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Density management and biodiversity in young Douglas-fir forests: Challenges of managing across scales

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Abstract

Concerns about the dominance of dense, young plantations in the Pacific Northwest have spurred interest in the effects of density management on various aspects of biodiversity. We review results from numerous large-scale management experiments (LSMEs) in terms of the early vegetation responses to thinning. In particular, we focus on the contributions of variable treatments, such as gap creation, unthinned patches and variable density thinning to within-stand variability. Density management resulted in changes in overstory and understory vegetation, but results were similar and independent of thinning intensity. Even light thinning operations initially reduced understory vegetation likely due to harvesting damage. The vegetation recovered quickly, but thinning resulted in a compositional shift towards invading, early seral species. Spatially variable treatments provide for variable canopy structure and understory vegetation and results from the LSMEs suggest incorporating these into thinning prescriptions may be beneficial where biodiversity is of concern. The need for spatially variable treatments is highlighted by the hierarchical habitat-selection framework of various wildlife species. This framework provides a basis for matching spatial variability in forest structure and vegetation to the spatial scales that wildlife species perceive and respond to. Silvicultural prescriptions that increase within-stand variability can provide important habitat features across multiple scales and enhance habitat quality beyond that provided by stand-level prescriptions.

Keywords: Thinning; Shrubs; Herbaceous cover; Habitat selection scales; Variable density treatments

1. Introduction

In recent years, forest management on public lands in the Pacific Northwest (PNW) has focused on issues surrounding biodiversity, especially on millions of hectares of young, even-aged stands in western Oregon and Washington that resulted from past clearcutting. Increasing recognition that historical stand development was considerably different from development of current plantations (Tappeiner et al., 1997) has raised concerns of possible extinctions of plant and wildlife species due to habitat loss. More immediate concerns include poor quality of wildlife habitat due to uniformly high overstory canopy closure and sparse understory vegetation in these young stands (McComb et al., 1993). To address these concerns, foresters have focused on understanding how these young stands can be managed to provide ecosystem functions and processes necessary to maintain regional biodiversity (Carey and Curtis, 1996; Hayes and Hagar, 2002).

Increasing vertical and horizontal structural heterogeneity within stands is of special concern in young stand management on public land in the PNW. This heterogeneity is important for diversity of wildlife habitat (MacArthur and MacArthur, 1961; McGarigal and McComb, 1995) and impacts other ecological functions and processes (Pickett and White, 1985; Holling, 1992). The PNW has diverse ecological regions, but attention has been focused on the mesic, low-elevation western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) zones, and the colder, mid-elevation true fir zones (*Abies* spp.) (Franklin and Dyrness, 1988). Little explicit information exists on the influences or requirements of structural features on habitat for most wildlife species. Historical (i.e., pre-European settlement) patterns of stand development therefore are used as a reference for the structures and stand complexity that likely will provide similar functions in managed forests (Hansen et al., 1991).

Natural disturbances historically were influential at several spatial scales, resulting in high within-stand heterogeneity in natural stands (Miles and Swanson, 1986; Spies et al., 1990; Tappeiner et al., 1997). Forests in the Oregon Coast Range historically regenerated over multiple decades (Tappeiner et al., 1997), with a prolonged open shrub, herb, and sapling stage in

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Table 1
Summary of large-scale management experiments and retrospective studies

Study	Age at treatment (years)	Response[a] (years)	Reps	Density management treatments[b] (harvest intensity)	Spatial variability*	Reference
Designed experiments						
STUDS	30–33	1	3	C; light; moderate; heavy	Underplanted	Chan et al. (2006)
YSTDS	33–43	5–7	4	C; light; light w/gaps*; heavy	20% stand in 0.2 ha gaps	Hagar et al. (2004)
Suzuki	35–45	1–2	4	C; light; moderate	None	Suzuki and Hayes (2003)
UAMP	35–47	3	4	C; light w/gaps*; light; heavy	10% in 0.2 ha gaps planted w/regen; light and heavy trts underplanted	Tucker et al. (2001)
DMS	40–70	5	7	C; light; moderate*; variable*[c]	10% gaps and unthinned in 0.1, 0.2, 0.4 ha sizes	Cissel et al. (2006)
CFIRP	45–144	2	3	C; gaps*; heavy	33% in 0.2 or 0.6 ha gaps	Maguire and Chambers (2005)
DEMO	65–170	1–2	8	C; 75% retention with gaps*; 40% retention dispersed or grouped*; 15% retention dispersed or grouped*	1 ha gap and group retention areas	Aubry et al. (1999)
Retrospective studies						
Suzuki	52–100[d]	7–24	8	C; variable[e]	None	Suzuki and Hayes (2003)
Bailey	50–120[d]	10–24	32	C; variable[e]	None	Bailey et al. (1998)

Treatments were uniformly applied unless noted with an*.

[a] Years post-treatment of vegetation surveys used in Figs. 2–6.

[b] Unthinned controls noted as "C"; treatments ordered with decreasing residual basal area for referencing Figs. 2–6.

[c] Included residual densities of 100, 200 and 300 trees per ha, plus gap creation and unthinned areas.

[d] Age at time of sampling.

[e] Retrospective studies paired unthinned with nearby commercially thinned stands.

which spatial variability in tree regeneration likely was pronounced (Tappeiner et al., 1997; Franklin et al., 2002). A prolonged period of closed canopied forest followed the regeneration phase. Without major natural disturbances or human interference, the stem exclusion or closed-canopy phase is fairly stable and can last for several decades (Oliver and Larson, 1996; Franklin et al., 2002). During this phase, small-scale disturbances due to insects, disease, or wind damage were likely frequent, creating small canopy gaps that allowed surrounding trees to expand their crowns, promoting crown size differentiation (Spies et al., 1990; Oliver and Larson, 1996). Further, infrequent windstorms, landslides, and fires could disturb large patches (>1000 m^2), providing patch- and landscape-scale heterogeneity (Miles and Swanson, 1986; Morrison and Swanson, 1990; Lutz and Halpern, 2006). Creating similar patterns of structural diversity in young stands may require treatments different from those used for timber production. For example, rather than thinning to uniform spacing throughout the stand, managing for biodiversity necessarily includes activities on several disturbance and spatial scales, which may include variable density thinning, creating gaps and unthinned patches of different sizes, and creating two-storied stands through natural regeneration or underplanting (Carey et al., 1999; Hayes and Hagar, 2002; Puettmann et al., 2004).

