vapa, Pomu, Gash

^a Trees >5.0 cm dbh.

^b Tree species codes: Abam = *Abies amabilis*, Abco = *A. concolor*, Abgr = *A. grandis*, Abmas = *A. magnifica* var. *shastensis*, Actr = *Acer macrophyllum*, Alru = *Alnus rubra*, Cacth = *Castanopsis chrysophylla*, Cade = *Calocedrus decurrens*, Conu = *Cornus nuttallii*, Pimo = *Pinus monticola*, Pipo = *P. ponderosa*, Psme = *Pseudotsuga menziesii*, Thpl = *Thuja plicata*, Tshe = *Tsuga heterophylla*.

^c Based on cover; includes understory trees (<5.0 cm dbh). Species codes in addition to those above: Acci = *Acer circinatum*, Acgld = *Acer glabrum* var. *douglasii*, Actr = *Achlys triphylla*, Amal = *Amelanchier alnifolia*, Bene = *Berberis nervosa*, Coca = *Cornus canadensis*, Cococ = *Corylus cornuta* var. *californica*, Gash = *Gaultheria shallon*, Libo2 = *Linnæa borealis*, Oxor = *Oxalis oregana*, Pomu = *Polystichum munitum*, Ptaq = *Pteridium aquilinum*, Smst = *Smilacina stellata*, Symo = *Symphoricarpos mollis*, Vame = *Vaccinium ovalifolium*, V. *alaskense*, Vapa = *V. membranaceum*, Vapa = *V. parvifolium*, Xete = *Xerophyllum tenax*.

^d One treatment unit with tree ages of 400-520 yr; the remaining units with tree ages of 200-325 yr.

Experimental and Sampling Designs

Aubry et al. (1999) describe the DEMO experimental design and harvest prescriptions in an introductory paper in this volume. To review, at each of the eight study blocks (replicates), six harvest treatments have been randomly assigned to 13-ha experimental (treatment) units. Treatments differ in the level (percentage of basal area) and/or spatial pattern (dispersed vs. aggregated) of retained trees as follows: (1) 100% retention (control); (2) 75% retention (harvested as three circular, 1-ha gaps—henceforth the “gap” treatment); (3) 40% dispersed retention; (4) 40% aggregated retention (as five, circular 1-ha retention patches); (5) 15% dispersed retention; and (6) 15% aggregated retention (as two, circular 1-ha retention patches) (see Figure 1). By design, these treatments produce distinctly different patterns of variation in stand structure and environment: relatively homogeneous conditions in the control and dispersed retention treatments, and two contrasting conditions (intact forest and harvested area) in the aggregated retention and “gap” treatments. We employ two sampling designs to capture the contrasts and gradients in vegetation

response that are expected to arise from these treatments.

Sampling Design for Treatment Effects

The first sampling design, which permits analysis of treatment effects (e.g., Hypotheses 1-3, below), uses a set of permanent vegetation plots arrayed across a grid system at each site (63 or 64 grid points with 40-m spacing, Figure 1). The number and spatial distributions of sample plots vary by treatment, however. In the dispersed retention and control treatments, where stand conditions will be relatively homogenous, 32 plots are placed systematically at alternate grid points (Figure 1a). In the aggregated retention and gap treatments, where we expect two distinct post-harvest environments, plots are placed at all grid points within the aggregates (or gaps), and at a subset of points in the surrounding matrix (yielding 32 or 37 plots per treatment, Figure 1b).

Strong contrasts in harvest treatments will produce marked differences in the composition, size structure, and spatial distribution of overstory trees. We are particularly interested in the effects of these treatments on volume and basal area growth; stem

