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Changes in forest structure following variable-retention harvests in Douglas-fir dominated forests

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Abstract

Variable retention has been advocated for maintaining biological diversity after regeneration harvest of forest stands. The Demonstration of Ecosystem Management Options (DEMO) study was established to test the effects of varying levels and patterns of residual trees on a range of forest taxa, ecosystem processes, and public perceptions. Understanding responses to experimental treatments depends on how well stand structural targets defining those treatments are achieved, but also on inadvertent changes in non-target structural attributes. DEMO treatments were specified by six levels and patterns of retained basal area: 100% retention (control), 75% aggregated retention (three 1-ha gaps cut within the treatment unit), 40% dispersed retention (regular distribution of residual trees), 40% aggregated retention (five uncut 1-ha aggregates), 15% dispersed retention (regular distribution of residual trees), and 15% aggregated retention (two uncut 1-ha aggregates). Treatments were applied randomly to 13-ha experimental units at each of six blocks in western Oregon and Washington. Treatment implementation produced the desired range of non-overlapping proportions of residual basal area. Other unspecified stand attributes such as tree density, stand density index, and canopy cover generally paralleled reductions in basal area, but quadratic mean diameter increased in the dispersed treatments due to selective retention of larger trees. Resulting stand structures were strongly dependent on initial conditions. Many differences in relative diameter distributions were observed before and after treatment, although they were changed less by aggregated retention. Strong differences in stand structure among blocks were highlighted by principal components analysis of diameter distributions, but experimental units converged on more similar structures at successively lower levels of retention. Indices of vertical complexity depicted by canopy area profiles showed strong responses to treatments, as did indices of horizontal variability in crown-area profile. Changes in tree species composition were small, although Douglas-fir (*Pseudotsuga menziesii*) became less dominant at lower levels of retention. The combination of differing initial conditions and differing treatments created variation in residual stand structure that is independent of the categorical treatments and that may help explain residual variation in responses to these discrete treatments.

Keywords: Crown-area profile; Green-tree retention; Habitat structure; *Pseudotsuga menziesii*; Stand structure; Variable retention; Vertical complexity; Target structure

1. Introduction

Forests cover approximately 30% of the earth's surface and contain a major portion of the species inhabiting terrestrial ecosystems. The species diversity of forests is positively correlated with increasing structural complexity and spatial heterogeneity at a variety of ecological scales (Huston, 1994; Brokaw and Lent, 1999). Although natural disturbances can enhance species diversity (Pickett, 1976, 1980; Connell, 1978; Petraitis et al., 1989), anthropogenic disturbances that differ in severity, extent, and frequency from natural disturbance regimes can result in a forest landscape that may or may not support the desired or historical diversity of species (Cissel et al., 1999; Landres et al., 1999; Spies and Turner, 1999). Management of forests for timber may not result in the rates of extinction associated with more intensive changes in land use (e.g., deforestation, urban development; Lugo, 1988); however, effects of forest management for timber production must be understood to prevent local extirpation of species from managed forest landscapes. The challenge is to develop silvicultural systems that allow extraction of timber and regeneration of desired species in an economically viable manner, while maximizing social

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acceptability and minimizing adverse effects on biodiversity (Hunter, 1990; Spathelf, 1997; Frelich and Puettmann, 1999; Kerr, 1999; Seymour and Hunter, 1999).

Timber harvesting can significantly affect the presence and abundance of many forest species (Imbeau et al., 2001; Sullivan et al., 2001), although effects can be light at very low harvest intensities (Costa and Magnusson, 2002). Activities associated with varying levels of timber extraction can directly or indirectly influence the abundance or quality of coarse woody debris (Siitonen et al., 2000), soil microbes (Barg and Edmonds, 1999), wood-decomposing fungi (Sippola and Renvall, 1999), lichens (Rolstad et al., 2001), bryophytes (Hazell and Gustafsson, 1999), vascular plants (Traut and Muir, 2000; Bergstedt and Milberg, 2001), invertebrates (Schowalter, 1995), herpetofauna (Schlaepfer and Gavin, 2001), birds (Chambers et al., 1999; Tittler et al., 2001), and mammals (Sullivan et al., 2001). However, the processes by which these changes occur often remain unclear. Some responses are strongly correlated with residual stand density (Sullivan et al., 2001), but the proximal cause may reflect secondary or indirect effects such as severity of ground disturbance or amount of slash accumulation (Halpern, 1988; Halpern and McKenzie, 2001). In unmanaged forests, bird species diversity correlates with measures of vertical structure (e.g., foliage height diversity), in part because some taxonomic groups are distributed vertically in forest canopies (MacArthur and MacArthur, 1961; Brokaw and Lent, 1999). However, few studies have demonstrated that silvicultural treatments influence plant and animal responses by changing vertical structure of the vegetation (but see Sullivan et al., 2001). Horizontal variability in stand structure has been proposed as one mechanism that contributes to species diversity in old-growth forests (Halpern and Spies, 1995) and is the subject of wildlife research in managed forests (Carey and Johnson, 1995; Carey, 2000; Haveri and Carey, 2000). Significant progress on linking retention strategies and silvicultural treatments to responses of various taxa in these studies depends on detailed characterization of vegetation structure both before and after harvest. Moreover, sole focus on target structural attributes (e.g., proportion of retained basal area) may be inadequate without further consideration of 'non-target' attributes that also influence responses. Characterizing both target and non-target attributes is essential for developing silvicultural systems that reach the desired balance between economically viable production of timber, regeneration of desired tree species, and protection of other forest values.

The largest changes in forest biota generally occur after regeneration harvests under even-age silvicultural systems, the most notable being clearcutting (Halpern, 1988; Sullivan et al., 1999). Impacts to species associated with later stages of forest succession or development (i.e., late-seral species) are ameliorated to some extent by retaining live trees during timber harvest, whether implemented during the regeneration phase of conventional seed-tree or shelterwood systems (Beese and Bryant, 1999; Nyland, 2002) or as "variable-retention" regeneration harvests that are currently being explored for maintaining biological diversity (Arnott and Beese, 1997; Franklin et al., 1997; Aubry et al., 1999; Hazell and Gustafsson, 1999; Tittler et al., 2001; Lindenmayer and Franklin, 2002). In established stands that are relatively dense and uniform but not yet ready for regeneration harvesting, thinning can stimulate understory vegetation and enhance biological diversity (Alaback, 1982; Bailey et al., 1998; Thomas et al., 1999; Sullivan et al., 2001; Thysell and Carey, 2001). In contrast to thinning and other traditional intermediate treatments, however, the primary objective of variable retention is to mitigate effects of regeneration harvests on late-successional species by maintaining an older cohort of trees and other structures through the next rotation (Lindenmayer and Franklin, 2002). The goal is to maintain some taxa characteristic of mature stands in the short-term, to expedite recovery to pre-harvest conditions in the long-term, and to retain features that enhance the structural complexity of future stands (Franklin et al., 1997; Lindenmayer and Franklin, 2002).

Little information is available to guide decisions about optimal retention levels or patterns for variable-retention harvests. The responses of some species may be linear with respect to harvest intensity, whereas others may show nonlinear or threshold responses. Moreover, ecological responses to retention may be strongly influenced by the spatial distribution of retained trees (i.e., regularly dispersed versus aggregated). The Northwest Forest Plan calls for retaining green trees in at least 15% of the harvest unit, with 70% of these retained in aggregates of 0.2–1.0 ha (Tuchmann et al., 1996). In response to the dearth of scientific evidence supporting these guidelines, a regional interdisciplinary experiment, Demonstration of Ecosystem Management Options (DEMO), was initiated in 1994 to test ecosystem responses to differing proportions and spatial distributions of retained trees (Aubry et al., 1999; Franklin et al., 1999). Assessment of the long-term responses of plants, animals, specific ecological processes, and public perceptions constitute the core investigations of DEMO (Halpern and Raphael, 1999). However, these long-term responses will be influenced by short-term responses in at least two ways. First, residual stand structures will place bounds on future stand development and thereby control other long-term responses. Second, short-term responses of many plant and animal populations will determine, to some degree, the potential for long-term recovery from disturbance. Even under very simple specification of a single harvest treatment, differences in initial stand conditions (e.g., tree density, size, and spatial distribution) may result in considerable variation in residual stand structures among replications. These differences in stand structure may be key to interpreting biological responses and explaining variability in response to treatment. Similarly, explicit description of treatment effects on stand structure may help to distinguish between those responses that are inescapable consequences of a given level or pattern of harvesting and those that can be mitigated by modifying particular harvest criteria, harvesting operations, or post-harvest treatments. Furthermore, responses of some taxa may be closely related to residual stand structure and others to amount of material removed, disturbance associated with harvest, or elimination of specific structural features.

The objective of this paper was to test whether treatments specified by a given percentage of basal area retention produced proportional changes in other features of stand structure that potentially influence biological responses. These features included four general aspects of stand structure: (1) average stand attributes such as tree size and density, (2) tree species composition, (3) vertical complexity, and (4) horizontal heterogeneity. The variable-retention treatments in DEMO were designed to impose specific changes in 'target' structural variables (i.e., level and spatial distribution of basal area), but had no explicit guidelines for 'non-target' attributes (e.g., diameter distribution, species composition, vertical structure). Three hypotheses about average stand attributes were tested:

Hypothesis 1a. The percentage of retained basal area matches the target specified in the treatment definition.

Hypothesis 1b. Tree density, stand density index (Reineke, 1933), and canopy cover will decline in proportion to removed basal area.

Hypothesis 1c. Quadratic mean diameter will increase in dispersed retention treatments, but remain unaffected by aggregated retention.

Because treatments were not intended to affect tree species composition, two other hypotheses were tested:

Hypothesis 2a. Overstory tree species richness and diversity will not differ among treatments.

Hypothesis 2b. Overstory species composition will not change in response to treatment.

Vertical complexity in forests can be assessed indirectly by quantifying the variability in size-class structure or more directly by characterizing the vertical distribution of crown layers. Treatment effects on vertical complexity were evaluated by testing two hypotheses:

Hypothesis 3a. Relative diameter distributions will be truncated in dispersed treatments, but remain unchanged in aggregated treatments.