To address the question of whether density management practices for timber production are sufficient to promote biodiversity or whether alternative practices are required, large-scale management experiments (LSMEs) (Monserud, 2002) were initiated in young stands (30–60 years old) dominated by Douglas-fir in western Oregon and Washington (see Table 1 for a subset covered in this paper). LSMEs test short- and long-term responses to operationally applied treatments, are designed to address multiple objectives and measure a wide variety of responses. Treatments varied but were aligned along a density gradient. LSMEs typically have large treatment blocks (13–60 ha) to provide an opportunity to investigate not only average treatment responses, but also within-stand variability. Within-stand spatial heterogeneity was enhanced in selected treatments through creation of different-sized gaps, unthinned patches, or both (Table 1).

This review focuses on the impacts of density management on various vegetation components in young stands, including the overstory canopy and understory shrubs and herbs. Of special interest is the question whether uniform management at the stand scale is still suitable when biodiversity aspects are a main concern. The variability within treatments and studies in the LSMEs provides an indication of the potential for density management to enhance within-stand complexity, i.e., at smaller-than-stand scales. Alternatively, the consistency of responses across studies provides information about the potential to apply these treatments successfully across the landscape, i.e., at larger-than-stand scales.

Diversity of wildlife habitat is an important aspect of biodiversity. It is of special interest to federal and state forest management in the PNW and was therefore emphasized in many LSMEs. The importance of spatial scale in managing for wildlife habitat is well established (Johnson, 1980; Wiens et al., 1987) and we discuss this to illustrate the challenges of managing vegetation and structure across spatial scales and the associated impacts on biodiversity. We first discuss how spatial scales influence wildlife habitat (Johnson, 1980; Wiens, 1989; Holling, 1992). We next discuss how density management impacts canopy structure and understory vegetation at different spatial scales. Due to the recent implementation of the LSMEs our data are limited to short-term results, but our discussion includes long-term trends where they are becoming apparent.

2. Methods

2.1. Description of studies

Seven LSMEs surveyed understory vegetation and wildlife response to density management and were the basis for this paper (Monserud, 2002) (Table 1). Most studies were installed in young Douglas-fir stands. The studies covered a wide geographic area in western Oregon and Washington in the mesic, low-elevation western hemlock and Douglas-fir zones (Franklin and Dyrness, 1988). The Density Management Study (DMS) was replicated across the Oregon Cascades and Coast Range. The Demonstration of Ecosystem Management Options (DEMO) study included treatment sites from throughout western Oregon and Washington, and included mid-elevation true fir sites. The College of Forestry Integrated Research Project (CFIRP) and the Siuslaw Thinning and Underplanting for Diversity Study (STUDS) were installed in the central Oregon Coast Range. The Young Stand Thinning and Diversity Study (YSTDS) and the Uneven-Aged Management Project (UAMP) were installed in the Oregon Cascades. The STUDS, UAMP and YSTDS studies were installed in plantations, while the other studies were in naturally regenerated stands except for one replication of the DMS study. All studies had large treatment blocks (13–60 ha) that avoided the need to extrapolate small-plot results to operational scales (Monserud, 2002). The large treatment blocks also allowed incorporation of spatially variable treatments. Five studies incorporated gap creation of varying sizes and two included unthinned patches (Table 1).

2.2. Analysis

In our analysis, overstory canopy data and understory vegetation responses to the density management treatments were averaged across study replications. We address spatial variability as an indicator of scale through assessment of within-stand variability measures (standard deviation and coefficient of variation), and the specific contribution of gap creation or unthinned patches. To provide an overview, we limited our work to taxa-level responses (e.g., shrubs and herbs). Inherent site differences in understory composition among and within studies prevent a species specific analysis. Results from the LSMEs were 1–7 years post-harvest (Table 1). We generally used the latest data available and discussed the importance of differences in time since thinning in regards to their impacts on treatment responses.

3. Importance of spatial scale to wildlife habitat

The influence of overstory and understory vegetation cover and composition on wildlife populations has been well documented (MacArthur and MacArthur, 1961) and the dominance of young, even-aged Douglas-fir stands in western Oregon and Washington are of wide concern for wildlife and other biodiversity aspects (McComb et al., 1993; Hayes et al., 1997; Hayes and Hagar, 2002). Stand density management can elicit strong wildlife responses, but responses of specific species or populations are highly variable (Hansen et al., 1995; Carey et al., 1999). We suggest these apparently inconsistent wildlife responses may be partly due to differences between scales of treatments (usually at the stand-level) and scales at which wildlife perceive and utilize habitat. To overcome this apparent discrepancy, a hierarchical habitat selection framework is useful for assessing the effect of density management treatments and spatial heterogeneity on wildlife responses (Johnson, 1980; Holling, 1992; Bissonette, 1997). Wildlife perceive habitat at several scales, each associated with decisions about nesting sites, foraging and cover (Johnson, 1980). At the largest scale, first-order selection determines the geographic range of a species, followed by second-order selection of a home range. At smaller scales are the third-order selection of habitat use of patches within the home range, and the fourth-order is resource use within the patches. This hierarchical habitat selection is generally downward influenced, with the higher orders affecting the scale, quality and abundance of habitat selected at lower orders (Orians and Wittenberger, 1991), with notable exceptions (Wiens, 1989; Bissonette, 1997).

The specific extent of these scales for habitat selection varies considerably among wildlife species (Bissonette, 1997) (Fig. 1). For example, the home range selection of many small mammals in the PNW varies from a few square meters, an area usually even smaller than typical sampling plots in the LSMEs [e.g., a single mature conifer tree for the red tree vole (*Phenacomys longicaudus*)] to several thousand hectares, an area beyond single LSME installations [e.g., predators such as the Pacific martin (*Martes pennanti*)] (Zielinski et al., 2004). Patch selection (third-order) within the home range also varies in size, depending on the use (nest or den sites, or foraging) and species.