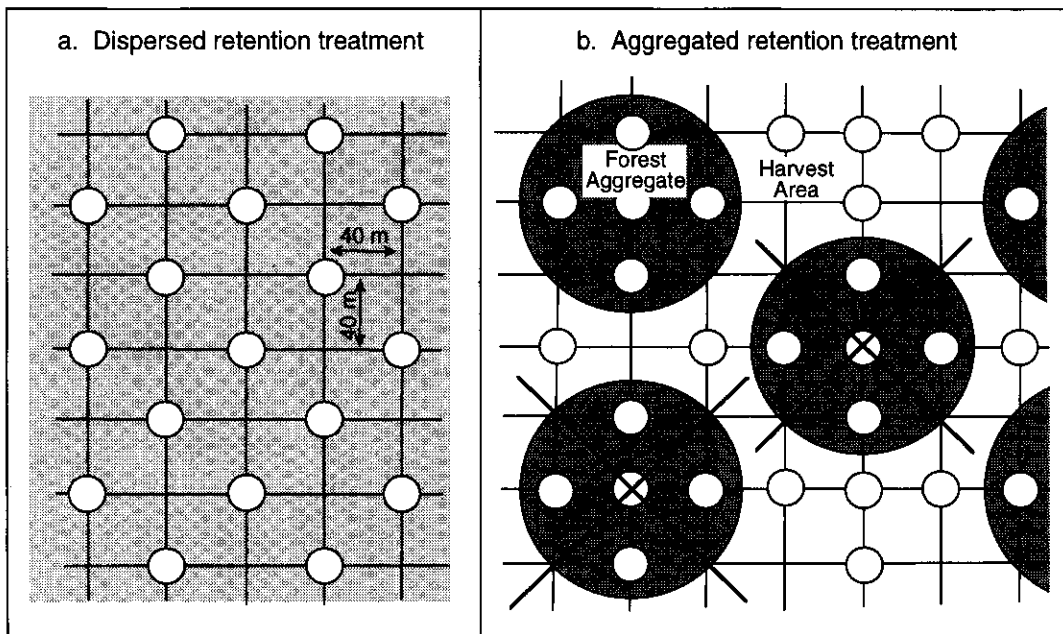


Figure 1. Plot locations (open circles) for sampling (a) relatively homogeneous conditions in the dispersed retention treatments and (b) contrasting conditions in the aggregated retention treatments. Control units are sampled as in (a); “gap” (75% retention) units are sampled using ca. 100 m long transects (dark lines in b, see also Figure 2).

TABLE 2. Variables of interest and derived statistics for the two primary sampling approaches (see Methods and Figure 2). X = variable sampled; blank = variable not sampled.

Variable	Treatment-level effects	Within-treatment ^a gradients	Derived statistics
Physical Site Characteristics			
Elevation, aspect, slope	X	X	
Topographic position, slope configuration	X	X	
Ground surface conditions (e.g., mineral soil, stone, litter, log)	X	X	
Coarse woody debris	X		volume and density (by species and decay class)
Post-harvest disturbance (e.g., vegetation damage, soil disturbance)	X	X	
Overstory Vegetation			
Canopy cover	X	X	
Tree diameters (>5 cm dbh)	X		density, basal area, volume, and diameter distributions (by species)
Tree characteristics (e.g., canopy class, vigor, crown ratio, damage)	X		
Tree mortality: physical conditions and causes	X		rates and causes of mortality (by species)
Tree heights: total, canopy depth	X		height and canopy depth distributions (by species)
Snags: diameter, height, decay class	X		density (by species, diameter, decay, and height class)
Understory Vegetation			
Lichens: presence/absence	X		species frequency and diversity
Bryophytes: presence/absence	X	X	species frequency and diversity
Herbs: cover, height	X	X	species frequency, diversity, and height distributions
Tall shrubs: cover, height	X	X	species frequency, diversity, and height distributions
Understory trees			
Seedlings (<10 cm tall): no. stems	X	X	frequency and density (by species)
Saplings (>10 cm tall, <5 cm dbh): cover, no. stems, height class, origin (natural vs. planted)	X	X	frequency, density, size structure, and rates of mortality (by species and size class)

^aConducted in the 40% aggregated retention treatments at Butte and Paradise Hills blocks only.

density; diameter, height, and canopy-depth distributions of canopy and sub-canopy trees; rates and causes of mortality; and recruitment and fates of snags (Table 2). A series of nested circular plots (Figure 2a) will be used to sample these overstory responses at 3-5 yr intervals. Permanently tagged trees will be measured for diameter, canopy position, structural attributes, and mortality. Tree height and crown depth will be measured for a subset of stems. Snags will be measured for diameter, height, decay class, and angle of lean.

As with the overstory, the forest understory is likely to respond to strong contrasts in harvest-

related disturbance (and resulting canopy conditions) among treatments. We are particularly interested in treatment effects on plant species diversity (richness and evenness); community composition and structure (the proportional representation of different plant groups or 'functional' types); and the establishment, growth, and mortality of regenerating trees (Table 2). We will also consider understory attributes that are known to influence the abundance and distribution of wildlife (e.g., plant cover and vertical stratification, recruitment and dynamics of coarse woody debris) (Table 2). A series of belt transects, intercept lines, and microplots nested within each tree plot will be used to sample