Hypothesis 3b. Vertical complexity will be reduced in dispersed treatments, but remain unchanged in aggregated treatments.

Treatments were designed to produce horizontal variability in the distribution of overstory trees. Retention of trees in aggregates was expected to increase spatial variability and dispersed treatments to reduce spatial variability. Two related hypotheses were therefore tested:

Hypothesis 4a. Plot-to-plot variability in vertical structure will decline in dispersed treatments.

Hypothesis 4b. Plot-to-plot variability in vertical structure will increase in aggregated treatments.

2. Methods

2.1. Study areas

To establish a broad geographic and ecological base of inference, six study blocks were selected to represent a diversity of forest types in western Oregon and Washington

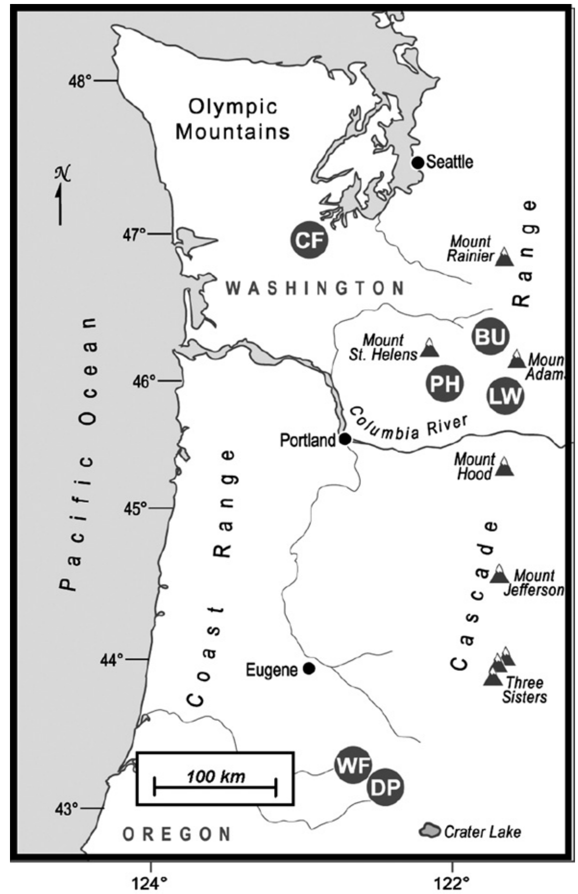

Fig. 1. Map of western Washington and Oregon with locations of the six DEMO study blocks. Block names from north to south are—CF: Capitol Forest, BU: Butte, PH: Paradise Hills, LW: Little White Salmon, WF: Watson Falls, and DP: Dog Prairie.

(Fig. 1). Two were on the Umpqua National Forest, Oregon (43.2°N, 122.3°W); three were on the Gifford Pinchot National Forest, Washington (46°N, 121.7°W); and one was on Capitol Forest in Washington (state land managed by the Washington Department of Natural Resources; 47°N, 123.1°W). The blocks encompassed markedly different physical environments, stand ages, and forest structures (Tables 1 and 2). 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).

Across blocks, elevations range from ca. 200 to 1700 m, slopes vary from gentle to steep, and nearly all topographic 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 (*A. concolor*) zones, respectively, and a third, Paradise Hills, occupies the colder, wetter, Pacific silver fir (*A. amabilis*) zone. Douglas-fir (*Pseudotsuga menziesii*) was the dominant tree species in all blocks, but associated species varied (Fig. 2).

Stand structure and understory composition also varied among blocks, reflecting differences in age, regeneration dynamics, disturbance history, and physical environment

Table 1
General topographic features and forest attributes for each of the six experimental blocks in the DEMO study

Location/block	Elevation (m)	Slope (%)	Aspect	Stand age (year)	Site index (m at 50 years)
Oregon: Umpqua National Forest					
Watson Falls	945–1310	4–7	Flat	110–130	40–43
Dog Prairie	1460–1710	34–62	SW	165	30
Washington: Gifford Pinchot National Forest					
Butte	975–1280	40–53	E–SE	70–80	27–32
Little White Salmon	825–975	40–60	NW–NE	140–170	30
Paradise Hills	850–1035	9–33	Variable	110–140	26–33
Washington: Department of Natural Resources					
Capitol Forest	210–275	28–52	Variable	65	37–41

Minimum and maximum values represent the range of treatment unit means.

(Tables 1 and 2; see also McKenzie et al., 2000; Halpern et al., 1999, 2005). Understories in some blocks contained very low cover and diversity of herbaceous species (Dog Prairie) while others hosted a dense herb and shrub community (Little White Salmon). Vine maple (*Acer circinatum*), Oregongrape (*Berberis nervosa*), salal (*Gaultheria shallon*), and huckleberry (*Vaccinium* spp.) were common in most blocks. Sites have had varying histories of recent disturbance (Aubry et al., 1999). Capitol Forest originated from natural regeneration following clearcut logging, Watson Falls was salvage logged between 1970 and 1978, and Dog Prairie was thinned in 1986. In contrast, blocks on the Gifford Pinchot National Forest were unmanaged.

2.2. Experimental design and treatments

Aubry et al. (1999) have described the DEMO experimental design and harvest prescriptions in detail. Briefly, at each block, six harvest treatments were randomly assigned to 13-ha experimental (treatment) units. Treatment units were square (360 m × 360 m) or slightly rectangular (320 m × 400 m). Treatments differed in the level (percentage of basal area) and/or spatial pattern (dispersed versus aggregated) of retained trees as follows (Fig. 3):

(1) 100%: 100% retention (control);
(2) 75%A: 75% aggregated retention (three circular, 1-ha patch cuts);
(3) 40%D: 40% dispersed retention;
(4) 40%A: 40% aggregated retention (five circular 1-ha forest aggregates);
(5) 15%D: 15% dispersed retention;
(6) 15%A: 15% aggregated retention (two circular 1-ha forest aggregates).

Aggregated treatments were implemented assuming that basal area was uniformly distributed across treatment units; i.e.,

Table 2
Average overstory conditions in the six experimental blocks prior to harvest

Attribute	Watson Falls	Dog Prairie	Butte	Little White Salmon	Paradise Hills	Capitol Forest
Douglas-fir						
Tree density (no./ha)[a]	246	219	798	124	191	232
Basal area (m^2/ha)	34.0	73.9	50.1	66.4	39.7	56.4
Quadratic mean diameter (cm)	43	66	29	83	52	57
Stand density index[b]	547	1001	944	823	590	815
Other conifers						
Tree density (no./ha)	144	126	348	37	551	94
Basal area (m^2/ha)	13.4	15.1	5.8	3.6	33.3	4.7
Quadratic mean diameter (cm)	31	40	16	32	28	26
Stand density index	229	250	142	62	631	93
Hardwoods						
Tree density (no./ha)	7	–	2	76	<1	36
Basal area (m^2/ha)	<0.1	–	<0.1	0.6	<0.1	2.9
Quadratic mean diameter (cm)	8.2	–	10	9	66	32
Stand density index	1	–	<1	17	1	52
All species						
Tree density (no./ha)	397	345	1147	237	742	362
Basal area (m^2/ha)	47.4	89.0	56.0	70.7	73.1	64.1
Quadratic mean diameter (cm)	39	58	26	63	36	48
Stand density index	786	1269	1105	978	1259	985

[a] Trees with diameter ≥ 5 cm.
[b] Reineke (1933).

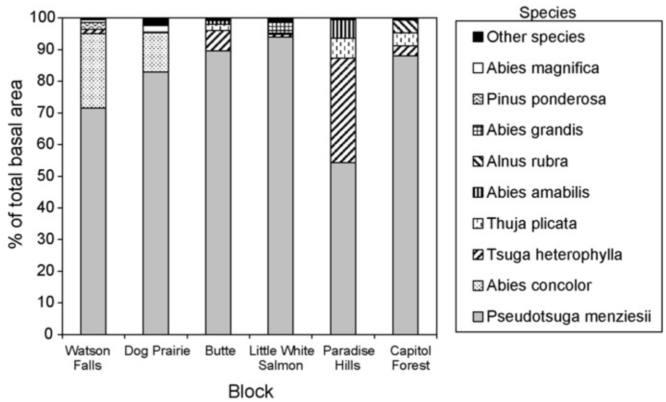

Fig. 2. Average overstory tree species composition (based on percentage of total basal area) among the six experimental blocks prior to treatment. Other species include *Abies lasiocarpa*, *A. procera*, *Acer macrophyllum*, *Alnus rubra*, *Castanopsis chrysophylla*, *Calocedrus decurrens*, *Chamaecyparis nootkatensis*, *Cornus nuttallii*, *Fraxinus latifolia*, *Pinus contorta*, *Picea engelmannii*, *Pinus monticola*, *Populus trichocarpa*, *Prunus emarginata*, *Rhamnus purshiana*, *Taxus brevifolia*, and *Tsuga mertensiana*.

areas retained were equal to 15, 40, and 75% of the treatment unit for 15%A, 40%A, and 75%A, respectively. Residual basal area was therefore not expected to match exactly the nominal level due to natural variation in the spatial distributions of trees. Likewise, because experimental units within a block varied in initial basal area, basal area in the aggregated treatments could depart considerably from 15, 40, and 75% of the control treatment basal area. In the dispersed treatments, residual basal areas were designed to equal the total basal area retained in the 1-ha aggregates of the respective aggregated treatments. Consequently, residual basal area of a specific unit receiving dispersed retention was not expected to be identical to 15 or 40% of its initial basal area. Residual trees in dispersed treatments were selected from dominant or co-dominant crown classes.

