

Patterns in spatial extent of gap influence on understory plant communities

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Abstract

Gap formation in forests can have impacts on forest ecosystems beyond the physical boundary of the canopy opening. The extent of gap influence may affect responses of many components of forest ecosystems to gap formation on stand and landscape scales. In this study, spatial extent of gap influence on understory plant communities was investigated in and around 0.1 and 0.4 ha harvested canopy gaps in four young Douglas-fir (*Pseudotsuga menziesii*) dominated stands in western Oregon. In larger gaps, the influence of gap creation on understory plant communities in surrounding forests was minimal. The area showing evidence of gap influence extended a maximum of 2 m beyond the edge of the canopy opening, suggesting that the area affected by gap creation did not differ greatly from the area of physical canopy removal. In smaller gaps, influence of the gap did not extend to the edge of the canopy opening. In fact, the area in which understory vegetation was influenced by gap creation was smaller than the physical canopy opening. Gap influence appears to be limited to areas where ruderal or competitor species are able to replace stress-tolerator species, likely due to elimination or reduction of these species by physical disturbance or competition. The limited gap influence extent exhibited here indicates that gap creation may not have a significant effect on understory plant communities beyond the physical canopy opening. This suggests a limited effectiveness of gaps, especially smaller gaps, as a tool for management of understory plant diversity, and perhaps biodiversity in general, on a larger scale.

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1. Introduction

Canopy gaps have long been seen as an important component of forested ecosystems (Watt, 1925, 1947; Bormann and Likens, 1979; Spies et al., 1990). Recently, creation of gaps has become a focus of managers attempting to emulate natural disturbance regimes (Runkle, 1991; Coates and Burton, 1997; Franklin et al., 2002). Canopy gaps are often considered in silvicultural prescriptions designed to produce and maintain late-successional habitat features in young forests (Hunter, 1993; Cissel et al., 2006; Davis et al., 2007). As a management tool, gap creation is aimed at increasing habitat heterogeneity and stand structural complexity (Runkle, 1991; Coates and Burton, 1997; Davis et al., 2007), both of which are often

associated with late-successional habitat conditions (Franklin et al., 2002; Muir et al., 2002).

The effects of gap formation on forest processes within the gap area (*sensu* Runkle, 1982), such as tree regeneration, stand structural development, and dynamics of the understory layer have been well documented (Canham and Marks, 1985; Collins and Pickett, 1988b; Spies et al., 1990; York et al., 2004). However, gap influence is not always limited to the physical canopy opening (Canham et al., 1990; Van Pelt and Franklin, 1999, 2000; Gray et al., 2002), and the extent of gap influence on the surrounding forest is less well understood (Coates et al., 1997; Menard et al., 2002). Research aimed at quantifying gap influence extent has focused on overstory tree responses (Payette et al., 1990), regeneration responses (Kobe, 1999; York et al., 2003; York et al., 2004), and modeling of tree growth and regeneration (Dube et al., 2001; Menard et al., 2002). Gap influence extent may vary widely depending on the parameter measured (Dube et al., 2001). Therefore, delineating the areal extent of gap influence in relation to aspects of biodiversity requires an ecologically integrative measure.

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Variation in understory plant communities may be a useful tool in quantifying gap influence extent and may be a good indicator of overall response of biodiversity to gap creation. Gap responses in understory plant communities may differ greatly from those of the overstory, especially in temperate forests where the understory is much more diverse and exhibits greater niche specialization (Gilliam, 2007). Due to this disparity, small-scale responses of species composition to gap formation in temperate forests are easier to quantify in understories than overstories, and variation in understory species composition may be useful in delineating areas influenced by gap creation. The understory also provides important habitat for other taxa in forest ecosystems and may be a good indicator of biodiversity in general (Hayes et al., 1997).

Utilizing characteristics of understory plants, for example classifying the understory community into functional groups, may further aid in detection of gap influence. Functional groups based on plant strategies such as those of Grime (1977), may be especially informative in this type of analysis. Grime advocates three strategies that have evolved in response to combinations of stress and disturbance intensity: (1) competitor species (adapted to low stress and low levels of disturbance), (2) ruderal species (adapted to low stress and high levels of disturbance), and (3) stress-tolerator species (adapted to high stress and low levels of disturbance). In forest understory plants, stress is most likely to be manifested in low availability of light and other resources under a closed canopy (Grime, 1977), and high intensity natural disturbance in these forests is primarily related to wildfire (Franklin et al., 2002). These functional groups are likely to be useful in highlighting the mechanisms responsible for understory community response to gap creation. In addition, investigating distributions of individual species may be instructive, especially for species known to be indicative of disturbed conditions (Halpern, 1989).