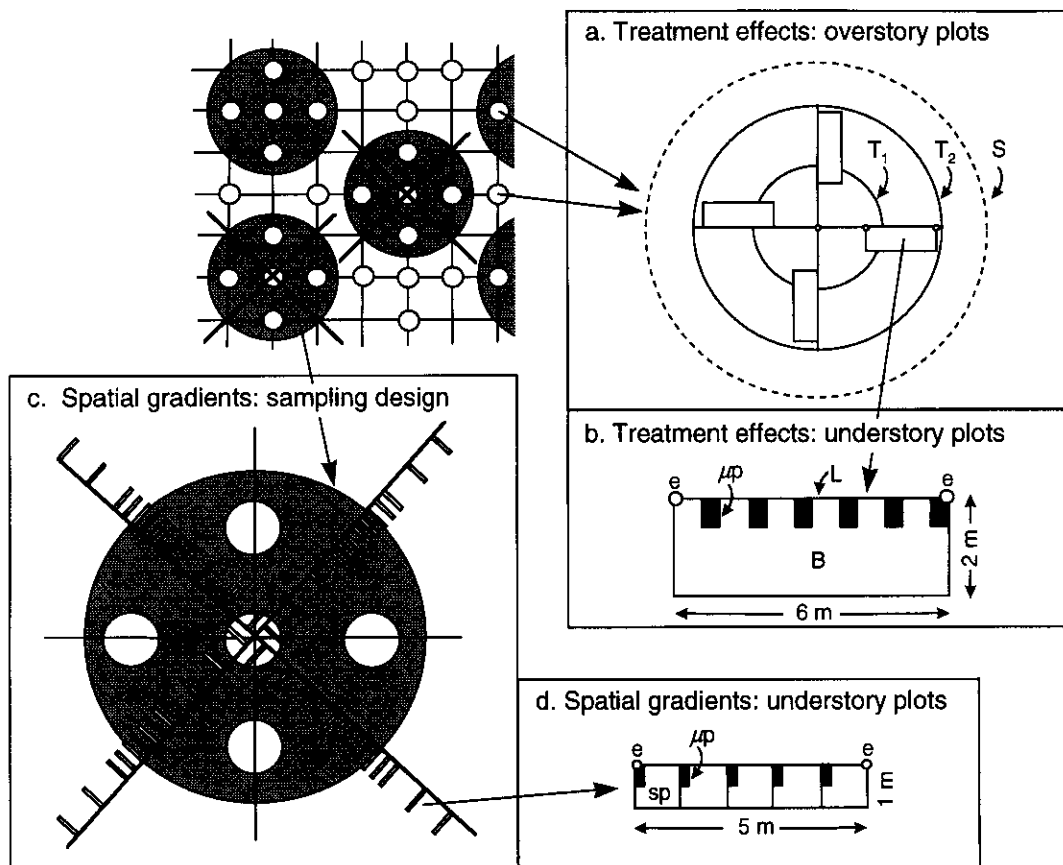


Figure 2. Plot and transect designs for sampling treatment effects (a, b) and spatial gradients (c, d) within aggregated retention units. For treatment effects, overstory characteristics (a) are measured within nested circular plots: 0.01 ha for trees 5.0-14.9 cm dbh (T_1), 0.04 ha for trees >15.0 cm dbh (T_2), and 0.08 ha for snags (S). Understory vegetation (b) is sampled with: belt transects (B) for density of saplings (trees >10 cm tall, <5 cm dbh); intercept lines (L) for cover/height of tall shrubs and saplings, disturbance assessments, and volume of coarse woody debris; and microplots (μp , 0.2 x 0.5 m) for ground surface characteristics, presence of bryophytes and macrolichens, cover and height of herbs and low shrubs, and density of tree seedlings (<10 cm tall). Overstory canopy cover is estimated with a spherical densiometer at the end points (e) of each intercept line. For spatial gradients in aggregated retention treatments (c), understory vegetation is sampled with 13 bands per transect. Within each band (d) are: subplots (sp, 1 x 1 m) for cover/height of all species and densities of tree seedlings/saplings; microplots (μp , 0.2 x 0.5 m) for presence/absence of bryophytes; and end points (e) for overstory canopy cover. See Table 2 for a complete list of variables.

the responses of understory species, changes in ground surface characteristics, and the types and levels of harvest-related disturbance (see Figure 2 caption for details). The nested plot design will also permit direct correlation of overstory and understory characteristics.

Sampling Design for Spatial Gradients Within Aggregated Retention Treatments

A second design will be used to sample fine-scale gradients in understory response within the ag-

gregated retention treatments (e.g., Hypotheses 4-7, below). This approach is limited to the 40% retention treatments at Butte and Paradise Hills. Here our focus is on the extent to which the 1-ha aggregates retain components of the original understory and/or ameliorate microclimatic conditions in the surrounding matrix. Bands of sample plots are arrayed along four orthogonal transects of ca. 100 m in length that span harvested, ecotonal (edge), and intact forest environments (Figure 2c). The perpendicular placement of transects permits examination of the effects of aspect on spatial

gradients in vegetation. Bands are spaced more closely (every 5 m) near the edges (ca. first 15–25 m) of the 1-ha aggregates where we anticipate sharper gradients in vegetation response, and more widely (every 10 m) in the harvested matrix and forest interior (Figure 2c). A series of sub-plots and microplots within each band (Figure 2d) will be used to sample changes in understory composition and structure (Table 2; see Figure 2 caption for details).

Hypotheses, Mechanisms, and Analytical Approaches

It is not possible in this paper to describe the full range of expected ecological or silvicultural responses to varying levels or patterns of green-tree retention. However, to stimulate future discussion and to guide ongoing inquiry and analysis, we have summarized our expectations in a table of predicted, qualitative responses to the six experimental treatments (Table 3). These predictions draw upon the results of empirical studies of natural disturbance and succession, plant-environment relationships, plant life history strategies, and vegetation responses to more conventional methods of silviculture (i.e., clearcut logging, commercial thinning). Others are more speculative and reflect general theory that is untested in these forest ecosystems.