Treatment units were logged by a skyline cable system (Capitol Forest), ground-based system (Watson Falls, Paradise Hills), or helicopter (Dog Prairie, Butte, Little White Salmon) (Halpern and McKenzie, 2001). Felling and yarding in all treatment units were completed within 3–7 months in each block (1997–1998). Damage to residual stems was generally low (Moore et al., 2002). Non-merchantable trees (subcanopy stems with dbh < 18 cm) were felled at Paradise Hills, felled if damaged at Watson Falls, and left standing at Butte; non-merchantable trees were largely absent in the remaining blocks. At Watson Falls, logging slash was piled away from vegetation sampling points and burned to reduce fuel loadings to permissible levels; slash was left untreated at the remaining blocks. Because treatment of non-merchantable trees and logging slash was kept constant within a block, their effects on treatment responses became part of the block effect. All harvest treatments within a block were also planted with the same density and mix of species; only the harvested portions of the aggregated treatments were planted. Planting densities ranged from 300 to 825 seedlings ha^{-1} and included predominantly Douglas-fir, with one to four additional species at all blocks except Capitol Forest (Maguire et al., 2006).

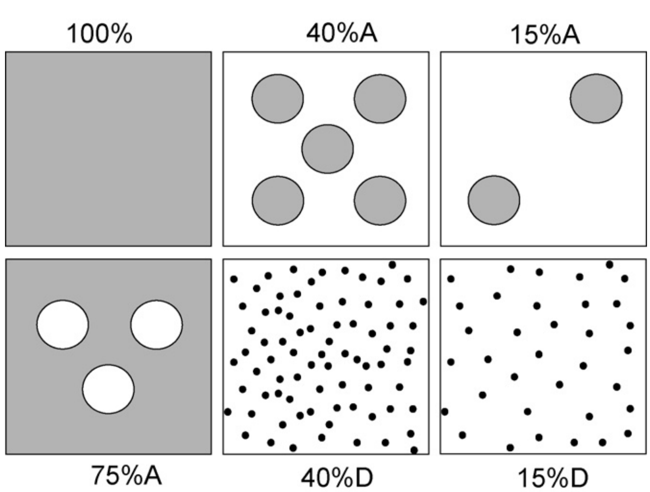

Fig. 3. Schematic representation of the six experimental treatments implemented in the DEMO study. Solid gray areas represent uncut forest (100 and 75% retention treatments) and uncut 1-ha forest aggregates (15%A and 40%A retention treatments); black dots represent individual trees (15%D and 40%D retention treatments).

2.3. Vegetation sampling

A rectangular sampling grid with 40-m spacing was established on each treatment unit, with points on the outside of the grid separated from the edge of the treated unit by a 40-m buffer. This yielded 63 or 64 sample points per treatment, depending on unit shape (7 × 9 or 8 × 8 grid). In the control and dispersed-retention treatments, 32 permanent plots were placed systematically at alternate grid points for the pre-harvest inventory. In the aggregated treatments, characterized by two distinct post-harvest conditions (cut and uncut), permanent plots were placed at all five grid points within each aggregate (40%A and 15%A) or cut patch (75%A), and at a subset of points in the surrounding matrix. This design resulted in 36 or 37 plots in 40%A and 32 plots in each of the other treatments. Pre-harvest overstory conditions were sampled in summer 1994–1996 with a set of nested circular plots at each sampled grid point: 0.01 ha for live and dead trees with diameter at breast height (D) ≥ 5 and <15 cm and 0.04 ha for trees with $D \geq 15$ cm. Within each plot, species and diameter (nearest 1 cm) were recorded for each tree, and total height and height to crown base were measured on a subsample of trees of each species. Taxonomic nomenclature followed Hitchcock and Cronquist (1973). During the summer after logging (1998 or 1999), post-harvest overstory conditions were sampled with a single 0.04-ha circular plot for all trees with $D \geq 5$ cm. Sampling intensity was increased to all 63 or 64 grid points in the two dispersed treatments (where tree densities were greatly reduced), but remained the same for all other treatments. An aluminum tag was nailed to each tree at breast height, and species and diameter (nearest 0.1 cm by diameter tape) were recorded. Within a treatment unit, a subsample of 40 trees from each species was selected for measurement of total height and height to crown base (nearest 0.1 m). If fewer than 40 trees were available for a given species, all individuals were measured. These height trees were further subsampled for crown width in 2002–2003 (nearest 0.1 m).

2.4. Derived measures of vegetation structure

2.4.1. Average stand attributes

Treatment unit attributes were computed from pre- and post-treatment plot data to establish initial and residual conditions, respectively. Total residual basal areas were compared to initial basal areas to estimate attained levels of retention. Other standard attributes were computed to further characterize stand structure, including tree density (trees per ha or tph), quadratic mean diameter (D_q), and stand density index (SDI; Reineke, 1933).

2.4.2. Species diversity and composition

To detect changes imposed by the treatments, three measures of tree species diversity were estimated for treatment units: species richness (S); Shannon index of species diversity (H; Shannon, 1948; Krebs, 1999); and Pielou index of species evenness (J; Pielou, 1966), with total basal area serving as the measure of abundance in the latter two. Jackknife estimates of species richness (Krebs, 1999) were necessitated by unequal post-treatment sample sizes among treatment units (63 or 64 in dispersed treatments versus 32–37 in others). To quantify changes in species composition, Renkonen's percentage similarity (Krebs, 1999) was computed from pre- and post-treatment samples (RPS = $\sum$ minimum(p_{1i}, p_{2i}), where p_{1i} and p_{2i} are the proportional abundance of species i in the pre- and post-harvest treatment unit, respectively).

2.5. Size class structure

Initial and residual diameter distributions were constructed by 5-cm classes, portraying differences in size structure of units before and after treatment.

2.6. Crown-area profile

Vertical structure of the treatment units was of primary interest due to its strong influence on light distribution, microclimate, wildlife habitat, and visual appearance. Crown cross-sectional areas at 0.5-m height intervals (Fig. 4) were estimated from crown shape models developed by Dubrasich et al. (1997), based on previous work with conifers (Biging and Wensel, 1990) and hardwoods (McPherson and Rowntree, 1988). The crown models were scaled to DEMO crown widths for the nine most common conifers—*P. menziesii*, *T. heterophylla*, *A. concolor*, *A. grandis*, *A. magnifica*, *A. procera*, *Calocedrus decurrens*, *Pinus monticola*, and *P. ponderosa*. For these nine species, crown width was estimated from dbh and crown ratio ($\mathrm{CW} = g_1 D^{g_2} [\mathrm{CR}]^{g_3}$ where CR is the ratio of live crown length to total tree height and g_k's are parameters estimated from the data). Crown widths for all remaining species were estimated from regional equations (Bechtold, 2004). Cross-sectional areas of individual tree crowns were summed at each height, and estimates of total canopy cross-sectional area per hectare were plotted against height to yield a crown-area profile for each treatment unit (Dubrasich et al., 1997). Missing total heights and heights to crown base were estimated from tree diameters by applying equations developed separately for each treatment unit, using standard methodology (Curtis, 1967; Ritchie and Hann, 1987). Total canopy cover was computed as the sum of the estimated crown projection areas, corrected for crown overlap (Crookston and Stage, 1999; Gill et al., 2000). Canopy cover for each aggregated treatment unit (75%A, 40%A, 15%A) was estimated as an area-weighted average of the harvested and unharvested portions of the treatment units.

Three sets of univariate indices were selected to portray specific aspects of crown-area profile considered relevant to responses of other taxa: vertical complexity, degree of species

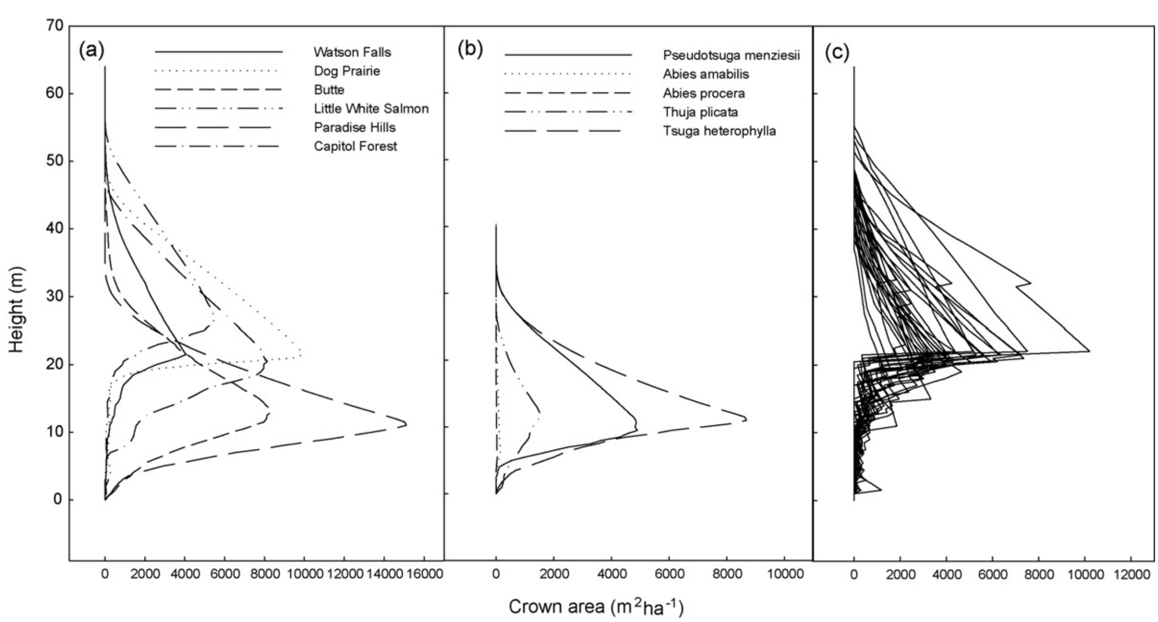

Fig. 4. Examples of pre-harvest crown-area profiles depicting overstory canopy structure on treatment units: (a) composite profiles for all species combined (100% retention units only); (b) profiles for individual species on a single treatment unit (100% retention at Paradise Hills); (c) composite profiles for individual plots within a treatment unit, all species combined (100% retention at Watson Falls).