Wildlife respond to thinning treatments at spatial scales characteristic of the species (Fig. 1) and hierarchical habitat-scale associations (Johnson, 1980) provide a framework for assessment of individual species responses to density management treatments (Orians and Wittenberger, 1991). However, effective density management for wildlife requires that we provide the habitat features for a target species (e.g., cover, food, nest sites) using spatial arrangements that match the scales the species perceives and responds to (Bissonette, 1997; Hayes and Hagar, 2002).

The linkage between spatial scales of wildlife habitat selection and silvicultural practices employed in the LSMEs is highlighted for a few selective species in Fig. 1. Treatments in the LSMEs span a wide range of spatial scales, from a few square meters to entire stands (typical stand size on industrial forest land in western Oregon and Washington is 23 ha; Briggs and Trobaugh, 2001). At the same time, the impact of these treatments on wildlife habitat is a function of the disturbance severity, defined as damage to understory vegetation. The

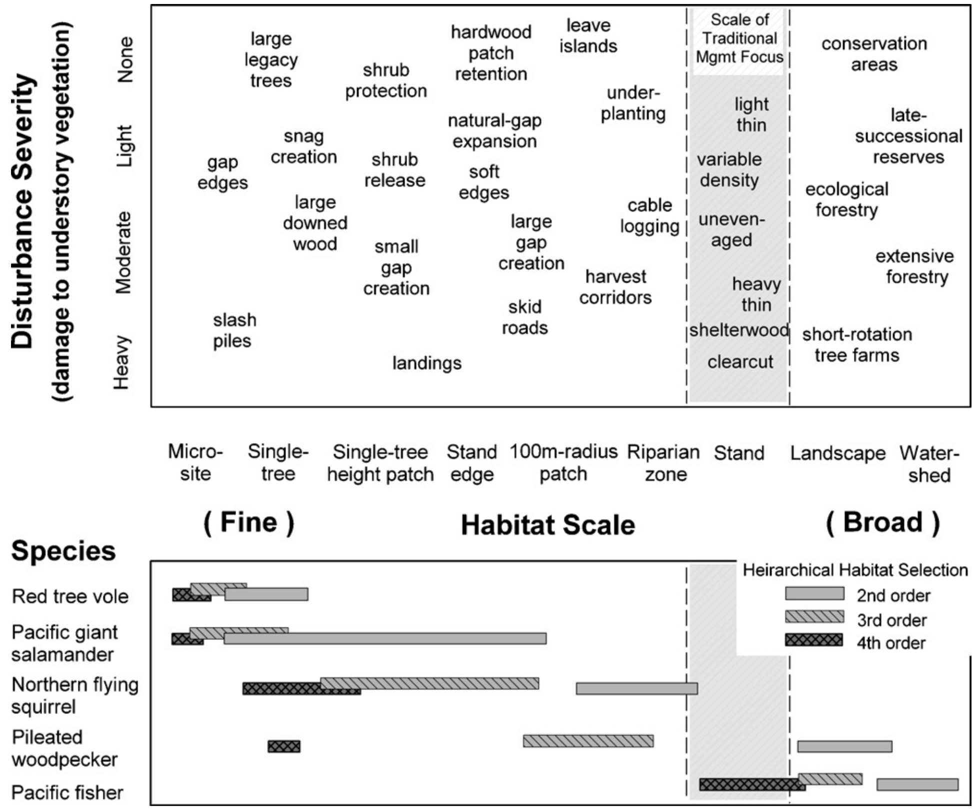

Fig. 1. Silvicultural prescriptions, harvest methods and management decisions impact stand structure and understory vegetation at different spatial scales (shown on an approximate log-scale) (top). Wildlife perceive and respond to habitat at species specific scales (bottom) that do not necessarily correspond to stand-level management. See text for explanation of hierarchical habitat selection orders.

treatments in the LSMEs provide for a continuous range of within-stand diversity, with a gradient from small-scale, high severity to large-scale, low severity impacts. Other practices, such as commercial thinning operations, result in disturbances on a range of spatial scales and severities, which vary between extraction corridors, felling areas and thinned patches (Fig. 1). The species listed in Fig. 1 highlight the scales, or combinations of scales, at which silvicultural treatments impact their habitat, and that these scales vary by species. The figure also points out that the focus of the LSMEs is at the stand or smaller than stand scales. Consequently, this paper focuses on density management at scales smaller than an individual stand. On the other hand, some wildlife species utilize multiple stands up to entire watersheds (Fig. 1) and harvest scheduling, conservation area planning, and watershed policy may impact their habitat quality (Turner et al., 2001). For discussions of these larger-scale issues the reader is directed to the extensive landscape ecology literature (e.g., Hunter, 1990; Turner et al., 2001).

4. Managing vegetation across multiple scales

In each of the following discussions, we first highlight the importance of canopy structure or understory vegetation on wildlife habitat. Next, we present short-term influences of density management treatments on these stand structural components, with a special focus on results from the LSMEs. We further present long-term responses to thinning from retrospective studies where available. For understory vegetation, we discuss the influences of density management on shrub and herb cover, species richness and composition, and the possible effects of exotic plants and interfering vegetation on diversity. Lastly, management implications are discussed with an emphasis on the importance of within-stand variability.

4.1. Canopy structure

4.1.1. Influence of canopy structure on wildlife

Increased canopy openness is the most obvious and immediate response to thinning. As an immediate structural response, canopy openness can benefit wildlife habitat through better access (Carey, 1996; North et al., 1999), higher visibility for spotting prey (North et al., 1999), and increased ground temperatures. Alternately, several mammal species in the PNW are associated with closed-canopy or shrub-dominated stands for protection cover (Hayes and Hagar, 2002). Other songbirds and small mammals appeared to favor thinned stands with gaps in the YSTDS (Hagar et al., 2004), and managing for semipermanent canopy openings is suggested to enhance habitat for many species (Carey, 1996; Carey et al., 1999). Given the high canopy variability within and among unmanaged stands (Spies, 1991), wildlife species are well adapted to a range of structures (McGarigal and McComb, 1995; Hayes and Hagar, 2002). Thus, diverse vertical canopy structures are expected to support diverse wildlife communities

(MacArthur and MacArthur, 1961; Hayes and Hagar, 2002). Because most measures of canopy openness used in wildlife studies do not explicitly consider horizontal heterogeneity (Dubrasich et al., 1997; Roth, 1976), little explicit information exists on the importance of vertical and horizontal heterogeneity for wildlife in the PNW. This leaves managers with the historical range of variability as the only reference for desired habitat characteristics of native wildlife. Creating historical patterns of canopy openings, spatial and vertical canopy structures and diversity in young stands will necessarily include management on a number of spatial scales, including gaps, unthinned patches, and variable density thinning (Tappeiner et al., 1997).