In the following sections, we explore a set of predictions in depth as examples of the types of questions that we have posed in this study. We focus on the response of the forest understory which contains the vast majority of plant species in these forests, and in which we anticipate short-term changes to be most dynamic. Our hypotheses consider three groups of taxa for which we anticipate distinct patterns of response. The first are “forest-interior” species: subordinate forest herbs that are not restricted to, but are found most frequently and with greatest abundance in, forest-interior and late-successional environments (e.g., coral-root [*Corallorhiza* spp.], prince’s pine [*Chimaphila umbellata*], rattlesnake-plantain [*Goodyera oblongifolia*], twayblade [*Listera* spp.], pyrola [*Pyrola picta*]; Spies 1991, Halpern and Spies 1995). Many of these herbs are sensitive to disturbances associated with logging and broadcast burning (R5 species of Halpern [1989]; see also Halpern et al. [1992]) and are thought to require long periods of time for populations to re-

cover following large-scale disturbance (Halpern and Spies 1995). The second group consists of “early-seral” or “open-site” species. These include annual, biennial, and perennial herbs (native and exotic) that typically dominate recently disturbed and early successional communities (I1–I4 species of Halpern [1989]; see also Dyrness [1973], Schoonmaker and McKee [1988], Halpern and Franklin [1990]). These taxa are characterized by long-distance seed dispersal, rapid growth rates, and high fecundities. The third group of interest, “forest dominants,” are woody and herbaceous species that dominate mature and old-growth forest understories. These taxa are tolerant of disturbance (R3 species of Halpern [1989]; e.g., *Acer circinatum*, *Berberis nervosa*, *Gaultheria shallon*, and *Polystichum munitum*) and can occupy a broad range of canopy conditions and seral stages (Spies 1991).

Hypothesized Responses Among Treatments

An underlying premise of green-tree retention is that the survival of organisms associated with forest-interior environments will increase with the proportion of live trees retained through harvest (Franklin et al. 1997). Conversely, invasion of early-successional or open-site species should decline with increased levels of retention. To date, these assumptions have not been tested empirically, nor have the forms of these relationships been articulated (e.g., as linear or non-linear functions, or as threshold responses). There is even greater uncertainty regarding possible differences in response within aggregated and dispersed retention (Franklin et al. 1997). We predict that these groups will respond as follows:

Hypothesis 1.—*The abundance and diversity of forest-interior species will increase with the percentage of green trees retained (Figure 3a).* This prediction rests on two likely outcomes of increasing levels of retention: (1) reduced levels of disturbance to soils and understory vegetation, and (2) greater amounts of shading from retained trees. The results of long-term, successional studies following clearcut logging and burning suggest that both conditions should promote survival of forest-interior species (Halpern 1989, Halpern et al. 1992, Halpern and Spies 1995). In these studies, species extinctions induced by harvest were correlated with the intensity of soil disturbance. In

TABLE 3. Hypothesized short-term (5-10 yr) responses of forest overstory and understory communities to varying levels and patterns of green-tree retention. Responses are relative and represent the *average* condition within each treatment unit (e.g., weighted by area of harvested matrix and forest aggregate), assuming no post-harvest thinning. See Aubry et al. (1999) for details of harvest plans and post-harvest prescriptions.

Forest Attribute	Level and Pattern of Retention			
	40%		15%	
	Dispersed	Aggregated	Dispersed	Aggregated
	100%	75%		
Overstory Characteristics				
Variability of tree sizes (>5 cm dbh) ^a	high	high	moderate	low
Growth release of retained trees	none	non-minor	minor	minor
Windthrow-related mortality of retained trees	low	low	low	low
Variability of snag sizes and decay classes ^b	high	high	moderate	low-moderate
Understory Characteristics				
Variability of tree sizes (<5 cm dbh) ^c	high	high	moderate	low-moderate
Diversity of tree species ^d	low	low	moderate-high	high
Growth rates of regenerating trees ^e	very low	low	moderate	moderate-high
Relative contribution of planted vs. natural regeneration (ratio) ^f	n/a	low	moderate	high
Number of understory vegetation layers ^f	high	high	moderate-high	low-moderate
Persistence of forest-interior species (vascular plants)	high	moderate-high	moderate	low
Change in cover of forest understory dominants	none	small decrease	moderate increase	large decline
Recruitment of early-seral, open-site species	very low	low	moderate	very high
Persistence of ground-layer bryophytes	high	moderate-high	moderate-high	low-moderate

^a Retained trees in dispersed retention treatments will be dominants and co-dominants.

^b All snags will be retained in forest aggregates. In harvested portions of treatments, existing snags will be retained where possible and 6.5 snags/ha will be created from live trees.

^c Non-merchantable trees will be retained where possible.

^d Includes early-seral and hardwood species.

^e Includes planted and natural regeneration. Harvested portions of each unit will be planted with a diversity of species. Planting density (ca. 300-600 trees/ha) and composition will vary by block, but will be consistent among treatments within a block.

^f Includes all size classes of understory trees (<5 cm dbh).