Table 3
Indices of crown-area profiles representing different aspects of structural diversity of the forest canopy

Variable	Definition	Range in post-harvest values
Crown-area profile summed across all species		
$S.D._{CA}$	Standard deviation of crown area among 0.5-m height intervals	584–10,398
H_{CA}	Shannon diversity index of crown area among 0.5-m height intervals	3.63–4.40
J_{CA}	Pielou evenness index of crown area among 0.5-m height intervals	0.85–0.94
Crown-area profile for individual species		
$S.D._{sp}$	Weighted mean standard deviation of crown area among 0.5-m height intervals	503–6,657
H_{sp}	Weighted mean Shannon diversity index of crown area among 0.5-m height intervals	3.60–4.17
J_{sp}	Weighted mean Pielou evenness index of crown area among 0.5-m height intervals	0.85–0.93
Crown-area profile for individual plots (summed across all species)		
$S.D._{plot}$	Weighted mean standard deviation of crown area among plots at a given height	931–7,843
H_{plot}	Weighted mean Shannon diversity index of crown area among plots at a given height	2.20–4.03
J_{plot}	Weighted mean Pielou evenness index of crown area among plots at a given height	0.64–0.99

stratification, and horizontal variability (Table 3). Of primary interest was the relative uniformity of the crown-area profile among height intervals (analogous to foliage height diversity; MacArthur and MacArthur, 1961). The first set of indices was therefore based on the crown-area profile for a treatment unit, summed across species. The vertical uniformity in this profile was expressed by three indices: the standard deviation of crown area among 0.5-m height intervals ($S.D._{CA}$); Shannon index of diversity among 0.5-m height intervals (H_{CA}); and Pielou index of evenness among 0.5-m height intervals (J_{CA}). Because canopy complexity may result either from stratification of species into layers or from presence of most species in all layers, indices were also computed for each species separately. Weighted-average indices ($S.D._{sp}$, H_{sp}, and J_{sp} in Table 3) were then determined by applying the total crown volume (integral of crown shape model) of each species as its weight. Finally, plot-to-plot variation in crown area provided a measure of the horizontal variability in stand structure at the scale of individual plots within treatment units (0.04 ha for trees with $D > 15$ cm). The last set of indices therefore entailed summing crown area at a given height for all species on the plot, then computing the standard deviation, Shannon diversity index, and Pielou evenness index for crown area among plots at a common height. This process was repeated for each height, and the weighted mean of all heights was calculated by weighting each height-specific index by total crown area at that height (yielding $S.D._{plot}$, H_{plot}, and J_{plot} in Table 3). For the indices of vertical structure (first two sets), a lower S.D., higher H, and higher J indicated greater uniformity and, hence, greater vertical diversity or complexity. For indices of horizontal structure (third set), a lower SD, higher H, and higher J indicated greater uniformity and, hence, lower heterogeneity or complexity.

2.7. Treatment evaluation

To assess changes in forest structure, treatments were regarded as nominal because retention levels were not designed to match exactly 15, 40, or 75% of initial basal area on each treatment unit (see Section 2.2). Retention levels were thus portrayed in three alternative ways, i.e., as a percentage of: (1) initial basal area of that experimental unit, (2) initial basal area of the control unit in that block, and (3) target basal area. Target basal area was defined as 100, 75, 40, and 15% of initial basal area in the control and aggregated treatments units (100%, 75%A, 40%A, and 15%A, respectively); however, the target basal areas for 40%D and 15%D were designed to be identical to the target basal areas in 40%A and 15%A, respectively. Because basal area was estimated by sampling with fixed-area plots, sampling error was associated with both pre- and post-harvest basal area estimates.

2.8. Statistical analysis

As expected in a large-scale field experiment, initial conditions of the 13-ha experimental units differed to varying degrees within each block. Although random assignment of treatments protected against bias arising from initial conditions, it was possible to obtain systematic differences among treatment units by chance. To test for this possible source of bias, all response variables were tested for treatment "effects" prior to harvest using ANOVA. Differences among treatment means were identified by Tukey's studentized range tests when an overall treatment effect was significant at $\alpha = 0.05$ (Zar, 1984). Differences in indices of vertical complexity were likewise tested by the Friedman nonparametric analog of a randomized block ANOVA, with multiple comparison tests performed on treatment rank sums (Zar, 1984). To control the experiment-wise error rate, P-values between 0.005 and 0.05 were considered marginally significant and values <0.005 were considered significant. Residuals from all ANOVAs were analyzed graphically to check whether transformation was needed to meet the assumptions of constant variance and normality (no transformations were needed).

Differences in post-harvest stand attributes and structural/compositional indices were also assessed by ANOVA or Friedman's test (followed by *post hoc* tests of means), as were changes in these indices (post-harvest minus pre-harvest). A separate ANOVA tested treatment effects on percentage similarity (RPS; see Section 2.4) of pre- and post-treatment species composition. Although some attributes such as total basal area were expected to differ significantly because they defined the treatments, outcomes for other attributes were contingent on the potential interaction between treatments and initial conditions within each treatment unit. As a result, differences in post-harvest conditions among treatments may reflect: (1) little or no change in some units that differed initially; (2) marked change in some units and little change in others, where all were initially similar; and (3) combination of varying levels of change and varying degrees of initial similarity among all units. Conversely, lack of differences in post-harvest conditions could conceivably mask treatment effects if large differences in initial conditions were eliminated or reduced by treatments.

Stand structure is inherently complex and can be viewed in myriad dimensions. However, many aspects of stand structure are strongly correlated with diameter distribution, and diameter at breast height is arguably the most easily and accurately measured dimension of individual trees. A series of two-sample K–S tests (Zar, 1984) was performed to test for significant differences in initial diameter distributions among treatment units within a block; similar tests were performed after treatment. In addition to K–S tests, a principal components analysis was conducted on pre- and post-treatment diameter distributions (density of trees in 5-cm diameter classes). This multivariate structural analysis provided insights into initial variation among treatment units, and changes in structure that were imposed by the treatments themselves.

3. Results

3.1. Treatment evaluation

Initial basal area did not differ significantly among treatments ($P = 0.97$; Table 4 and Fig. 5a), and variation among blocks ($P < 0.001$) was substantially larger than variation among treatment units within blocks. This expected between-block variation resulted in residual basal areas for a given level of retention that differed by as much as 250% (Fig. 5b). Regardless, most treatment units contained residual basal areas within 10% of their targets, although some were 20–

Table 4
Tests of treatment effects on pre-harvest condition, post-harvest condition, and change in condition (post- minus pre-harvest measurement; randomized block ANOVA)

Stand attribute	Pre-harvest	Post-harvest	Change
Total basal area (m^2/ha)	ns*	100 75A 40D 40A 15D 15A	100 75A 40D 40A 15A 15D
Douglas-fir basal area (m^2/ha)	ns	100 75A 40D 40A 15D 15A	100 40A 75A 40D 15D 15A
Trees density (no./ha)	ns	75A 100 40A 40D 15A 15D	100 75A 40A 40D 15D 15A
Quadratic mean diameter (cm)	ns	40D 100 15D 40A 75A 15A	40D 15D 100 75A 40A 15A
Stand density index	ns	100 75A 40D 40A 15A 15D	100 75A 40D 40A 15D 15A
Total canopy cover (%)	ns	100 75A 40D 40A 15D 15A	100 75A 40D 40A 15D 15A
Douglas-fir canopy cover (%)	ns	100 75A 40D 40A 15D 15A	100 75A 40D 40A 15D 15A
Tree species richness (S, no./trt)	ns	ns	ns
Shannon index (H)	ns	ns	15D 15A 40A 75A 100 40D
Evenness (J)	ns	15A 15D 40A 75A 100 40D	15D 15A 40A 75A 100 40D
Percentage similarity	—	—	100 40A 75A 15A 15D 40D
Canopy depth (m)	ns	ns	ns

Treatments are ordered from highest to lowest in mean response; lines connect treatment units that are not significantly different ($\alpha = 0.05$; Tukey studentized range tests). Treatment labels refer to the percentage basal area retention followed by D for dispersed or A for aggregated treatments. (*) Overall treatment effect in ANOVA not statistically significant at $\alpha = 0.05$.

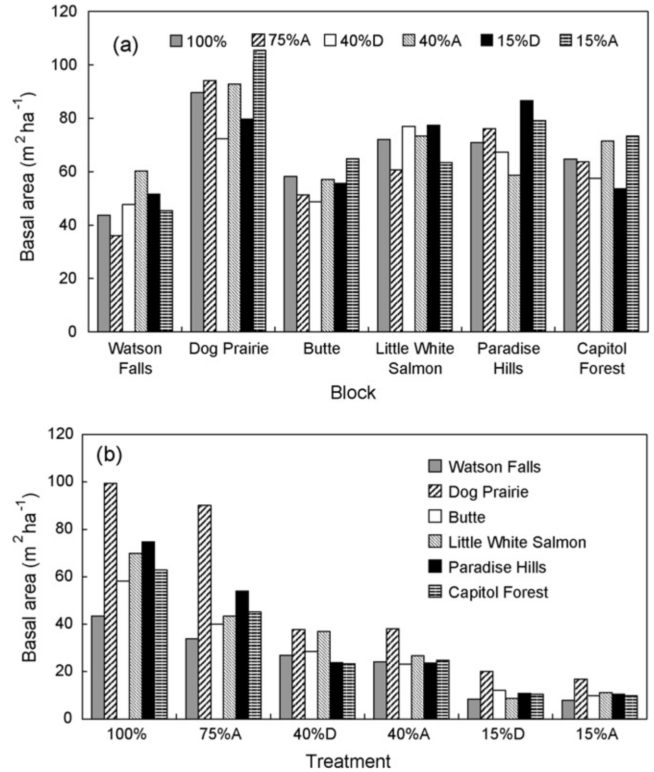

Fig. 5. Treatment unit basal area (m^2/ha) among the six experimental blocks (a) prior to harvest and (b) after harvest. Results of statistical tests on treatment effects are listed in Table 4. For treatment definitions see Section 2.2.

30% higher (Fig. 6a). Even in control units, estimates of post-harvest basal area differed by as much as 11% from pre-harvest estimates, underscoring the effect of sampling error on assessing the magnitude of discrepancies between target and residual basal area. Sampling error (standard errors) ranged from 2 to 16%, so the majority of deviations from target basal areas were less than the magnitude of the sampling error.