One approach to quantifying gap influence extent based on biotic responses is to treat gap influence as an edge effect emanating from the gap edge into the surrounding forest. Determination of depth of edge influence (DEI) in forests has received a great deal of attention (Chen et al., 1992, 1995; Cadenasso et al., 2003; Harper et al., 2005), and has an established methodology (Harper and Macdonald, 2001; Toms

and Lesperance, 2003). Response parameters investigated in DEI studies include: microclimate (Chen et al., 1995), tree mortality (Chen et al., 1992), tree growth (Chen et al., 1992; Laurance et al., 1998; McDonald and Urban, 2004), tree species distributions (Wales, 1972), tree regeneration (Chen et al., 1992), and understory vegetation (Fraver, 1994; Euskirchen et al., 2001; Harper and Macdonald, 2002b; Honnay et al., 2002). Although studies of edge influence have generally focused on edges resulting from large, natural or anthropogenic disturbances (e.g., clearcuts, old fields), methods developed for these purposes are also applicable to investigation of edges resulting from smaller forest canopy gaps.

The objective of this study was to better understand mechanisms that drive understory vegetation response, and the spatial extent of this response, to gap formation in managed forests. To accomplish this objective we (1) investigated the impact of gap creation on various components of the understory plant community and (2) determined the spatial extent and patterns of gap influence on the same components. To achieve these goals, we quantified depth of gap influence (DGI) on understory plant species composition, species diversity, functional group abundance, and the abundance of gap-indicator species. We estimated DGI separately for north and south facing gap edges and compared between two gap sizes.

2. Methods

2.1. Site descriptions

This research was conducted as a component of the Density Management Study (DMS), an ongoing investigation of the effectiveness of thinning treatments in fostering development of late-successional habitat features in young Douglas-fir forests. We focused on four DMS sites located in western Oregon, three in the Coast Range ecoregion (Omernick, 1987): Bottomline (BL), OM Hubbard (OMH), and North Soup (NS), and one in the Cascade Foothills ecoregion: Keel Mountain (KM). All study stands were even-aged and dominated by 40–70-year-old Douglas-fir (*Pseudotsuga menziesii*) in a single canopy layer. One site (KM) had a minor western hemlock (*Tsuga heterophylla*) component. Sites spanned a variety of

Table 1
Characteristics of DMS sites used in gap influence study

| | Bottomline | Keel Mountain | North Soup | OM Hubbard |
|-----------------------------|------------|---------------|---------------|---------------|
| Latitude (N) | 43°46'20" | 44°31'41" | 43°33'57" | 43°17'30" |
| Longitude (W) | 123°14'11" | 122°37'55" | 123°46'38" | 123°35'00" |
| Elevation (m) | 236–369 | 659–768 | 159–411 | 394–783 |
| Aspect | NW-NE | SW-NW | NW-N | NE-N |
| Slope (%) | 0–30 | 0–30 | 0–60 | 30–60 |
| Annual precipitation (cm) | 127 | 165 | 216 | 178 |
| Logging method | Cable yard | Cable/ground | Cable yard | Tractor/cable |
| Treatment date (month/year) | 7–11/1997 | 7/1997–9/1998 | 8/1998–9/1999 | 7–11/1997 |
| Soil texture | Clay loam | Loam | Clay loam | Loam/clay |
| Stand age (years) | ~65 | ~50 | >50 | ~45–50 |
| Mineral soil cover (%) | 1.1 | 0.9 | 3.0 | 4.9 |
| Site index (50 year) | 138 | 127 | 132 | 120 |

For more detail see (Cissel et al., 2006).

elevations, aspects, and stand histories. Site and treatment details are summarized in Table 1 and in greater detail in Cissel et al. (2006).

The DMS study stands that we investigated were thinned to 200 trees per hectare and included three sizes of circular gap openings (0.1, 0.2, and 0.4 ha). Harvesting was conducted in the summer of 1997 for BL and OMH, the summers of 1997 and 1998 for KM, and the summers of 1998 and 1999 for NS. Therefore, gap “ages” varied from 5 to 7 years at the time this study was conducted. This study focused on the 0.1 and 0.4 ha gaps, which had gap diameter to tree height ratios of approximately 1.0 and 2.0, respectively. Gap creation was implemented through operational harvesting and gap locations were determined by logging constraints and not by condition of overstory or understory vegetation. Therefore, locations of gaps, while not randomly assigned, are considered to be representative of typical stand conditions in the region. Gaps used as landings for timber extraction were avoided, but all gaps contained some ground-layer disturbance from harvesting operations.