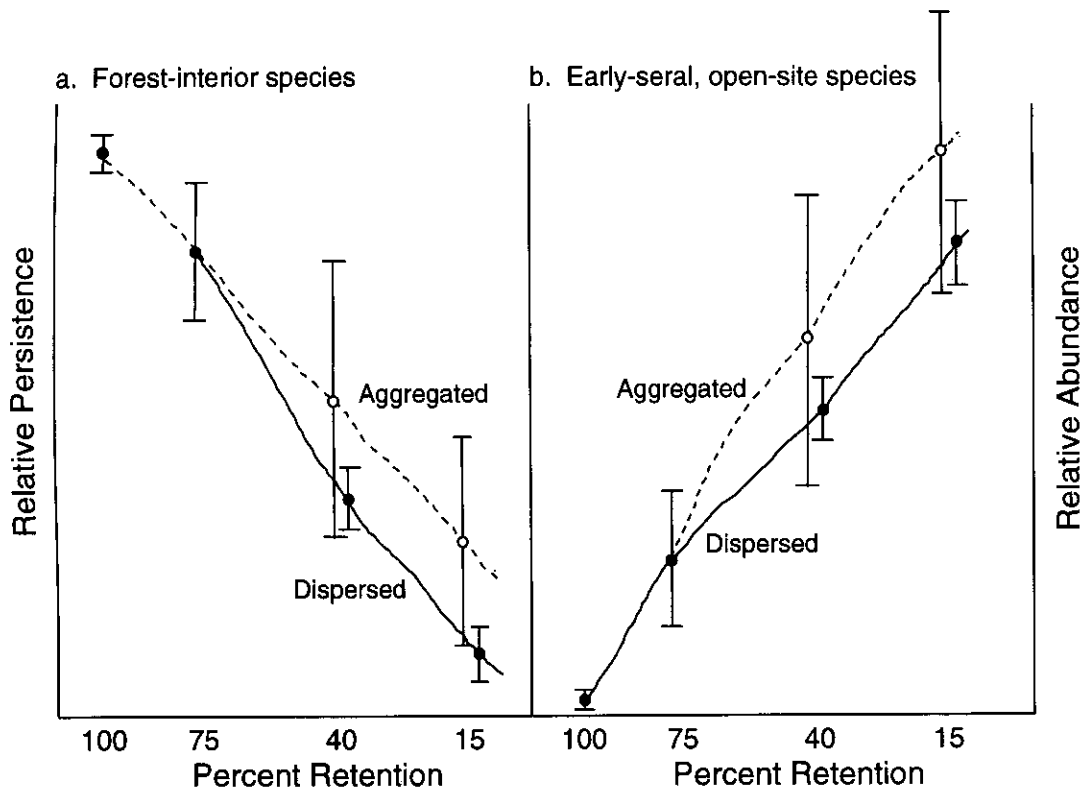


Figure 3. Predicted short-term, qualitative responses (mean and variance) to varying levels and patterns of green-tree retention for two groups of understory taxa: (a) forest-interior species and (b) early-seral or open-site species.

addition, even where forest soils remained undisturbed, removal of the overstory canopy was sufficient to cause mortality of some sensitive species.

Hypothesis 2.—*The abundance and diversity of early-seral, open-site species will decrease with the percentage of green trees retained (Figure 3b).* This hypothesis has a strong basis in life history theory (Grime 1977, Grace 1990). As light, potential establishment sites, and soil resources become more limiting with greater levels of retention, early-seral species are at a competitive disadvantage. In studies of post-harvest succession, these taxa typically show positive responses to disturbance intensity and negative responses to canopy closure (Dyrness 1973; Halpern 1988, 1989; Schoonmaker and McKee 1988; Halpern and Spies 1995).

Hypothesis 3.—*For both forest-interior and early-seral, open-site species, the mean and the variation in abundance and diversity will be greater*

in aggregated retention treatments than in dispersed retention treatments (Figure 3). We assume that in dispersed retention units, uniformly high levels of logging disturbance and associated microclimatic stress will lead to significant loss of forest-interior species and to widespread establishment of early-seral species. In contrast, in aggregated retention units we anticipate spatially distinct patterns of survival and invasion: in harvested portions of these units, survival of forest-interior species will be low and establishment of early-seral species will be high; conversely, in the retention patches, survival of forest-interior species will be high, and establishment of open-site species will be low.

Analytical Approaches for Hypotheses 1-3.—To test for the effects of treatments on species abundance and diversity, we will use analysis of variance (ANOVA) (or repeated measures ANOVA for long-term effects) coupled with planned comparisons of means (Sokal and Rohlf 1981). Due

TABLE 4. Variation in stand structure and species abundance prior to harvest among the six treatment units at Paradise Hills, Washington. Values are 1996 treatment means. Totals represent the summed cover of all species within a stratum (only selected species are shown).