The 75, 40, and 15% aggregated treatments were assumed to be attainable by cutting the corresponding proportion of area, but because trees were not distributed uniformly, percentage of basal area retained on these units differed somewhat from the nominal percentages (Fig. 6b). Likewise, the actual percentages relative to the controls differed from the nominal percentages (Fig. 6c), reflecting initial differences in basal area among treatment units within blocks (Fig. 5a). Regardless, when residual basal area was expressed as a percentage of initial basal area of each unit, the treatments achieved the desired objective of establishing three contrasting and non-overlapping levels of retention: 11–25% for 15% retention, 35–59% for 40% retention, and 71–94% for 75% retention (Fig. 6b). The retention classes were similar when based on controls, ranging from 13 to 21, 32 to 62, and 62 to 91%, respectively (Fig. 6c). Hence, with respect to Hypothesis 1a, the retained basal area percentages were generally commensurate with nominal levels.

3.2. Average stand attributes

Variation in initial tree density, quadratic mean diameter, and stand density index among blocks (pre-harvest ANOVAs, all $P < 0.001$) was again substantially larger than the

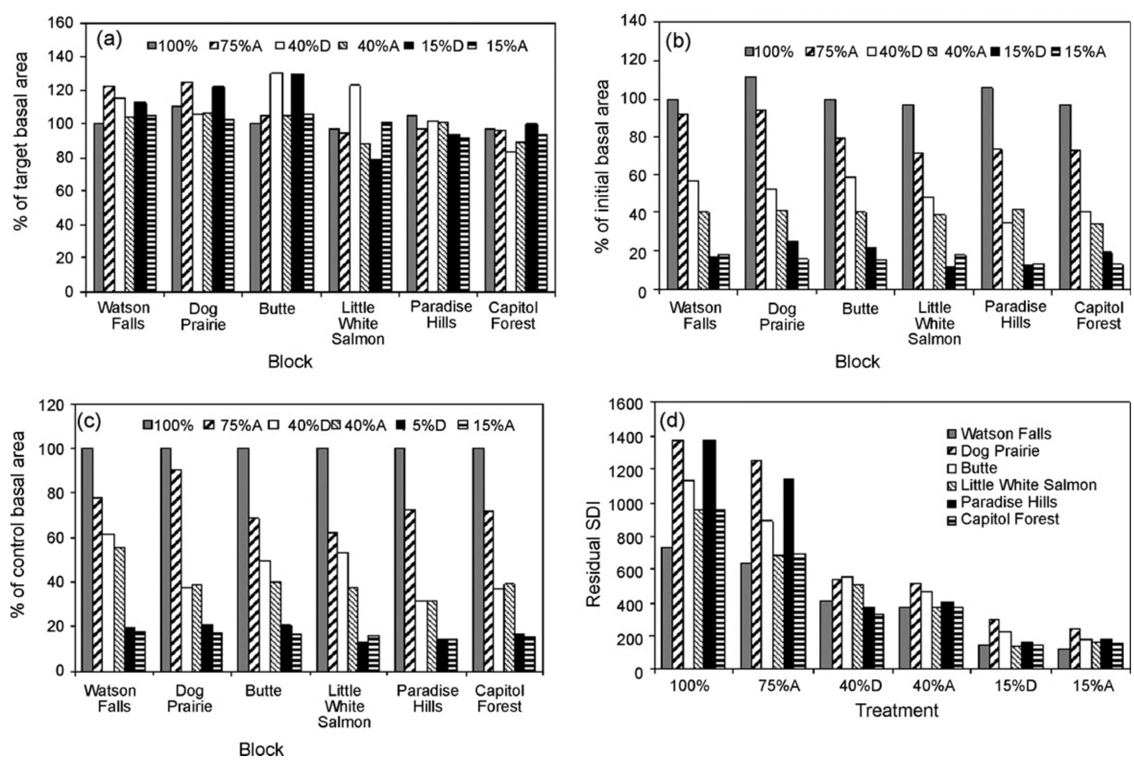

Fig. 6. Post-harvest basal area and stand density: (a) residual basal area as a percentage of target basal area (see Section 2.2 for definition of target); (b) residual basal area as a percentage of initial basal area; (c) residual basal area as a percentage of control treatment basal area; and (d) residual stand density index.

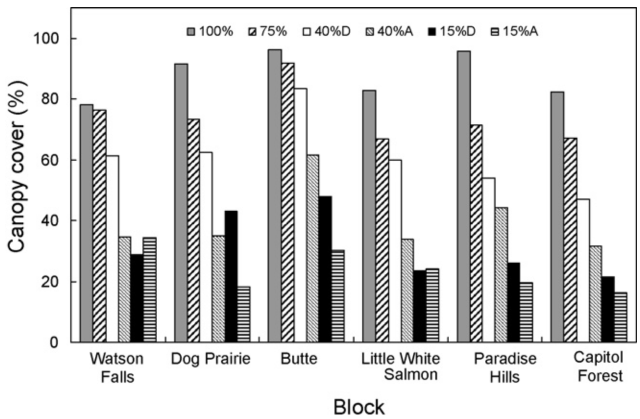

Fig. 7. Post-harvest canopy cover based on estimated crown widths, an assumption of circular crown projection areas, and degree of crown projection overlap expected from randomly distributed trees (see Section 2.4).

variation among treatment units within each block. Differences among treatments were all non-significant (pre-harvest ANOVAs, all $P > 0.81$; Table 4), as would be expected with random assignment of treatments to experimental units. Conversely, treatments imposed a significant change in each stand attribute ("change" ANOVAs, all $P < 0.0001$; Table 4), thus significant treatment effects on residual stand attributes were apparent (post-harvest ANOVAs, all $P < 0.006$; Table 4). Douglas-fir was the only species that exhibited significant differences in post-harvest basal area among treatments ($P < 0.0001$ for overall F-test; Table 4). Although pre-harvest canopy cover did not differ significantly among treatments ($P = 0.79$), post-harvest cover (Fig. 7) and change in cover were significantly different ($P < 0.0001$; Table 4). With respect to Hypothesis 1b, the rank of treatment units by residual tree density, stand density index, and canopy cover generally paralleled residual basal area (Table 4); however, the relative abundance of trees with relatively small mean diameters at Butte and Paradise Hills caused high stand density indices relative to their basal areas (Fig. 6d versus Fig. 5b). Trends for quadratic mean diameter were less clear, but the expected increase in dispersed treatments (Hypothesis 1c) was generally supported (Table 4).

3.3. Species diversity and composition

Tree species diversity did not differ among treatment units prior to harvest ($P > 0.22$). Treatments produced no significant change in species richness, but did significantly increase diversity (H) and evenness (J) in the 15% treatments ($P = 0.001$ for overall F-test; Table 4). Thus, Hypothesis 2a was supported by the lack of response in species richness, but not by the increase in species diversity and evennesss.

A marginal treatment effect was detected for percentage similarity between pre- and post-harvest overstory composition ($P = 0.01$), with multiple comparison tests indicating a marginally significant difference only between the control and 40% dispersed retention (Table 4). Average percentage similarity was 90% for 40% dispersed treatments and 99% for controls; overall change in species composition was therefore inferred to be only slight, confirming Hypothesis 2b.

3.4. Size class structure

Significant differences in diameter distribution were found prior to treatment among treatment units within a block (Table 5). These differences were attributable, in part, to variation in the number of small trees ($D < 15$ cm; Figs. 8 and 9), but many differences remained even when small trees were excluded from the analyses (Table 5). Initial differences also shaped post-harvest distributions. Considering only trees with $D > 15$ cm, three of the six 40%D–40%A pairs and two of the six 15%D–15%A pairs were not significantly different before harvest, and none of these pairs became significantly different after treatment (Table 5). All of the 40%D–15%D pairs exhibited significantly different diameter distributions both before and after harvest treatments. Although diameter distributions of all 40%A–15%A pairs were also significantly different before harvest, treatments surprisingly caused two of six to become statistically indistinguishable after harvest. In the one block where the 100%, 75%A, and 40%A treatments were similar before treatment, the diameter distributions remained similar after treatment, supporting the expectation that the aggregated treatments would retain their initial size structure (Hypothesis 3a). Likewise, in five cases where pairs

Table 5
Tests on similarity of diameter distributions among treatment units within a block

Block	Before treatment, size classes ≥ 5 cm						Before treatment, size classes ≥ 15 cm						After treatment, size classes ≥ 15 cm					
	100%	75A%	40%D	40%A	15%D	15%A	100%	75%A	40%D	40%A	15%D	15%A	100%	75%A	40%D	40%A	15%D	15%A
Watson Falls	–	–	–	–	–	–	ab	–	a	b	–	a	abc	a	bd	c	–	d
Dog Prairie	a	a	–	–	–	–	a	a	b	ac	b	c	a	a	bc	a	b	c
Butte	–	–	a	a	b	b	a	–	b	ab	c	c	a	–	b	ab	c	c
Little White Salmon	a	–	ab	a	–	b	ab	–	ab	a	–	b	a	a	a	a	–	a
Paradise Hills	–	–	–	–	–	–	–	a	a	–	b	b	–	a	–	ab	c	bc
Capitol Forest	–	a	–	a	–	–	–	a	b	ab	–	–	a	b	ab	bc	c	–

Diameter distributions were characterized by tree density in 5-cm classes. Treatment labels refer to the percentage basal area retention followed by D for dispersed or A for aggregated treatments. Treatments with a common letter are not significantly different ($\alpha = 0.01$; Kolmogorov–Smirnov tests) and those designated by a dash (–) are significantly different from all others.