2.2. Study design and data collection

Gap transects used for sampling understory vegetation, substrates, and environmental variables were established between July 1 and August 31, 2004. We sampled eight gaps (four each of 0.1 and 0.4 ha sizes) at three sites (KM, OMH, NS) and six gaps (three of each size) at a fourth site (BL), resulting in a total of 15 gaps of each size. Transects originated at gap center and extended 23 m beyond the gap edge, defined as the line extending between the boles of the nearest surrounding canopy trees (Runkle, 1982), into the surrounding forest understory to the north/northeast (between 0° and 60°) and south/southwest (180° from N/NE bearing; Fig. 1). Gaps were selected according to suitability for the transect layout, with the stipulation that transects avoid (at a distance greater

than the total transect length) other gaps, leave islands (unthinned patches), or the boundaries of the treatment or site.

Understory vegetation (<6 m in height) was sampled in plots (hereafter transect positions) made up of sets of five contiguous 4 m² square sampling quadrats (hereafter subplots) established parallel to transects (Fig. 1). Transect positions included: south forest matrix (SM; centered 54 m south of gap center in 0.4 ha gaps and 36 m in 0.1 ha gaps, distances are approximate, actual distance depended on diameter of gap), south edge (SE; ~36 m, ~18 m), south gap interior (SG; only in 0.4 ha gaps, ~18 m), gap center (C), north gap interior (NG, only in 0.4 ha gaps), north edge (NE), and north forest matrix (NM). In addition, interior forest plots, defined as having no gap influence, were obtained from a stand scale study of vegetation response to thinning treatments (Cissel et al., 2006). Plots in this survey were randomly located within the thinned treatment area and consisted of four 18.55 m² circular vegetation sampling subplots within a 0.1 ha plot area. Sampling of these plots was conducted during the summers of 2003 (KM, OMH, BL) and 2004 (NS). Plots were only selected as interior forest plots if they were 30 m or more from any natural or management-related gap greater than or equal to 0.1 ha in size.

Ocular estimates of percent cover were made for all vascular plant species (with cover < 6 m in height) in each subplot in the transect survey and the stand scale survey. Taxonomic nomenclature follows the USDA Plants Database (USDA-NRCS, 2005). Cover was estimated in classes with 1% increment up to 10% cover (1%, 2%, 3%, etc.) and in 5% increments beyond that (15%, 20%, 25%, etc.).

2.3. Data analysis

2.3.1. Understory community variables

We used indicator species analysis (ISA) to identify species that were indicative of gap locations in both gap sizes. This

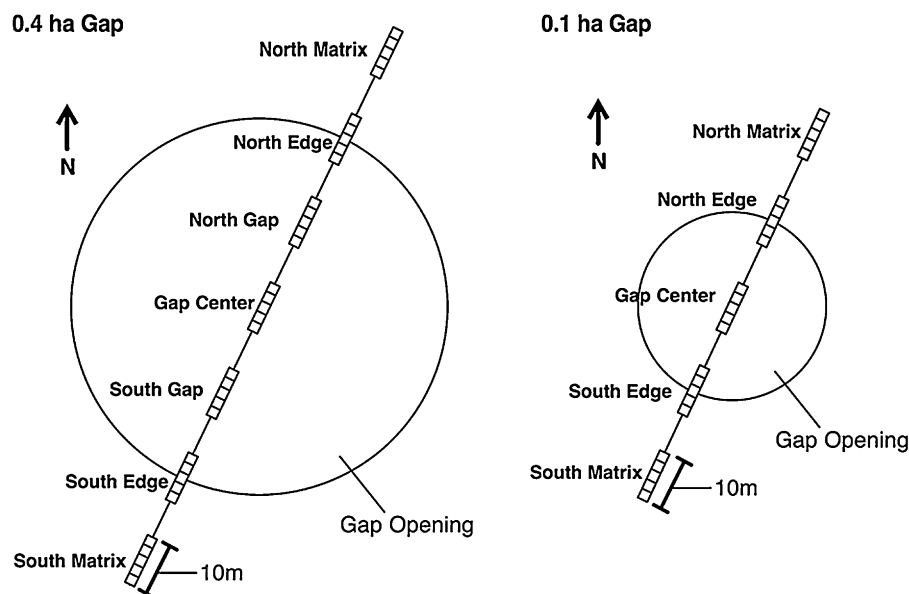


Fig. 1. Layout of gap-transects for both gap sizes; all elements are to scale. Figure illustrates an ideal case, in reality gaps were not perfectly round and actual distances along transects varied slightly. Orientation of gap transects is depicted as approximately N/NE (22.5°), but varied between 0° and 60°.