Forest Attribute	Treatment Unit					
	100%	75%	40%		15%	
			Disp.	Aggr.	Disp.	Aggr.
Overstory Structure						
Tree density (no./ha)	1005	512	877	642	684	732
Basal area (m ² /ha)	70.9	76.1	67.3	58.7	86.7	79.1
Percent Cover of Understory Strata and Selected Species						
Herb stratum (total)	12.7	36.8	19.4	33.5	7.4	6.4
<i>Berberis nervosa</i>	0.3	7.9	1.5	0.2	1.2	0.5
<i>Cornus canadensis</i>	0.9	2.2	1.6	6.7	0.6	1.1
<i>Gaultheria shallon</i>	2.7	9.3	1.2	1.4	0.1	—
<i>Xerophyllum tenax</i>	7.7	10.7	10.2	8.5	2.4	1.7
Tall shrub stratum (total)	6.5	23.4	7.0	28.6	4.0	5.8
<i>Vaccinium membranaceum</i>	0.4	4.6	1.1	10.7	0.2	1.0
<i>V. ovalifolium/V. alaskaense</i>	3.2	7.7	4.0	13.7	2.3	4.4
<i>V. parvifolium</i>	2.5	5.7	1.8	1.9	1.2	0.3
Understory tree stratum (total)	2.5	2.3	8.8	13.6	0.9	3.5
<i>Abies amabilis</i>	1.1	0.2	2.1	10.4	0.6	3.1
<i>Tsuga heterophylla</i>	0.8	1.9	6.0	2.2	0.2	0.2

to the patchy nature of plant species distributions, we have found high levels of variation in frequency, cover, and diversity among pre-harvest treatment units within some blocks (e.g., Table 4). Thus, to improve our ability to detect treatment-level effects we will analyze for *changes* in species frequency, cover, or diversity relative to initial (pre-harvest) conditions. Analysis of covariance (ANCOVA) may be used to test for effects of other potentially important variables (e.g., level of disturbance, cover of coarse woody debris). Species abundance will be measured as frequency of occurrence at varying spatial scales (microplots, transects, and plots) and as mean plot-level cover. Species diversity will be expressed as richness and heterogeneity (Hill 1973) at the same spatial scales. To examine the effects of treatments on the *variability* of responses (*Hypothesis 3*), similar analyses will be conducted using the coefficients of variation of these parameters. Significance levels will be adjusted for multiple comparisons using the sequential Bonferroni method as described by Rice (1989).

Additional correlation and regression analyses will be conducted at smaller spatial scales (e.g., transects or plots) to explore finer-scale relationships with forest canopy cover, shrub-layer development, ground surface conditions, and har-

vest-related disturbance. These relationships may vary with, or independently of, changes in the level and pattern of retention.

Hypothesized Gradients Within Aggregated Retention Treatments

Aggregates (retention patches) are predicted to serve as refugia for plant species that are sensitive to disturbance or to open-canopy conditions, and as sources of propagules for surrounding harvested areas (e.g., Busing et al. 1995, Halpern and Spies 1995, Franklin et al. 1997). Given the slow rates of dispersal of some understory species (Jules 1997), decades of observation may be required to fully judge the potential of aggregates to serve as sources for recolonization of late-seral species. However, the short-term effectiveness of aggregates as local refugia can be tested by monitoring species' persistence following harvest. The following hypotheses address the extent to which the floristic composition of forest aggregates is maintained through harvest:

Hypothesis 4.—*Within aggregates, species associated with forest-interior or late-seral environments will decrease in abundance and diversity with proximity to the aggregate edge (Figure 4).* This prediction assumes that in fragmented