4.1.2. Density management

Young Douglas-fir stands are typically characterized by a closed canopy of the dominant overstory tree layer (Spies, 1991; Oliver and Larson, 1996). High tree-to-tree competition limits development of understory vegetation, and gaps due to mortality of smaller, less competitive trees are quickly filled by expansion of neighboring trees (Oliver and Larson, 1996; Franklin et al., 2002). Common management practices for timber production attempt to ensure the overstory canopy layer fully occupies site resources, and are designed for maximum timber value production (Marshall and Curtis, 2002). The added objective of increasing understory vegetation for wildlife habitat and other ecological functions likely will require more intensive density management in order to ensure adequate resources for understory development (McComb et al., 1993; Hayes et al., 1997).

While canopy closure is related to understory light levels (Monsi and Saeki, 1953) and therefore understory vegetation and other habitat features, treatments in the LSMEs were prescribed using trees per hectare or percentage of residual basal area (for comparison, they are listed by residual basal area). In all LSMEs, canopy closure in unthinned stands was very high (Fig. 2), with estimates often above 90%. Low-intensity thinnings, which leave residual basal areas above 30–40 $m^2\ ha^{-1}$, consistently have fairly little impact on canopy closure. Quite likely these low-intensity thinnings, reflecting typical timber production practices, mainly removed trees of suppressed or intermediate crown classes in the lower canopy layers, i.e., trees that were at least partially overtopped. In more intensive thinnings, codominant, and even dominant, trees have to be removed to achieve the required reduction in stand density. In treatments with residual basal area below 30–40 $m^2\ ha^{-1}$ canopy closure dropped off quickly with lower basal area (Fig. 2). Despite differences in stand history, initial density, and measurement methodology, a threshold pattern of canopy closure to basal area was consistent (Fig. 2). Heavier thinning than typically prescribed for timber production may be necessary to reduce canopy closure enough to alter understory light levels and associated environmental and resource conditions significantly (McComb et al., 1993; Hayes et al., 1997).

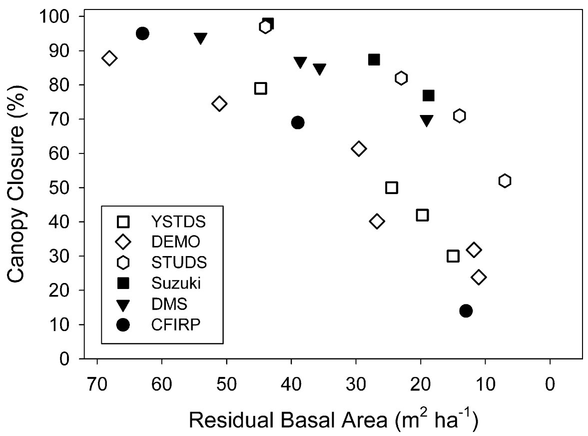

Fig. 2. Canopy closure 1–7 years following density management is strongly related to the residual basal area. Table 1 lists treatments in order of residual basal area. Canopy closure in the studies was estimated in different ways, accounting for the two apparent trends. The DMS, STUDS and Suzuki studies used wide-angle hemispherical photographs, while the others used narrow-angle densitometers.

Creation of canopy gaps is being considered as an alternative to evenly spaced thinning to improve growing conditions for regeneration (Coates and Burton, 1997; York et al., 2003) or understory vegetation (Beggs, 2005; Fahey, 2006). Gap size is also an important criterion for wildlife habitat. Gaps are characterized by a steep environmental and resource gradient from gap centers to edges and further into the forest (Canham et al., 1990; Battles et al., 2001; York et al., 2003). Canopy closure in the center of 0.4 and 0.1 ha gaps in the DMS study was 62% and 75%, respectively, due to the influence of surrounding trees (based on 0–60° fish-eye images) (Fahey, 2006).

Complex vertical canopy structures are of interest when managing for biodiversity because they have been associated with increased songbird diversity and use (Carey, 1996). Foliage height diversity (FHD) (MacArthur and MacArthur, 1961), or similar diversity measures of vertical foliage display, are low in young Douglas-fir stands with typically short, compacted crowns and a sparse or absent mid-canopy layer (Dubrasich et al., 1997; Beggs, 2005). Canopy structures are not very dynamic and different intensities of low thinning did not increase FHD in young Douglas-fir stands over the short-term in the YSTDS study (Beggs, 2005). On the other hand, spatial variability in canopy closure was more affected by density management. Canopy closure in unthinned stands at the YSTDS varied around 14% (expressed as coefficient of variation of canopy closure estimated in 0.1 ha plots), whereas adding gaps within evenly spaced thinning treatments increased the variability to 79% (Beggs, 2005). Heavy evenly spaced thinning also increased within-stand variability in canopy closure (to 53%), but the ecological implications are quite different as heavy thinning does not provide for strong edge contrasts or large openings. These contrasts are important as early results of gap studies suggest that the influence of gaps on light levels, vegetation, and other attributes is more restricted to the gap area than previously hypothesized (Coates, 2000; Beggs, 2005; Fahey, 2006). The impact of gaps needs to be referenced in the context of the surrounding stand, however. For example, the same gap size has a different ecological effect in stands where the surrounding stand has been thinned (Beggs,

2005) than in stands with no treatment outside the gaps, such as the CFIRP study (Ketchum, 1995).

Even heavy thinning only produces a transient response in canopy closure. Douglas-fir in particular has rapid crown expansion following thinning, with canopy closure quickly increasing towards full canopy closure (Oliver and Larson, 1996; Bailey et al., 1998). Canopy closure following thinning has been documented at 2–3% per year, with very high within-site variability that masked any possible density effects (Beggs, 2005; Chan et al., 2006). Canopy expansion was delayed by three years in the STUDS study (Chan et al., 2006) and may be common in dense stands. On the other hand, previous thinning perhaps can increase the capacity of trees to expand their crowns after subsequent thinning. Canopy closure rates in Douglas-fir stands that were thinned previously were about twice as high as those in the studies described above, with very rapid expansion immediately after thinning (Newton and Cole, 2003).