analysis highlighted the types of species that respond to gap creation and allowed us to study the spatial distributions of these species as a measure of gap influence. ISA, implemented using PC-ORD v4.1 (McCune and Medford, 1995), evaluates the faithfulness of species to transect position groups based on relative species frequencies and abundances. Indicator species for each gap size were defined as those significant at the $p < 0.1$ level. We also classified species into disturbance response-based functional groups to help highlight the mechanisms responsible for gap-related patterns and to allow for comparisons among sites and gaps. Plant strategy groups were defined as: competitor, ruderal, and stress tolerator (Grime, 1977). Species were assigned to Grimean guilds based on life history characteristics, shade tolerance, and disturbance response strategies (see Table 2 in Grime, 1977; Fahey, 2005).

To assess patterns in understory plant composition we developed a univariate community composition variable, obtained from non-metric multidimensional scaling (NMS; McCune and Grace, 2002) ordination of the full set of transect plots (all sites, both gap sizes). All ordinations were run using the “slow and thorough” autopilot setting in PC-ORD v4.1 (McCune and Medford, 1995) with “random” starting configurations using Sorensen’s distance measure. Each ordination was rotated to maximize the amount of community variation explained by the first axis, scores from this axis were then used as a univariate community response variable, known hereafter as the “NMS community composition variable”. In order to obtain scores for reference forest interior plots (for use in DGI analysis: Section 2.3.2) in the ordination space defined by the transect data, we used the NMS Scores procedure in PC-ORD v4.1 (McCune and Medford, 1995). This procedure fits new plots into an existing ordination space using an iterative approach to find the best fit position for each new plot individually (McCune and Grace, 2002). Use of this procedure allowed us to define the ordination space based on the data of interest (transects), while utilizing plots from the larger stand survey as reference (no gap influence) plots.

We also investigated species diversity using patterns in Simpson’s diversity index (Simpson, 1949), which was calculated as:

$$D = 1 - \sum_{i=1}^s p_i^2 \quad (1)$$

where p_i is the proportion of total cover in species i and s is the total number of species (Magurran, 2004). In this form, the index represents the likelihood that two randomly chosen units of cover will belong to different species (McCune and Grace, 2002). For the reference plots, values of Simpson’s diversity measure were adjusted to the mean of the forest matrix transect plots to account for differences in plot size in the two surveys.

2.3.2. Depth of gap influence

To assess DGI on the variables discussed above we employed the critical values approach (Harper and Macdonald, 2001, 2002a). This method uses randomization tests to compare

mean values of response variables at different distances along transects to values obtained from reference (interior) forest plots. Critical values of response variables were the 2.5 and 97.5 percentiles of 5000 permuted means, and a significance level of $\alpha = 0.01$ was used to evaluate our results. Mean values of response variables on transects were considered significantly different from reference forest levels if they lay outside these critical values (Harper and Macdonald, 2001). DGI was defined as the location where two or more consecutive values fell outside the critical values threshold (Harper and Macdonald, 2001). This analysis was performed on selected indicator species, plant functional groups, understory plant species diversity, and understory community composition. For this analysis, indicator species were chosen based on their ubiquity across sites and gaps within each site (Fahey, 2005).

3. Results

3.1. Indicator species analysis

Using indicator species analysis, we successfully identified a number of species indicative of gap interior positions in each gap size. The set of indicator species for each gap size included ruderal (R) and competitor (C) species as well as native (N) and exotic (E) species. In general, the indicators for the large gap size were ruderal species while those for the small gaps size were typically competitor species. In the large gaps the indicators of the gap interior positions included: *Agrostis exarata* (R, N), *Aira caryophylla* (R, E), *Chamerion angustifolium* (R, N), *Cirsium vulgare* (R, E), *Elymus glaucus* (R, N), *Epilobium ciliatum* (R, N), *Madia exigua* (R, N), and *Pteridium aquilinum* (C, N). In the small gaps the indicator species were: *Anaphalis margaritacea* (R, N), *C. angustifolium* (R, N), *Digitalis purpurea* (R, E), *E. ciliatum* (R, N), *P. aquilinum* (C, N), *Ribes sanguineum* (C, N), *Rubus luccodermis* (C, N), *Rubus spectabilis* (C, N), *Rubus ursinus* (C, N), *Rumex acetosella* (R, E), and *Whipplea modesta* (C, N). For each gap size, three indicator species that were found at all sites and in most gaps within each site were selected for use in the DGI analysis (see Section 3.2 below).