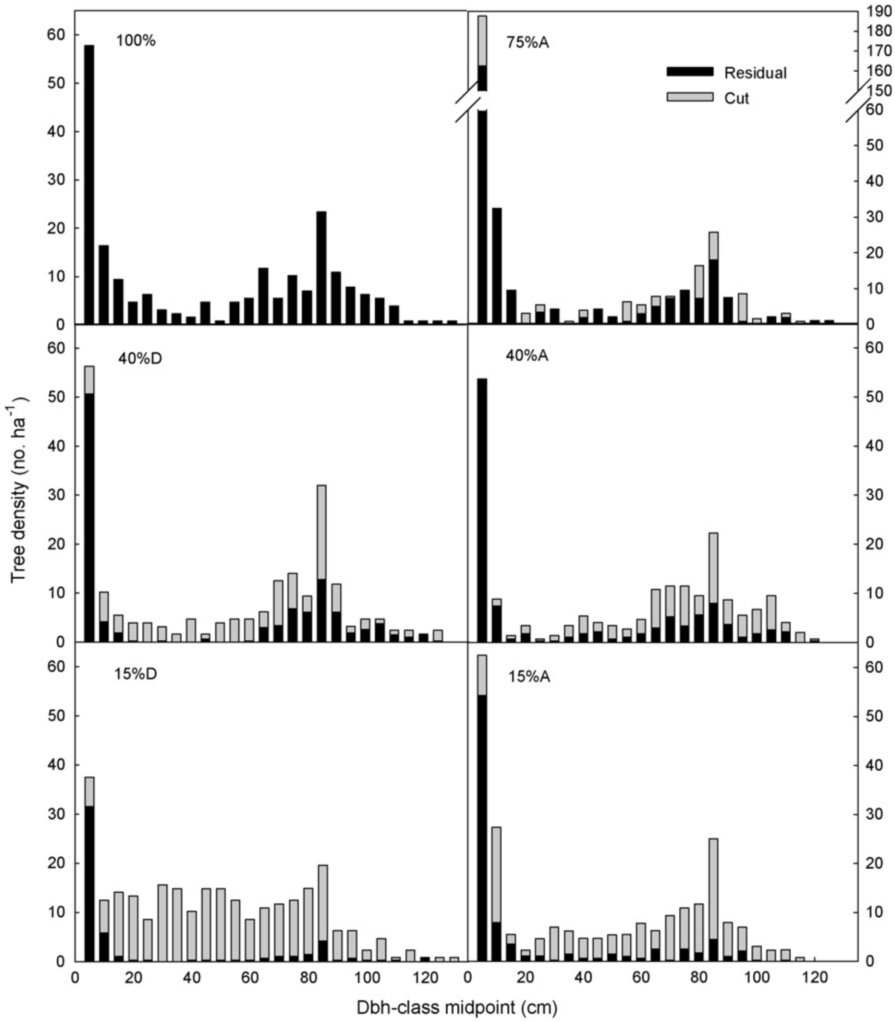

Fig. 8. Tree diameter distributions showing residual and cut trees in each treatment unit at Little White Salmon. Diameter classes are labeled by midpoint, with the exception that diameter class "5" corresponds to the interval 5–7.5 cm.

from the aggregated-control set (100%, 75%A, 40%A, and 15%A) were not significantly different, four remained indistinguishable after treatment. Conversely, six pairs that were significantly different before harvest were not after harvest. Looking below the 15-cm diameter class, a sufficient number of small trees remained to produce a substantial second mode in the smallest diameter classes of the distributions, despite removal of most suppressed, intermediate, and some codominant trees in the main canopy of dispersed treatments (e.g., Figs. 8 and 9).

Principal components analysis of diameter-class data underscored the large block-to-block variation relative to within-block variation, consistent with the ANOVAs and K–S tests (Fig. 10). The first principal component accounted for 35% of the variance and, as indicated by eigenvector loadings, was associated with the relative density of trees in the 5–45 and 65–115 cm diameter classes. The second principal component accounted for 20% of the variance and was associated with the density of trees in the 45–65 cm classes. Prior to harvest, treatment units within blocks formed fairly distinct groups along gradients in stand structure represented by the first two principal components (Fig. 10a). Likewise, after treatment, the control treatments maintained maximal multivariate distances, but 75, 40, and 15% retention treatments moved to successively more similar stand structures among blocks (Fig. 10b).

3.5. Crown-area profile

Random allocation of treatments to experimental units produced the expected result of no initial differences in crown-area-profile indices among treatments (Table 6). One exception was plot-to-plot variability in crown area (H_{plot}, J_{plot}). Multiple comparison tests revealed that aggregated treatments (15%A and 40%A) had significantly greater horizontal canopy evenness (J_{plot}) than all other treatments, and that 40%A had significantly greater diversity (H_{plot}).

Vertical complexity of the canopy was clearly changed by retention harvests (Table 6). The standard deviation of crown area among heights both within ($\mathrm{S.D.}_{\mathrm{sp}}$) and across species ($\mathrm{S.D.}_{\mathrm{CA}}$) was significantly reduced by all treatments relative to the control ($P < 0.0001$ for Friedman test). This reduced

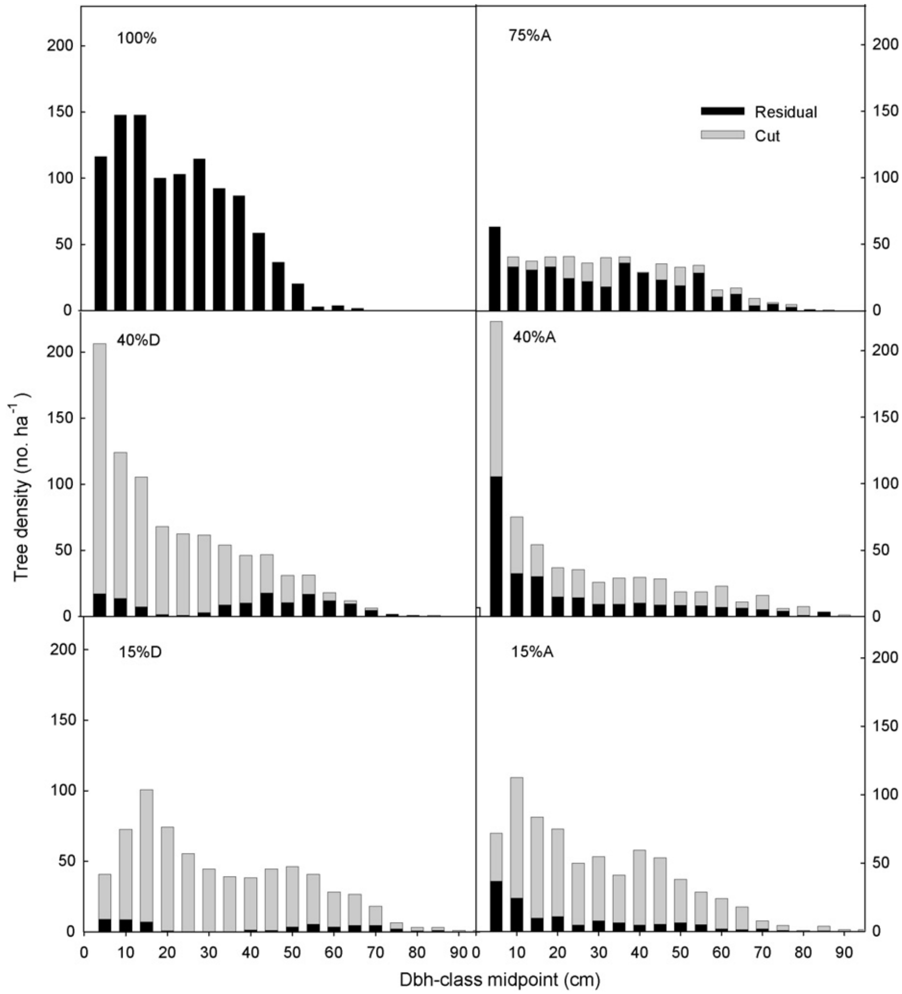

Fig. 9. Tree diameter distributions showing residual and cut trees in each treatment unit at Paradise Hills. See Fig. 8 for other details.

variation was a direct result of the reduction in stand density and a large decline in total crown area at its peak in the middle of the canopy, moving the composite crown-area profile to greater uniformity among heights as retention level declined (Table 6 and Fig. 11). Because canopy depth, or the number of height intervals over which crown area was distributed, was not affected by treatment (Table 4), uniformity ($S.D._{CA}$) over that interval was greater, contrary to Hypothesis 3b.

The weak and somewhat random initial treatment differences in plot-to-plot variation of crown-area profile (H_{plot}, J_{plot}; Table 6) underscore the importance of assessing change in these indices to interpret treatment effects. Consistent with Hypotheses 4a and 4b, dispersed treatments (40%D, 15%D) significantly reduced plot-to-plot variability relative to controls (100%), and aggregated treatments (75%A, 15%A, and to a lesser extent 40%A) significantly increased horizontal variability relative to the control ($P < 0.0001$ for Friedman test on $S.D._{plot}$; Table 6). Consistency between change in H_{plot} and change in J_{plot} (Table 6) indicates that the increase in heterogeneity in aggregated treatments can largely be attributed to greater differences in cover at a given canopy level between cut and uncut portions of the treatment units.

4. Discussion

4.1. Treatment evaluation and structural variation

The experimental treatments imposed in this study achieved the desired range in level and pattern of retention. Apparent discrepancies between residual and target basal areas were inevitable for several reasons. First, residual basal area of each unit was estimated from plot data, rather than by measuring all trees; hence, sampling error prevented knowledge of the exact magnitude of discrepancies from the target basal area. Second, for practical reasons pre- and post-harvest measurement protocols varied slightly with respect to plot size (for small trees) and measurement precision (1 cm before harvest, 0.1 cm after harvest). Third, up to 4 years of growth and mortality had accrued between pre- and post-harvest measurements. Lastly, harvesting operations can inadvertently miss trees marked for removal and damage trees targeted for retention. The combined magnitude of the first three effects was indicated by the basal area of the control expressed as a percentage of target basal area (Fig. 6a).