Windstorms and disease that kill trees are common in young stands (Lutz and Halpern, 2006) and may result in natural gaps of widely varying sizes (from single trees to entire stands). Without periodic disturbances, however, thinned stands will develop towards uniform, closed-canopy conditions (Oliver and Larson, 1996). Retrospective thinning studies have shown that canopy closure recovered to >90% within 10–30 years after thinnings (Bailey et al., 1998; Suzuki and Hayes, 2003) with a timber production objective. These thinnings were likely lighter than those considered for understory vegetation release, suggesting that full canopy closure may occur later in stands managed for understory vegetation. Even widely spaced stands will reach full canopy cover. Open-grown Douglas-fir crowns can obtain 10–15 m diameters within 40–50 years (Paine and Hann, 1982), consequently managing for understory vegetation and diverse habitat features will require either multiple, or heavy thinnings. Alternatively, variable density thinnings with areas of extremely low density or gap creation may provide long-term openings. The rates of gap recession have not been directly measured in the PNW. Estimates derived from open-grown crown-width trajectories (Paine and Hann, 1982) suggest that gap creation of 25, 36 and 51 m diameters, (0.05, 0.1 or 0.2 ha, respectively) would be reduced to 15, 26, and 40 m in diameter, respectively, within 20 years.

4.1.3. *Implications for management*

Home ranges of many songbirds and small mammals in the PNW are between 2 and 5 ha. Wildlife habitat for these species often requires contrasting fine-scale habitat features in close juxtaposition within these home ranges (Hayes and Hagar, 2002). Density management that incorporates gap creation and other spatially variable treatments can increase within-stand heterogeneity in canopy structure and thus provide suitable habitat at the spatial scales the wildlife perceive and can utilize (Fig. 1). In contrast, uniform thinning will tend to create uniform canopy openings and structures that may be more suitable to wildlife species with larger home ranges (Fig. 1).

Horizontal heterogeneity in the canopy appears to be common in older, unmanaged stands, where canopy gaps vary between 25 and 2500 m^2 (Spies et al., 1990). Creating variable canopy conditions over the long-term can be achieved in many ways. Uniform thinning does not appear to be a viable, long-term option, unless very wide residual spacing is used. Gap creation and variable density thinning increases canopy openness (Fig. 2) and within stand variability. However, only gaps are likely to persist long-term, provided that tree regeneration in the gaps is slow or absent. Deciduous trees have more open, spreading crowns than conifers, but most will be overtopped by conifers eventually. Managing large deciduous tree patches to minimize overtopping by conifers will be advantageous for developing large crowns, large durable snags, and heavy seed production. Many songbird and bat species nest or roost in deciduous trees, and retention of these in thinning operations can provide vital features in otherwise suitable habitat (Hayes and Hagar, 2002).

Foliage height diversity is usually low in young, single-storied canopies. Low-thinning removes a distinct portion of the canopy layer and thus will decrease or at best, maintain FHD. Thinning operations that purposely leave a diversity of tree and crown sizes may be necessary in monoculture stands. Even then, species like Douglas-fir will close in over time and canopy layers will become more homogenous (Marshall and Curtis, 2002). Alternatively, regeneration of an under- and eventually mid-story tree layer will increase FHD. Survival and growth of regenerating conifers are strongly related to the understory light levels (Gray and Spies, 1996) and provide a good example of how creating spatial diversity in overstories may have long-term effects. Regeneration of shade-intolerant conifers is not likely in small gaps (<0.1 ha) or in the understory except in widely spaced stands (Maas-Hebner et al., 2005). Shade-tolerant species can survive in small gaps or under dense canopies, but will not grow quickly under these conditions (Taylor, 1990). Dense conifer regeneration can suppress other understory vegetation and variable density thinning or creating gaps of different sizes may help avoid this on larger scales (Alaback and Herman, 1988; Bailey and Tappeiner, 1998).

4.2. *Understory vegetation*

4.2.1. *Influence of understory vegetation on wildlife*

Young stands with high understory vegetation cover and diverse composition will benefit many wildlife species especially where this habitat is rare, such as in dense unthinned stands (Hayes and Hagar, 2002; Beggs, 2005). A positive wildlife response to thinning in young stands has been attributed to increased understory vegetation cover and diverse composition (Carey et al., 1999; Suzuki and Hayes, 2003; Hagar et al., 2004). Providing within-stand heterogeneity of understory vegetation can further increase the odds that suitable habitat will be available at the correct spatial scales for multiple species.

Understory deciduous trees and shrubs are especially important habitat, as they provide berries and seeds (Wender et al., 2004), small mammal cover (Martin and McComb, 2002), contribute to foliage height diversity, and are an

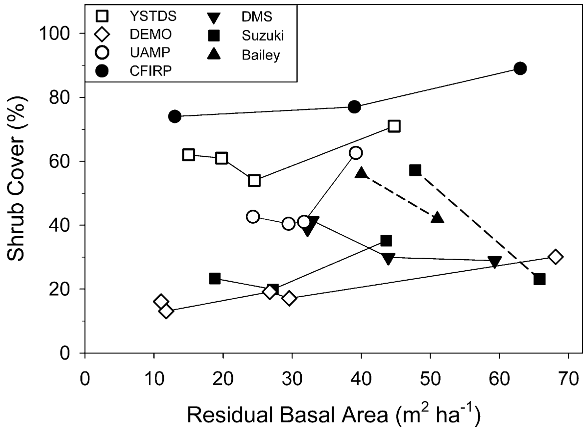

Fig. 3. Shrub cover responses 1–7 years following density management treatments (solid lines). Unthinned stands have the highest basal area in each study. See Table 1 for treatments listed in order of residual basal area. Retrospective studies (dashed lines) are averages for stands thinned 10–30 years previously, with the corresponding unthinned stands.

important substrate for lichen growth. Abundance of arthropods, an important food source for most neotropical songbirds, has been linked to the deciduous shrub component (Schowalter, 1995; Muir et al., 2002). A diverse understory composition is also beneficial, as deciduous shrubs, grasses and forbs are generally more palatable than evergreen plants and thus serve as an important food source for small mammals and invertebrates (Muir et al., 2002).