3.2. Depth of gap influence

Gap influence on understory plant community composition was largely limited to gap interiors, according to critical values analysis of the NMS scores variable. DGI, as defined by locations where NMS scores reached critical values thresholds indicating no difference from reference forest conditions, differed between gap sizes and edge orientations (Fig. 2a and b). In large gaps (0.4 ha), DGI was limited to between 0 and 2 m beyond gap edges (into the thinned forest matrix) on north edge transects, and between 2 and 4 m from gap edges (inside gaps) on south edge transects (Fig. 2a). The location of influence was reversed by edge orientation and was much smaller in 0.1 ha gaps, where depth of gap influence was between 4 and 14 m from gap edge on the north edges and between 0 and 2 m from gap edge on the south edges (Fig. 2b).

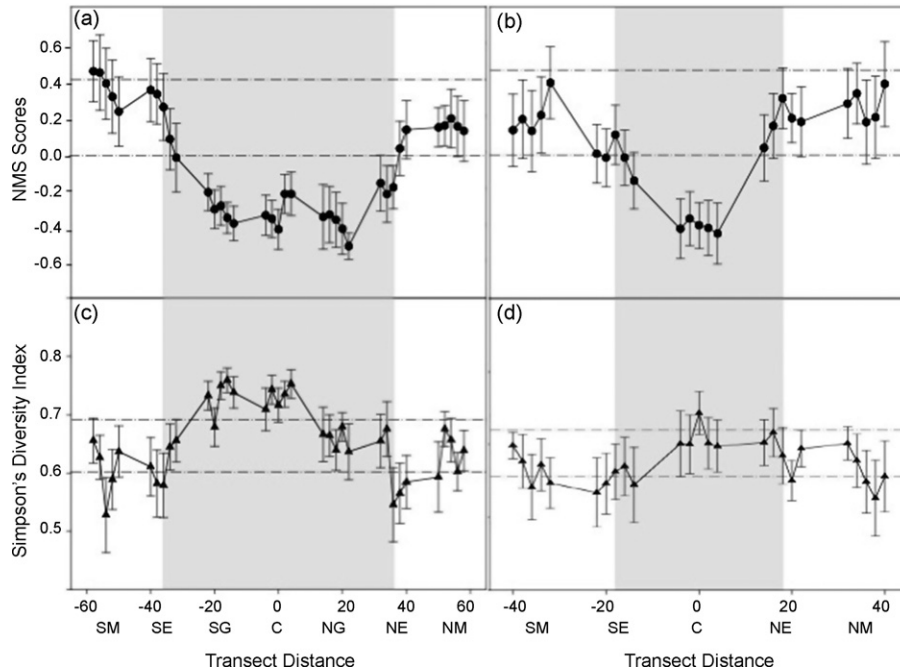


Fig. 2. Mean values of NMS community composition variable and Simpson's diversity index across 0.4 ha gaps (a and c) and 0.1 ha gaps (b and d). Bars represent standard errors. Gray shaded areas represent gap interior. Dotted lines represent critical values for forest interior condition for each variable.

Edge effects on understory plant diversity showed a more complex pattern. Simpson's diversity index was lower than reference levels at edge locations in both gap sizes, and higher than reference in center and south gap locations in 0.4 ha gaps (Fig. 2c and d). Gap influence on species diversity was skewed south in 0.4 ha gaps (Fig. 2c) and north in 0.1 ha gaps (Fig. 2d),

which was the opposite of the pattern seen in composition. Gap interior influence on species diversity was obvious only in the larger gap size and was limited to the gap center and south gap positions (Fig. 2c).