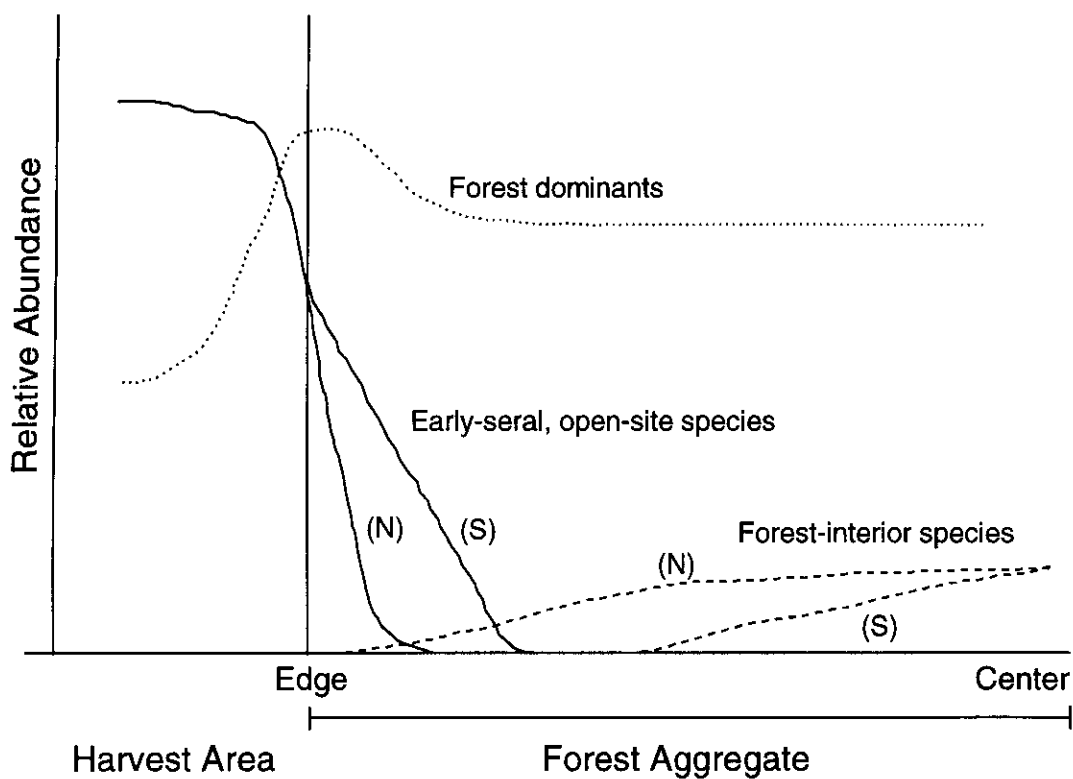


Figure 4. Hypothesized short-term, qualitative responses of three groups of understory taxa as a function of distance from the edge of a 1-ha forest aggregate (radius of ca. 56 m). Responses are expected to differ between north- (N) and south- (S) facing edges.

habitats, the distributions of forest-interior species are shaped by edge effects, manifested as gradients in microclimate, herbivory, or the abundance of competing species. Even if forest structure is retained, forest fragments experience greater variability in air and soil temperature, higher levels of light, greater wind speed, and lower humidity than do larger intact stands (Chen et al. 1992, Matlack 1993). In low-elevation forests of the Pacific Northwest, altered microclimates can extend more than 200 m inward from the forest edge (Chen et al. 1995). (By comparison, the 1-ha aggregates in the current experimental design have radii of ca. 56 m). To what extent understory plants exhibit parallel gradients in response is unclear (Wales 1972; Matlack 1993, 1994a, 1994b; Fraver 1994). Empirical support for the effects of edges on forest understories is scarce in the Pacific Northwest. In the Klamath Mountains of northern California, Frost (1992) found that the abundance of some forest herbs declined for dis-

tances of up to 60 m from the forest-clearcut boundary. However, some of the more sensitive herbs observed in these mixed coniferous forests—those with affinities for cooler, moister environments—lie near their southern distributional limits. Our gradient analyses will indicate whether similar patterns are found in the more mesic environments of western Oregon and Washington.

In addition to microclimatic effects, forest edges may also be associated with greater rates of herbivory (Alverson et al. 1988) or regeneration/release of woody plants that can outcompete smaller herbaceous species (Frost 1992) (see Hypothesis 6). Although some forest-interior species may maintain their current distributions, we expect short-term declines in abundance and diversity toward the forest edge. As edge contrasts decline with time (as regenerating stands develop), we expect the gradual recovery of some of these species.

Hypothesis 5.—*Early-seral, open-site species will decline in abundance and diversity with distance into the forest aggregate; gradients in abundance and diversity will be steeper and shorter than those of forest-interior species (Figure 4).* It has been observed in other forest ecosystems that changes in microclimate and local disturbance regime along the forest edge may promote the invasion of exotic or ruderal taxa (Ranney et al. 1981, Laurance 1991, Brothers and Spingam 1992, Frost 1992). The distances to which early-seral species invade may be more closely linked to the depth of edge-related disturbance than to gradients in microclimate, thus we expect relatively short, steep gradients in response. As the effects of disturbance diminish with time, we expect these gradients in seral species distributions to become less apparent.

Hypothesis 6.—*The dominant forest understory species will show positive responses to the creation of edges, peaking in abundance within a short distance of the forest aggregate-harvested matrix boundary (Figure 4).* Many of our dominant understory taxa (e.g., *Vaccinium* spp., *Gaultheria shallon*, and *Acer circinatum*) possess morphological or physiological traits (e.g., extensive rhizome systems, variable leaf morphology, and/or potential for rapid vegetative spread) that confer resistance to disturbance and enable vigorous expansion once resource conditions improve (Alaback and Herman 1988; Halpern 1988, 1989; Huffman et al. 1994; O'Dea et al. 1995). It is likely that increases in light along the boundaries of newly created forest aggregates will induce rapid lateral and vertical growth of these taxa.

Hypothesis 7.—*Edge effects, as defined by the distances to which early-seral species penetrate or forest-interior species are lost (and by the magnitude of these changes), will be greater where environmental conditions are more stressful (i.e., along south- and west-facing edges as opposed to north- and east-facing edges) (Figure 4).* This prediction is based on the assumption that environmental conditions that inhibit forest-interior species and enhance establishment of open-site species are accentuated along south- and west-facing aspects (Wales 1972, Ranney 1977, Matlack 1993, Chen et al. 1995, Murcia 1995). In the Pacific Northwest, these aspect-related effects may be magnified by greater rates of treefall or canopy damage along south- and west-facing edges due to the strongly directional nature of winter storms.