4.2.2. Shrub cover

Only recently have studies been designed to specifically quantify vegetation responses to density management in young Douglas-fir stands (Fig. 3). During the first 1–7 years after thinning, total shrub cover was 12–22% lower than the unthinned controls. These decreases did not seem to be related to the age differences in the data, however early dynamics are likely important. Short-shrub cover in the YSTDS study was reduced by 50% compared to the unthinned controls 1–2 years after harvest for all treatments, but was similar to the controls after 5–7 years (Beggs, 2005). The single exception to decreasing shrub cover was attributed to large increases in short, clonal shrubs in the DMS study (Fig. 3) (Berryman and Puettmann, unpublished results). Tall shrub cover, in particular, appears to be markedly reduced by density management (Beggs, 2005; Berryman and Puettmann, unpublished results). Possible causes include photoinhibition due to changes in light and microclimate (Powles, 1984), but more likely mechanical damage during harvest and slash cover are responsible. LSMEs responded very consistently across a wide geographic range, with the main source of variability appearing to be the initial shrub cover, as referenced by unthinned controls which had the highest basal area in each study (Fig. 3). The wide geographic range and the marked differences in composition across sites precluded species-level analyses.

The large treatments blocks in the LSMEs include a range of vegetation conditions. The within-stand variability in shrub cover is generally high (CV >100%) in unthinned stands (Berryman and Puettmann, unpublished results). Density management tends to homogenize shrub cover slightly when pre-treatment cover is relatively high. In contrast, thinning tends to increase shrub cover and greatly increase within-stand variability where shrub cover is absent before treatment (Harrington et al., 2005). High uniform shrub cover of a few species might reduce diversity of function, and treatments such as variable density thinning or gap creation have been proposed to increase spatial variability in shrub cover and thus stand diversity.

Gap creation has been suggested as one option to increase within-stand variability of understory vegetation. Shrub cover within gaps is greatly reduced in the first year after thinning (Beggs, 2005), likely due to mechanical damage and slash cover. Shrub cover responds quickly following harvest, however, and recovers within 5–7 years, but levels are still slightly less than the unthinned controls (Beggs, 2005; Fahey, 2006). These differences may be a result of harvesting damage and disappear soon, given that light levels in the center of 0.1 and 0.4 ha gaps at the DMS study were 37% and 60% of open conditions, respectively, compared to 25% under adjacent forest canopies thinned to 200 trees per hectare (tph) (Fahey, 2006).

Understory vegetation in small gaps (<36 m diameter) was strongly influenced by the residual forest during the first few years after thinning at the DMS study. The surrounding stand effectively reduced gap influence by 4–14 m on the north side but had no effect on the south side, as demonstrated by similar understory vegetation cover and composition of the interior gap edges to the surrounding forest (Fahey, 2006). Only large gaps (0.4 ha) influenced understory vegetation within the surrounding forest, but the spatial extent was limited to less than 4 m (Fahey, 2006).

In contrast to early thinning results, retrospective studies, which documented conditions 10–30 years post-harvest, generally showed no effect or a strong increase in tall- and short-shrub cover (Bailey et al., 1998; Suzuki and Hayes, 2003; Lindh and Muir, 2004). Canopy closure in stands thinned one to three decades earlier was generally very high (>90%) (Bailey et al., 1998; Suzuki and Hayes, 2003), but the stands still appeared able to retain a tall shrub layer. Slow development and persistence of tall shrubs after damage during harvest may be the principal reason for a delayed response, as the common species are well adapted to understory shade, developing through vegetative regeneration (Huffman et al., 1994; Tappeiner et al., 2001). Also, this persistent shrub layer may respond vigorously to subsequent thinning or canopy gaps as the stands age, further increasing the within-stand heterogeneity (Tappeiner et al., 2001). In western British Columbia, unthinned young plantations showed an inverse relationship between overstory canopy cover and shrub cover (Klinka et al., 1996), which suggests that long-term development will depend primarily on overstory cover. The distinction between early and late responses to thinning also needs to consider trends in stand dynamics where stands develop higher shrub and herb cover as they move from the stem exclusion to the understory initiation and old-growth stages (Spies, 1991; Wender et al., 2004).

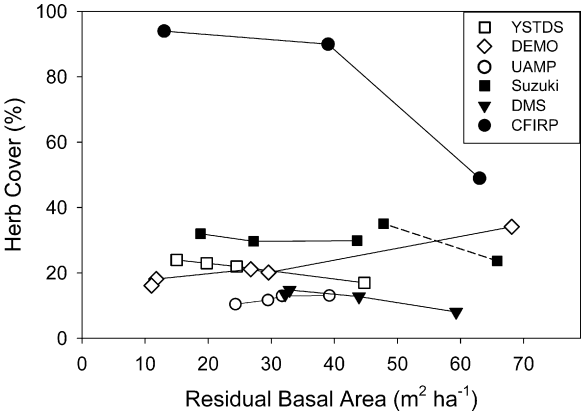

Fig. 4. Herbaceous cover responses 1–7 years following density management, and long-term responses from retrospective studies. See Fig. 3 for note regarding study type designations.

4.2.3. Herbaceous cover

Herbs are an important component of stand structure, since they are a major food source for arthropods and small mammals (Muir et al., 2002). Herbaceous cover was generally less responsive to density treatments than shrub cover (Fig. 4) and increasing herb production may present a significant challenge for management. Herb cover generally responds either neutrally or slightly negatively to thinning across a wide range of residual densities and spatial patterns (Fig. 4). Exceptions to this trend include the CFIRP study at the eastern edge of the Oregon Coast Range where herb cover increased to nearly 90% (Ketchum, 1995). Herb cover in unthinned stands was relatively high, and detailed analyses of thinned stands showed a strong response of annual herbs. Site-specific factors, including pre-treatment vegetation cover and composition, stand heterogeneity, and site quality may dominate post-treatment response patterns (Pabst and Spies, 1998), making broader inferences tenuous without further understanding of specific factors that influence vegetation response at a site.