DGI differed among plant strategy groups and responses of these groups varied between gap sizes and edge orientations

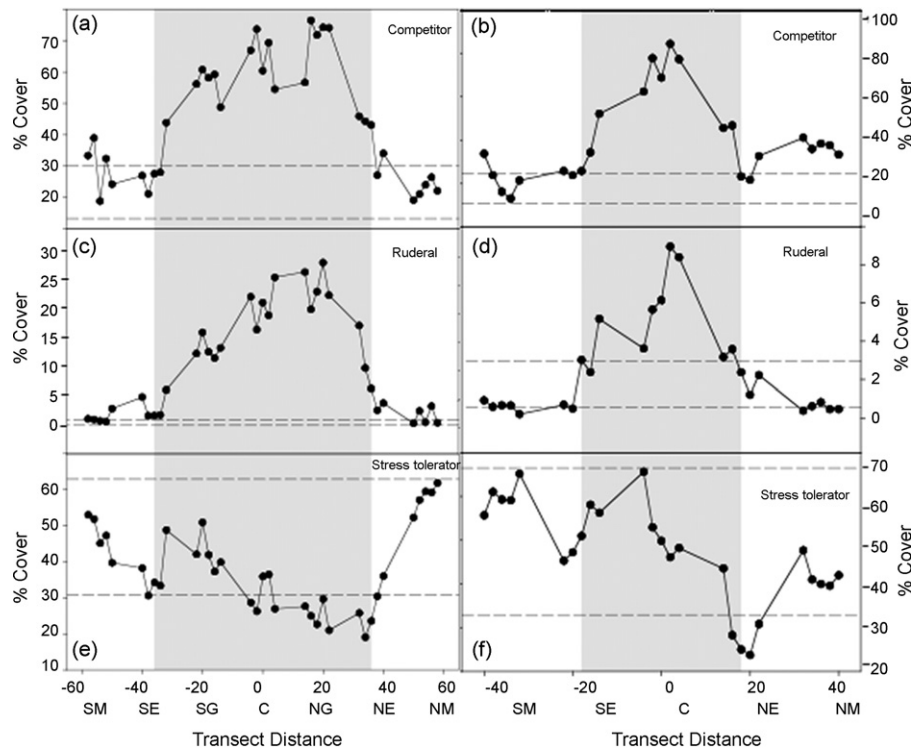


Fig. 3. Mean cover of Grime (1977) strategy groups by transect position in 0.4 ha (a, c, e) and 0.1 ha gaps (b, d, f). Gray shaded areas represent gap interior. Dotted lines represent critical values for forest interior condition for each group.

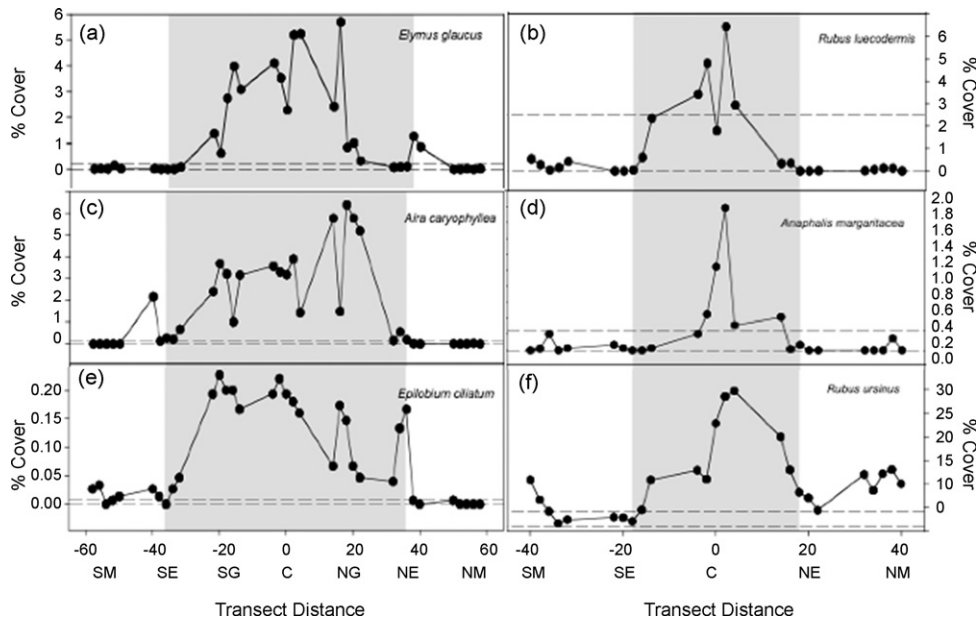


Fig. 4. Mean cover of selected gap-indicator species by transect position in 0.4 ha (a, c, e) and 0.1 ha (b, d, f) gaps. Gray shaded areas represent gap interior. Dotted lines represent critical values for forest interior condition for each species.