The unimportance of achieving the exact target basal areas can also be given further perspective by realizing that the

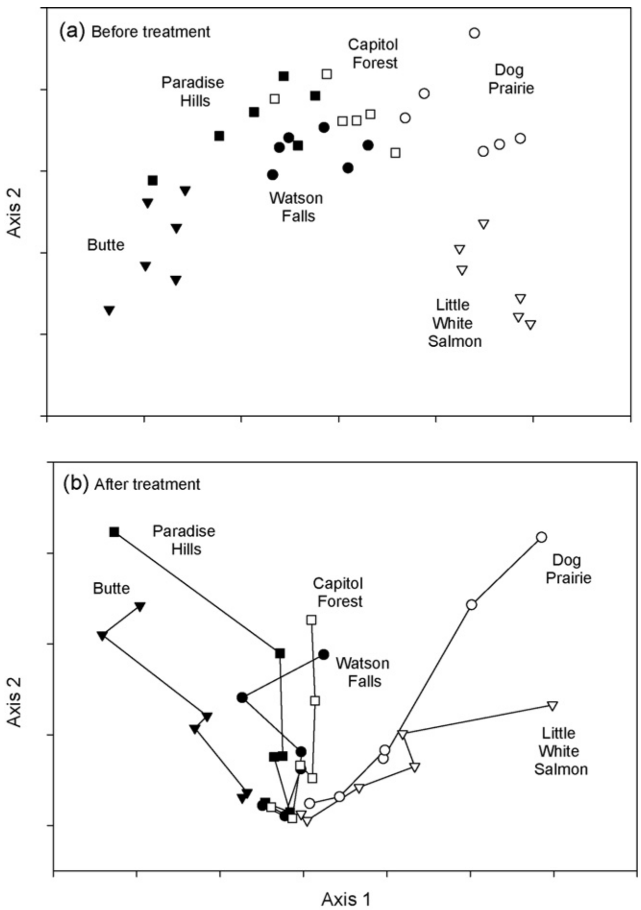

Fig. 10. Location of DEMO treatment units along stand structural gradients represented by the first two principal components of diameter distributions: (a) before treatment, and (b) after treatment. Diameter distributions were summarized as the number of trees per hectare in successive 5-cm diameter classes. Symbols closest to block labels in (b) are the control treatments, with lines connecting successive treatments in the following order: 100%, 75%A, 40%D, 40%A, 15%D, and 15%A.

initial basal areas of treatment units, and of aggregates within treatment units, were not known exactly because they also were estimated by plot sampling. Sampling units within treatment units were necessary because the 13-ha DEMO units were much larger than conventional research plots (usually <0.5 ha) to ensure operational and ecological relevance. Residual basal areas that come very close to the target basal areas can be achieved even in large treatment units, if sufficient resources are allocated to measuring initial conditions, marking trees, supervising timber harvesting, and eliminating losses to logging damage. In DEMO, however, a tradeoff was made between cost and accuracy of implementing the variable-retention harvests, as would be the case when implementing any other silvicultural prescription. The primary objective was to achieve four distinct levels of basal area retention, realizing that the effects of modest deviation in residual basal area from targets can be addressed more effectively with covariates during analysis than by attempting to eliminate it entirely in the field.

Substantial variation in other, non-target aspects of initial and residual stand structure was apparent among experimental units receiving the same treatment. A significant amount of variation in ecological responses to the nominal level or pattern of retention may therefore be accounted for by these attributes of stand structure. Some variation may have been an inevitable consequence of treatment implementation, but more often it reflected variation that was not explicitly controlled for in the experiment. Characterizing both target and non-target structural changes imposed by harvest treatments can help distinguish direct from indirect responses of the non-tree taxa and other ecosystem components, as well as account for differing human perception of visual quality. Several approaches can therefore be used to test treatment effects in this type of experiment. The first and most obvious approach is a randomized block ANOVA, which considers treatments as categorical. In this approach a treatment effect can be partitioned into separate effects of retention level and pattern. Additional variation due to deviation from nominal or target levels of retention would typically be ignored unless a covariate was added to the model. The ANOVA approach was adopted for initial analyses of biological responses to DEMO treatments to provide inferences on the level of experimental (and operational) units (e.g., Halpern et al., 2005; Schowalter et al., 2005; Maguire et al., 2005, 2006). In this approach, variation in initial and residual structure of treatment units within a block was ignored, but, block effects accounted for structural variability among blocks.

An alternative or complementary approach would augment or replace nominal or categorical treatments with measured post-harvest retention level (the target stand structural attribute) as a single continuous variable. If responses are proportional to level of retention, then treating the latter as continuous should improve the power of statistical models (i.e., lower error sum of squares and greater error degrees of freedom). Other covariates such as canopy cover and indices of vertical complexity, in the context of regression analysis, may help to explain the variation in response at a given retention level. Our structural analysis of diameter distributions and canopy area profiles revealed the degree to which replicates receiving the same nominal treatment displayed different pre- and post-harvest structures. Furthermore, different treatments imposed on units with different initial stand structures sometimes resulted in greater similarity in residual structure. For example, diameter distributions of some treatment units were significantly dissimilar before treatment but became similar after treatment, despite the expectation that harvests would cause the distributions to diverge. The response of some ecosystem components to level of basal area retention may also depend on the resulting size-class distribution, so identification of this interaction between target and non-target structural attributes becomes critical to understanding and minimizing impacts to biodiversity from future treatments. Indices of non-target structural attributes such as crown-area profile have emerged as significant predictors of some DEMO responses (for example, canopy arthropods and birds), even when treatment effects were undetectable by ANOVA (Maguire et al., 2005).

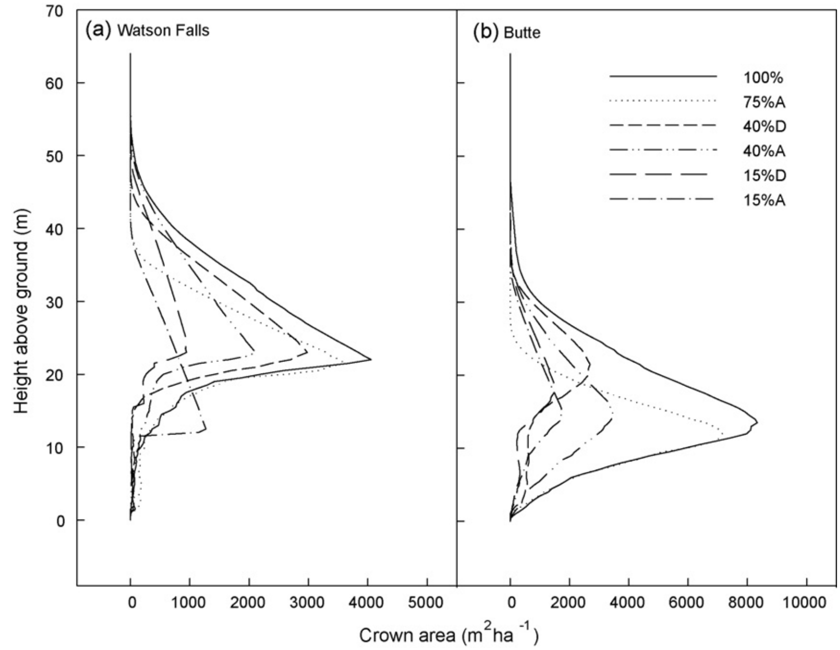

Fig. 11. Post-treatment crown-area profiles by treatment at Watson Falls and Paradise Hills.

Table 6
Tests of treatment effects on indices of canopy area profile complexity, including initial indices, post-harvest indices, and change in indices (post- minus pre-harvest; Friedman's tests)

Stand attribute	Pre-harvest	Post-harvest	Change
Crown-area profile summed across all species			
SD_{CA}	n.s.*	100 75A 40A 40D 15A 15D	100 75A 40D 40A 15D 15A
H_{CA}	n.s.	n.s.	15A 40A 15D 75A 100 40D
J_{CA}	n.s.	15A 15D 75A 40A 100 40D	15A 15D 75A 40A 100 40D
Crown-area profile for individual species			
SD_{sp}	n.s.	100 75A 40D 40A 15A 15D	100 75A 40D 40A 15D 15A
H_{sp}	n.s.	n.s.	n.s.
J_{sp}	ns	15A 15D 75A 40A 100 40D	15D 15A 40A 75A 100 40D
Crown-area profile for individual plots (summed across all species)			
SD_{plot}	n.s.	15A 75A 40A 100 40D 15D	15A 75A 40A 100 40D 15D
H_{plot}	40A 15D 15A 100 40D 75A	40D 15D 100 40A 75A 15A	40D 100 15D 40A 75A 15A
J_{plot}	40A 15A 100 75A 15D 40D	100 40D 15D 40A 75A 15A	40D 100 15D 40A 75A 15A

Treatments are ordered from highest to lowest by rank sum; lines connect treatment units that are not significantly different ($\alpha = 0.05$). Treatment labels refer to percentage basal area retention followed by D for dispersed and A for aggregated treatments. See Table 4 for detail on indices. (*) Overall treatment effect in ANOVA not statistically significant at $\alpha = 0.05$.

Residual stand structure, however, may not be the only or primary driver of ecosystem response. Some taxa may respond to the proportion of basal area removed if removal is closely correlated with the proportion of habitat disturbed or the proportional change in microclimate (Heithecker and Halpern, 2006). However, absolute amount of residual basal area may drive other responses, for example, those dependent on the amount of foraging substrate or the visual appeal of the remaining stand. Because the structural features to which different species respond will vary, incorporating both target and non-target structural indices into future analyses may ensure a more complete understanding of biological responses. A better appreciation of these functional links is essential for designing silvicultural treatments that balance timber harvest and tree regeneration with maintenance of biological diversity.

4.2. Changes in average attributes of stands

The stand attributes examined in this paper provide a comprehensive view of forest structure that will help to explain responses to variable-retention harvests (e.g., Maguire et al., 2005). One important structural difference was the significantly greater canopy cover in dispersed treatments than in aggregated treatments—as much as a two-fold difference (Fig. 7). Under the initially closed conditions found in all the treatment units, crowns of various canopy layers commonly overlap, so that as smaller trees are removed basal area declines more rapidly than canopy cover. The regular spacing of residual trees in dispersed treatments (40%D and 15%D) precluded any crown overlap, so the reduction in canopy cover was much less than the reduction in basal area. In contrast, canopy cover of aggregated treatments was very close to the basal area retention level. Higher canopy cover in the dispersed treatments (particularly at 40% retention) may play an important role in ameliorating microclimatic stress in harvested areas, particularly in comparison to harvested areas with no residual cover in the aggregated treatments (Heithecker and Halpern, 2006). This moderating influence offers potential benefits for shade-dependent understory plants (Halpern et al., 2005) and other organisms associated with cooler and moister environmental conditions at the forest floor.