Within-stand variability of herbs appears to be proportional to average cover values, suggesting microsite characteristics may be an important influence (Dyrness, 1973; Pabst and Spies, 1998). Thinning appears to increase within-site variability of herb cover in areas where stand-level herb cover increases (Harrington et al., 2005). Otherwise, the variability tends to remain unchanged and relatively high across treatments (CV > 60%) (Berryman and Puettmann, unpublished results). Gap creation did not appear to increase herb cover in the DMS or YSTDS studies (Fig. 4) (Beggs, 2005; Fahey, 2006), but competition from rapidly increasing shrub cover may have confounded the impacts of overstory removal (Beggs, 2005).

Ten to 30 years after thinning, herb cover was higher in thinned than unthinned stands (Bailey et al., 1998; Thysell and Carey, 2001). Herb response to thinning, however, may be negatively correlated with the response of the competing shrub and tree layers (He and Barclay, 2000). Herb cover in thinned stands was twice as high (approximately 25%) as unthinned or old-growth (approximately 10%) stands (Alaback and Herman, 1988; Spies, 1991; Bailey et al., 1998; Hanley, 2005).

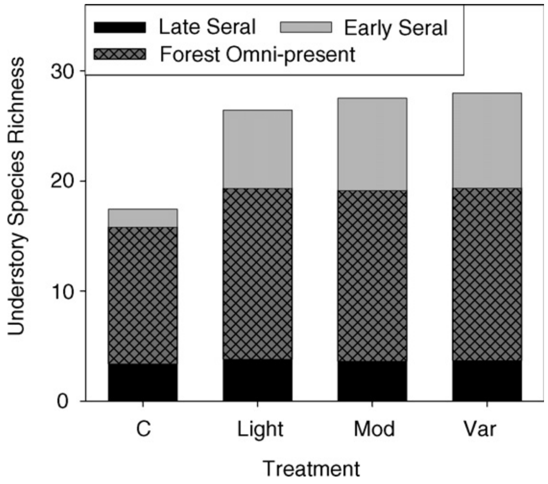

Fig. 5. Average species richness (# per 20 m^2 understory vegetation plot) in the Density Management Study (DMS) (Table 1). Species were grouped by seral types. Treatments were unthinned control (C), light, moderate, and variable density thinning.

4.2.4. Species richness and composition

The rapid canopy closure rates of young plantations affect floristic composition of vegetation during the early phases of stand development (Dyrness, 1973; Halpern, 1989; Puettmann and Berger, 2006). This leads to concerns whether vegetation composition in plantations develops similarly to that in old-growth stands in the Oregon Coast Range, which started at much lower densities and likely had high spatial variability (Tappeiner et al., 1997). Early results indicate that species composition after thinning is shifted towards an early seral type independent of thinning intensity and is characterized by increasing occurrence and cover of early seral and invading species (Halpern, 1989; Beggs, 2005) (Fig. 5). This compositional shift happens usually 1–2 years after thinning and appears to persist for 10 years or longer (Halpern, 1989; Beggs, 2005; Puettmann and Berger, 2006).

The LSMEs covered a wide array of site conditions and pre-treatment understory vegetation that were spatially variable within a site and compositionally variable among sites. Pre-treatment vegetation and abiotic plot characteristics exerted the strongest influence on post-treatment composition, followed by disturbance intensity (Dyrness, 1973; Halpern and Spies, 1995; Bailey et al., 1998; Pabst and Spies, 1998). Understory vegetation on old-growth sites that were clearcut and burned developed towards a composition similar to the pre-disturbed old-growth stands within 20–40 years (Schoonmaker and McKee, 1988; Halpern and Spies, 1995), demonstrating the trend for understory vegetation to return to mature forest conditions.

Thinning and gap creation increased spatial heterogeneity of species composition, but these effects in the DMS study were largely restricted to invading early seral species (Fig. 6). The increased variability in the heavily thinned stands suggests that microsite characteristics (such as soil disturbance and light levels) influence the occurrence of early seral species (Fig. 6). Although detailed information was not collected, conditions

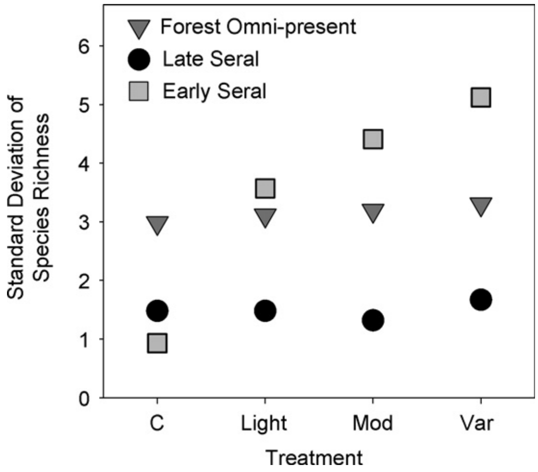

Fig. 6. Standard deviation of species richness computed for understory vegetation plots at the treatment block level and averaged over sites for the Density Management Study (DMS). Species were grouped by seral types. See Table 1 and Fig. 5 for treatment descriptions.

that favor invading species in clearcuts also likely would facilitate their establishment in thinned stands.

Larger gaps (0.4 ha) in the DMS study showed distinct compositional shifts characteristic of clearcuts, with much higher cover of invading early seral species (Fahey, 2006). On the other hand, relative to adjacent thinned stands, vegetation in small gaps (0.1 ha) shifted compositionally towards competitor (*sensu* Grime, 1977) forest-residual species. Thus, small gaps, such as created by low-intensity natural disturbances in PNW forests (Spies and Franklin, 1989) did not cause a distinct species shift, but they may benefit rare late-seral species over a longer period.