(Fig. 3). Ruderal and competitor species groups showed strong gap influence in both gap sizes, but this effect extended beyond gap edges only in large gaps (Fig. 3a–d). The competitor species group showed a symmetrical pattern in both gap sizes, whereas the ruderal and stress-tolerator groups both showed a strong skew of the gap effect toward the north side of the gap regardless of gap size. Also, in both gap sizes, the stress-tolerator group was below reference forest levels on the north, but not south, side of gaps (Fig. 3e and f).

Patterns in DGI on indicator species varied among species, although broad patterns were discernable. In general, above-reference abundance of gap-indicator species extended farther from gap center on north sides of transects than on south sides (Fig. 4). In larger gaps, the three species investigated (*E. glaucus*, *A. caryophylla*, and *E. ciliatum*) all showed a northward skew in their distributions, and each also showed evidence of being above reference levels outside of physical gap openings (Fig. 4a, c, and e). In small gaps, only *R. ursinus*, an almost ubiquitous competitor species, existed at above-reference abundance beyond the gap edge. The other two species, *A. margaritacea* and *R. luecodermis*, had elevated distributions that were largely limited to the physical gap opening (Fig. 4b, d and f).

4. Discussion

4.1. Spatial extent of gap influence

The “understory gap” may not be an easily definable concept as it appears to have multiple dimensions and differs greatly depending on disturbance type, gap size, and the aspects of the understory in question. However, one pattern that appears consistent is that gap influence on composition of understory vegetation communities does not extend greatly beyond the

physical canopy opening (*sensu* Runkle, 1982). Edge influence emanating from harvested gaps in our study was similar to that found at other temperate forest edges when cover or composition of understory species was measured (Euskirchen et al., 2001; Harper and Macdonald, 2002b). In addition, increases in gap size may have greater impact on gap influence on understory vegetation than expected based on physical gap size alone. The much greater DEI seen in interfaces between clearcuts and intact forest (Chen et al., 1992) suggests that this effect may continue to increase with increasing gap size beyond the range studied in our experiment. However, Kayler et al. (2005) found a gap influence of less than 10 m on understory community composition around a 1 ha group selection. This study only examined the south edge of the opening though, and edge influence extent on the north edge may have been substantially greater. A caveat to the results of our study is that the forest surrounding the gaps was thinned, which may have lessened the contrast between the gap and forest understory environments. An undisturbed forest matrix may have exhibited more or less gap influence depending on the variables of interest. For example, where the forest is undisturbed understory composition may be even less likely to exhibit gap influence (Kayler et al., 2005), but the abundance of competitor species may be more likely to exhibit gap influence (see Section 4.1.3).

4.1.1. Understory species composition

In larger gaps, the only area in the thinned forest matrix that exhibited understory community composition similar to that found inside gaps was a small area beyond the north edge. The northward skew in understory composition suggests a light driven response, as north gap edges receive elevated levels of radiation in the northern hemisphere (Canham et al., 1990). Our results suggest that Runkle’s (1982) “extended gap” definition

is not entirely appropriate for assessing the influence of elevated light availability on understory species composition in gaps. The “light gap”, a modified version of the extended gap offset slightly to the north, may best describe gap influence on understory vegetation in large gaps.

In smaller gaps, gap effects on understory species composition did not extend into the surrounding forest matrix. Our data suggest that small gaps are unlikely to have an influence on overall community makeup that extends even to the edge of the physical canopy opening, at least in the first few years after gap creation. Other investigators have obtained similar results and have related a negative gap edge effect to small opening sizes (Hughes and Bechtel, 1997; York et al., 2003).

4.1.2. Understory species diversity

Spatial extent of gap influence on understory species diversity did not follow a simple pattern. In general, edge locations appear to support lower understory plant species diversity than surrounding thinned forest or gap interiors. Gap influence on diversity exhibited both an interior (high diversity) component and an edge (low diversity) component. While other studies have found that edges support higher species diversity (Brothers and Spingarn, 1992; Fraver, 1994; Euskirchen et al., 2001), Harper and Macdonald (2002a,b) found mixed results, i.e., both higher and lower levels of diversity in edge locations, and Matlack (1994) found no increase in diversity at edge locations. These studies generally concentrated on well-established edges between highly dissimilar systems (such as an old-field forest or clear-cut edge) where two distinct vegetation communities intersected. In small forest canopy gaps, distinctions between gap communities and forest understory communities are not expected to be as great as at old-field or clear-cut edges because differences in environment across the edge are not as great (Cadenasso et al., 2003). This lack of edge contrast, which may be especially pronounced in our study system because of the thinning of the forest matrix, may help explain why diversity was not heightened at edges in this analysis.