Analytical Approaches for Hypotheses 4-7.—Analyses of spatial gradients within aggregated retention treatments will be used to elucidate how species abundance (frequency and cover) and diversity vary with distance from the forest-aggregate edge (Hypotheses 4-6, Figure 4). Abundance or diversity measures will be fit to linear or nonlinear regression models (Sokal and Rohlf 1981, Zar 1984). For species that exhibit a significant correlation between abundance and distance from edge, the form of the most appropriate model (e.g., linear, logarithmic, or exponential) may provide insight into the mechanism(s) of decline or advance (e.g., invasion or die-back as isolated individuals or in a wave-front; *sensu* Matlack 1994a). To examine possible aspect-related differences in these effects (Hypothesis 7, Figure 4), we will test for the significance of an aspect term in multiple regressions of abundance on distance and aspect. Multiple regression will also be used in exploratory fashion to test for relationships with other biotic and/or abiotic factors that vary at finer spatial scales and that may influence, or be influenced by, edge-related phenomena (e.g., tree cover, ground surface conditions, local disturbance, or associated vegetation). The sequential Bonferroni method will be used to adjust significance levels for multiple comparisons (Rice 1989).

The 1-ha sized aggregates in the current design are relatively large with respect to the range of prescribed patch sizes (0.2 to >1.0 ha) for green-tree retention units on federal matrix lands (USDA and USDI 1994). However, they are much smaller than are necessary to escape microclimatic effects associated with edges (Chen et al. 1995). Although our studies do not explicitly test for the effects of aggregate size, the results of these gradient analyses may suggest whether smaller aggregates might serve as plant refugia, or whether edge effects are such that larger retention units are necessary to maintain particular species or groups of species.

The Scientific Challenges of Large-scale, Interdisciplinary Experiments

Numerous challenges arise in designing and implementing large-scale, interdisciplinary experiments, particularly when these studies are motivated by concerns over natural resource management or policy. The DEMO experimental design and its component studies represent the products of a long and iterative process in which we have incorporated

diverse ecological interests, a rigorous experimental design, and the needs and concerns of land managers and the public (Abbott et al. 1999, Aubry et al. 1999, Franklin et al. 1999). Many of our decisions represent tradeoffs: they resolve particular problems but in turn may limit statistical power, ecological or silvicultural inference, or harvest efficiency. In this section, we provide several examples of the conceptual and methodological challenges that have shaped our studies.

Sample area and sample size: inherent tradeoffs in interdisciplinary studies. If the spatial scales of sampling in this experiment were not constrained by interdisciplinary linkages, vegetation studies could employ greater replication of smaller-sized treatment units, thus enhancing statistical power. However, vegetation measurements are integral to interpreting faunal responses (Lehmkuhl et al. 1999) which, by necessity, must be examined at larger spatial scales (13 ha). As a consequence, our ability to detect treatment effects for some components of the forest community may be compromised by the relatively small numbers of sample units.

Experimental rigor versus site-specific management approaches. To minimize the potential confounding of post-harvest activities with retention treatments, our silvicultural prescriptions require that site-preparation and tree-planting specifications are consistent among all harvest units within a block (Aubry et al. 1999). However, where experimental units occupy different environments, support different plant communities, or generate different densities of slash, this consistency may lead to a prescription that is less than optimal for silvicultural objectives. Ecological interpretations, as well as the applicability of particular results for managers, must be tempered by these considerations.

Natural variation in vegetation composition and structure. Despite attempts to minimize within-block variability, at some sites topographic configurations, land designations, and past management activities (e.g., adjacent harvest units or roads) precluded the establishment of six, 13-ha experimental units within a forest of homogeneous topography, vegetation, and stand history. Consequently, stand age, forest structure, and species composition vary among experimental units prior to treatment (Table 4). This heterogeneity has implications for interpreting the experimental treat-

ments and resulting ecological responses. For example, because the total basal area retained in forest aggregates dictates the total basal area retained in dispersed units, pre-treatment differences will skew the true proportion of basal area retained.

Variation in vegetation structure and composition prior to treatment (Table 4) must also be considered in interpreting post-harvest responses. To minimize these effects, we will focus on *changes* in abundance/diversity between pre- and post-harvest communities. Nonetheless, where competitive interactions are important determinants of species responses, and where there are large differences in the initial abundance of competitors, effects of treatments may be difficult to detect.

Separating effects of logging disturbance from effects of retention: short-term versus long-term considerations. A primary goal of our research is to elucidate the effects of varying levels and patterns of green-tree retention on forest community development. Although there has been concerted effort to minimize effects of confounding variation (Aubry et al. 1999), operationally, levels of disturbance will change markedly with the proportion of basal area removed and with the pattern in which it is removed. Thus, it is likely that short-term responses of vegetation will reflect differential patterns of logging disturbance as much as, or more than, patterns of retention. Sampling of post-harvest disturbance characteristics will permit an analysis of these effects. As disturbance effects diminish with time, canopy effects may dominate understory responses, although legacies of differential disturbance may continue to shape successional trajectories (Halpern 1988). Thus, green-tree retention strategies incorporate more than variation in the level and spatial arrangement of retained structures—they encompass an array of co-varying patterns and processes. To the extent that we can distinguish disturbance effects from those associated with canopy structures, we may better understand the mechanisms that shape vegetation response and more successfully guide new strategies for forest management.

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