Unthinned patches have been proposed to promote diversity and better mimic natural stand development patterns, especially patterns of spatial diversity in overstory cover and species composition (Carey et al., 1999). The abrupt edge between clearcut and unthinned patches did not appear to alter the composition of the unthinned patches at the DEMO study beyond about 10 m into the patch (Nelson and Halpern, 2005). No species were lost in 1 ha uncut patches, but this may become a concern in smaller patches. Likewise, 59 out of 61 forest residual species persisted immediately after harvest in the surrounding clearcut blocks (Nelson and Halpern, 2005). Uncut patches within recently thinned stands functioned similarly. Small patches that were 36 and 50 m in diameter (0.1 and 0.2 ha, respectively) at the DMS study were compositionally similar to the thinned stand (200 tph residual density), whereas the interiors of 71 m diameter patches (0.4 ha) were compositionally similar to the unthinned stands (Wessell, 2006). Unthinned patches of any size supported several species not present in the thinned stands, suggesting the value of these patches to within-stand heterogeneity and potential for propagation into adjacent areas.

In general, species loss due to thinning was not of great concern in the LSMEs. However, the thinning impact on species abundance and cover can have a pronounced effect on wildlife habitat and other ecosystem functions. The high cover of early seral invading species is expected to be short-lived as canopies close to near pre-treatment levels. It is not clear, however, whether these species will be entirely lost from the thinned stands even after several decades (Halpern and Spies, 1995; Bailey et al., 1998; Puettmann and Berger, 2006). Retrospective studies have documented a long-term increase in species richness and a compositional shift towards early seral species following thinning, mainly due to increased grasses, sedges and nitrogen fixing species, while unthinned sites were similar to nearby old-growth (Bailey et al., 1998). This continued presence may be an important consideration in latter thinnings, as many species propagate clonally and can respond vigorously if already established in the stand (Tappeiner et al., 2001).

4.2.5. Exotic and interfering species

Despite being rare in mature conifer stands (Halpern, 1989), exotic (i.e., non-native) plant species are a ubiquitous concern in PNW forests, especially since they tend to dominate site resources and markedly reduce native species richness (Heckman, 1999). In a similar manner, clonal shrubs and tree regeneration can dominate the understory vegetation layer and, as so-called interfering species, out compete other species (Alaback and Herman, 1988; Deal and Tappeiner, 2002). Thinning disturbs existing vegetation and frees up resources, compounding the risk that interfering species will expand and dominate understory vegetation. Alternatively, exotics tend to be localized to heavily disturbed areas, such as roads and clearcuts, but they are also common in unmanaged riparian areas (Heckman, 1999; Parendes and Jones, 2000). Exotics were rare in the LSMEs, with average cover generally less than 5% (Beggs, 2005; Nelson and Halpern, 2005) and a reported maximum of 11% (Thysell and Carey, 2001). Cover values were variable, however, and treatment areas which included gap creation and were near seed sources of exotic species had cover values of 25% and 14% at the CFIRP (Ketchum, 1995) and YSTDS studies (Beggs, 2005), respectively. In clearcuts, cover of exotic species diminishes rapidly after crown closure (Halpern and Spies, 1995; DeFerrari and Naiman, 1994) and we would expect similar trends in thinned stands. Exotics important to PNW forests tend to be ruderal herbs (*sensu* Grime, 1977) and occupy a niche of highly disturbed sites, which are relatively rare in natural forests (Heckman, 1999).

The response of tree regeneration is of special interest to foresters, as advanced regeneration of crop species is desirable in many situations. Too much regeneration, however, especially of shade-tolerant species, can provide a ‘‘secondary stem exclusion’’ that results in nearly complete loss of shrub and herb cover (Alaback and Herman, 1988; Bailey and Tappeiner, 1998). Although none of the short-term results of the LSMEs documented this response, other long-term observations in coastal Oregon and southeast Alaska (Alaback and Herman, 1988) indicated that western hemlock in particular regenerated prolifically after thinning, promoting a discontinuous understory vegetation response. Unthinned and widely spaced stands showed very low cover due to high shade and dense hemlock regeneration, respectively, whereas moderately thinned stands did not result in dense western hemlock regeneration and thus had high shrub and herb cover (Alaback and Herman, 1988).

Similarly, high uniform shrub cover can develop through vegetative reproduction and may out compete the herb layer (Huffman et al., 1994) or tree regeneration (Bailey and Tappeiner, 1998). This risk is most pronounced when few shrubs species are relatively abundant in the understory before thinning (He and Barclay, 2000; Deal and Tappeiner, 2002; Hanley, 2005) or where the disturbance intensity is high. Alternatively, on sites with diverse shrub layers before thinning, short-term results did not confirm trends towards homogenous expansion of interfering shrub species (Beggs, 2005).

4.2.6. Implications for management

Understory vegetation responds to density management in many ways, but the primary response seems to be a shift in composition towards early seral species in gaps or thinned stands (Fig. 5). Thinning can therefore provide animal browse that is otherwise absent in dense stands (Hanley, 2005; Harrington et al., 2005). In addition, heavy thinning or gap creation may be necessary to promote flowering and seed production in understory shrubs and forbs, as these appear to depend on light levels (Lindh and Muir, 2004; Wender et al., 2004). Harvesting activities will damage understory vegetation, especially tall shrubs, but the decrease in cover may be short-term (5–7 and 10–30 years for short- and tall-shrubs, respectively). In areas where tall shrub cover is of special concern, harvesting activities may be designed to protect shrub patches. Alternatively, on nutrient limited sites fertilization may increase understory vegetation growth without the need to alter density management regimes (Prescott et al., 1993).

In stands managed primarily for wildlife, variable density thinnings may minimize the risk of an understory shrub layer that is dominated by a single or few species (Alaback and Herman, 1988; Bailey and Tappeiner, 1998; Deal and Tappeiner, 2002). Also, gaps can provide a food source and microclimate favorable for many arthropod species and openings for aerial insect capture by songbirds (Hagar et al., 2004). The choice of gap size influences the contrast in vegetation composition between the gap interior and the surrounding thinned or unthinned forest (Fahey, 2006), and can provide a range of necessary habitat features in close arrangement. Only larger gaps, which allow invasion of early successional species, will likely alter habitat condition over the long-term. Understory responses to small gaps or homogenous thinnings are likely short-lived due to the aggressive crown expansion of young Douglas-fir (Halpern and Spies, 1995; Puettmann and Berger, 2006).

Large unthinned patches can further increase within-stand heterogeneity and retain a late-seral understory composition. They can also provided habitat for a number of low-mobility amphibian and mollusk species harmed in thinning operations. Unthinned patches may therefore act as a source of these for the surrounding stand (Wessell, 2006).

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