4.3. Changes in species composition

The only dramatic effect of the treatments on species composition was a reduction in the dominance of Douglas-fir. Although species richness was not affected at the scale of treatment units, greater proportional removal of Douglas-fir basal area tended to enhance evenness (J) and, hence, diversity (H) of the overstory in dispersed retention harvests. This result may have broad ecological significance because changes in diversity of the canopy layer could conceivably affect the diversity of associated species (Huston, 1994; Palik and Engstrom, 1999). Although this study was not designed to test the ecological effects of manipulating tree species diversity, opportunities may exist for exploring its potential effects where the relative abundance of species was changed by treatments.

4.4. Changes in stand structure

Initial diameter distributions were extremely variable within each block, underscoring the need to interpret responses to nominal treatment levels in light of both residual structure and the portions of the initial distribution that were removed. Under certain circumstances, different levels of removal from diameter distributions that are very different initially could produce relatively similar stand structures. Consequently, if particular taxa respond to residual structure rather than proportional removal of initial structure, treatment differences could be negated or reduced. Furthermore, if a given species responds to the presence or density of a single stand component, then considerable variation in stand structure could be imposed with little corresponding response provided this component remains unchanged (e.g., Artman, 2003).

Differences in post-harvest crown-area profiles largely paralleled variation in diameter distributions; however, some differences between crown-area profiles and diameter distribution were inevitable due to variation in the allometric relationship between tree diameter and crown width, not only among species but also within species growing in stands of varying density. For the same reason, differential removal of species can lead to differing crown-area profiles under an equivalent level of retention. The vertical complexity of aggregated retention units was expected to remain unchanged by treatment, under the assumption that stand structure was uniform across the entire unit; however, rejection of this hypothesis underscored the spatial variability in initial structure of treatment units. Even the three 1-ha cut patches in 75%A caused a reduction in vertical complexity, suggesting that local stand structures were sufficiently different that they contributed significantly to the composite crown-area profile.

Crown-area profiles provided an expedient method for characterizing the gross canopy structure of a stand, and provided information relevant to habitat suitability, particularly for canopy-dwelling species. Forests with greater vertical complexity tend to support a wider range of niches and, consequently, greater species richness (Brokaw and Lent, 1999). One additional advantage of crown-area profiles is the opportunity to assess stand porosity, or the amount of open space between crowns that could be an important component of wildlife habitat (Dubrasich et al., 1997).

4.5. Horizontal variability

Aggregated treatments produced significantly greater plot-to-plot variability in basal area and crown-area profile than did the control or dispersed treatments. Although this result was virtually guaranteed by treatment specifications, the relative differences among treatments were more difficult to predict. Treatment effects on horizontal variability – measured by both post-harvest condition and change from initial condition – were influenced by three factors: pattern of retention, level of retention, and degree of spatial variability in initial stand structure. The reduction in vertical complexity imposed by aggregated retention (as discussed above) was achieved under a very significant increase in horizontal variation.

Profiles within the 1-ha aggregates were similar to those found over the entire treatment unit prior to harvest, and provided a very different environment and appearance from profiles of dispersed treatments. The most significant feature of the aggregates within 40%A and 15%A, however, is likely their potential function as an undisturbed refuge, regardless of how representative of the original stand structure each aggregate was. Although the ecological effects of size, shape, and degree of isolation of residual patches cannot be addressed in this study, previous work on forest fragments at coarser spatial scales suggests that these effects may be significant (e.g., Forman et al., 1976; Berglund and Jonsson, 2001). Past research on species diversity in forest remnants was inspired by island biogeographic theory and landscape ecology (MacArthur and Wilson, 1967; Burgess and Sharpe, 1981; Forman and Godron, 1986), but some theoretical and empirical research has been extended to spatial scales as small as individual trees (e.g., Southwood and Kennedy, 1983; Fenton and Frego, 2005). The efficacy of aggregates for maintaining late-successional species should increase along the gradient from isolated, individual trees to larger intact aggregates consisting of many hectares. The 1-ha aggregates in the DEMO study tested the effect of variable retention at a spatial scale relevant to the size of typical regeneration units in the Pacific Northwest. These aggregates serve as refugia for many plants on the forest floor in the short-term but may be susceptible to edge effects over longer periods (Nelson and Halpern, 2005a,b).

Other studies have addressed the spatial variability produced by intermediate harvests, as opposed to the regeneration harvests that are the focus of variable retention. For example, variable density thinning (VDT) has been advocated for creating a mosaic of overstory densities, understory vegetation, and species diversity in stands with initially uniform tree density (Wilson and Carey, 2000; Thysell and Carey, 2001). Although variable-density thinning and variable-retention harvests differ in their silvicultural objectives and contexts, the net effect on habitat variability may be similar. One fundamental difference is that variable-density thinning imposes gradients in residual stand density within the target stand, whereas variable-retention harvests as applied in DEMO either homogenize stand density (dispersed treatments) or create two strongly contrasting conditions (cut versus no cut in aggregated treatments). The spatial scale at which variability in overstory and understory structure is achieved remains an important consideration because that scale will influence both abiotic and biotic responses.

4.6. Silvicultural implications

Detailed characterization of stand structure within these variable-retention treatments facilitates comparisons with other studies. Previous studies have tended to examine a relatively narrow range of treatments, often retrospectively (e.g., Franzreb, 1978; Summerville and Crist, 2002), an approach that does offer the advantageous of relatively immediate inferences. Initial conditions and treatment history are typically coarse or unavailable in retrospective studies, but current stand structure can be characterized in detail. Stand structure therefore becomes the link among observational, retrospective, and experimental studies. Responses to a wide range of harvest treatments have been evaluated, including regeneration harvests under clearcut (Heliölä et al., 2001), shelterwood (Beese and Bryant, 1999), seed tree (Sippola and Renvall, 1999), or selection systems (Lewis, 2001); intermediate treatments such as thinning (Hagar et al., 1996; Siitonen et al., 2000; Sullivan et al., 2001); and modified regeneration cuts such as ‘‘green-tree’’ or variable-retention harvests (Beese and Bryant, 1999; Hazell and Gustafsson, 1999; Tittler and Hannon, 2000; Tittler et al., 2001). Residual stand density and harvest intensity vary widely in these studies, but a synthesis or meta-analysis of results should be possible if sufficient descriptions of residual stand structure and change from initial structure are provided (e.g., Monserud, 2002).

Silvicultural systems have often been viewed (and sometimes practiced) as a set of rigid treatment regimes with little capacity for modification. However, a rich variety of silvicultural systems has been applied worldwide, underscoring the fact that any classification of silvicultural systems belies the mix and variety of systems that have been explored (Troup, 1928; Matthews, 1991). In practice, silvicultural treatments and systems are inherently dynamic and can evolve in response to changing objectives. The treatments applied in DEMO feature some basic elements of variable-retention ‘‘systems’’ that are yet to be fully articulated (Franklin et al., 1997; Lindenmayer and Franklin, 2002). The design of systems based on the variable-retention concept will continue to evolve as results accumulate from experiments like DEMO. The character of the systems that eventually emerge will almost certainly vary with differences in objectives and local conditions: many decisions remain after setting a target retention level, including size, crown class, and species of leave trees, as well as the spatial arrangement of aggregates, cut patches, and dispersed trees. Auxiliary management activities only weakly associated with the retention treatment (e.g., specific slash disposal methods) must also be considered in the design of variable-retention systems because they may impose undesirable effects on some components of biodiversity and are therefore key to designing mitigation measures. Finally, density management of the regenerating cohort will play an important role in long-term responses to variable-retention treatments because regeneration will exert strong influences on ground vegetation and forest-floor conditions (Alaback, 1982; Bailey et al., 1998; Sullivan et al., 2001). The initial effects of harvest-related disturbance will gradually diminish as stands age and the understory cohort gains prominence.

The DEMO study was designed to yield information on long-term responses of forest ecosystems to varying levels and patterns of residual trees. Different species and processes will display different types and rates of response, yet forest policy will continue to evolve well before experiments like DEMO come to full fruition. Although the more profound and persistent effects of these treatments will not become apparent for many years, the short-term changes in overstory structure and the coincident responses of forest taxa are intended to provide the type of timely and quantitative information that is too often neglected in ecological research (Pitelka, 1994).

5. Conclusions

Ecologically significant differences in residual stand structure resulted from variable-retention harvesting, even among units in which a similar percentage of initial basal area was retained. Tests on the nine hypotheses suggested that:

Hypothesis 1a. Retained basal area, expressed as a percentage of the control unit in that block or as a percentage of initial basal area in each unit, departed only slightly from targets specified by nominal treatment levels.

Hypothesis 1b. Residual tree density and stand density index were directly proportional to intended retention levels, but canopy cover in dispersed treatments was proportionately higher due to regular spatial distribution of residual trees with no crown overlap.

Hypothesis 1c. Quadratic mean diameter in 40%D increased significantly because the largest and most wind-firm trees were retained.

Hypothesis 2a. Overstory tree species richness was not changed significantly by the variable-retention treatments, although a slight decline in dominance by Douglas-fir resulted.

Hypothesis 2a. Percentage similarity of pre- versus post-harvest overstory species composition differed little among treatments.

Hypothesis 3a. Diameter distributions were generally not truncated in dispersed treatments because many submerchantable trees were left; however, dispersed retention imposed a significant change on the initial diameter distribution and aggregated treatments did not.

Hypothesis 3b. Dispersed treatments homogenized vertical canopy structure by distributing crown cover more evenly among canopy layers.

Hypothesis 4a. Plot-to-plot variability in vertical structure declined in dispersed treatments.

Hypothesis 4b. Plot-to-plot variability in vertical structure increased in aggregated treatments.

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