4.1.3. Functional group patterns

The observed patterns in species composition and diversity in relation to gaps can be largely explained by assessing functional group patterns. The functional group distributions in large gaps suggest that much of the observed response in species composition and diversity may be attributable to elevated abundance of ruderal species and diminished abundance of stress-tolerator species. Factors such as physical disturbance and propagule availability have a significant influence on understory species composition (Collins and Pickett, 1988a,b; Beatty, 2003), and as ruderal species are dependent on disturbance by definition, physical disturbance of existing vegetation is certainly partly responsible for observed gap response (Fahey and Puettmann, 2007). However, the directional nature of the response suggests this is not the only factor influencing the observed patterns. The northward skew of these group distributions suggests a light driven control on the

occurrence of ruderal and stress-tolerator species at levels different from those observed in the adjacent thinned forests. On the north side of larger gaps, ruderal and competitor species are able to replace stress-tolerator species more fully, presumably because they can benefit from high levels of direct solar radiation (Fahey and Puettmann, 2007), which create a highly competitive environment. This could explain why gap influence on surrounding forests was minimal even in large gaps. Physical disturbance of existing vegetation outside of gaps was minimal, therefore, gap influence is likely to occur only in places where stress-tolerator species are replaced by either ruderal or competitor species through competitive interactions, i.e., the highly competitive environment near the north gap edge.

Functional group patterns may also partially explain differences in gap influence exhibited in the two gap sizes. Small gaps may have been dominated by competitor species in part because of the lower levels of ground-layer disturbance associated with this gap size (Fahey, 2005). In the absence of high levels of disturbance, ruderal species are unable to take advantage of canopy removal and subsequent reduction in abundance of stress-tolerant species. In small gaps, levels of direct radiation may not have been elevated enough to cause competitive reduction of stress-tolerators except at the very center of the gaps, resulting in the negative gap influence extent observed in smaller gaps.

4.1.4. Gap-indicator species

Gap-indicator species displayed a range of patterns in relation to gap openings, emphasizing the idea that disturbance response in the understory layer may vary greatly among species (Halpern, 1989). Unfortunately, few of the indicator species were common enough to be studied in the DGI analysis, and the full range of variation in gap influence on distributions of these species is unknown. Distributions of gap-indicator species that were investigated were mostly consistent with the functional group identity of the species. The identity of gap-indicator species differed between the two gap sizes, likely due to the functional relationships discussed previously. Indicators for larger gaps tended to be ruderal species, while those for smaller gaps were generally competitor species. This pattern is likely responsible for much of the difference in gap influence between the gap sizes, but linking these differences to individual species is not possible in this study. Determination of gap influence on specific species of interest, such as invasive or late-successional habitat associated species, may be possible using the methodology employed here, but the patchy distribution of most understory plants would constitute a considerable challenge to such an analysis (Beatty, 2003).

4.2. Temporal trends in gap influence

Edge effects (Matlack, 1994; Harper et al., 2005) and species distributions in disturbed systems (Halpern, 1989) are temporally variable. Certain functional groups and gap dependent species may decline in importance as the disturbance becomes more temporally remote. The relationship between the

ruderal species group and gap influence patterns suggests a short-lived gap effect, as these species will most likely decline in abundance as the forest redevelops over time (Halpern and Spies, 1995). Changes in species composition are a secondary process in relation to edge creation, and DEI on composition is therefore hypothesized to increase over time in systems in which forest redevelopment does not occur (Harper et al., 2005). In this study system, though, compositional differences between gap and forest interior may become less pronounced over time as tree species regenerate in gaps. Gap areas may develop the dense overstory and depauperate understorey that is characteristic of early stand development and may therefore eventually host lower levels of understorey diversity (Halpern and Spies, 1995; Franklin et al., 2002). Edge structure, the three-dimensional arrangement of material at the edge, can also have a significant influence on edge effects (Didham and Lawton, 1999; Cadenasso and Pickett, 2001) and is likely to change over time as well (Harper et al., 2005). For example, the edges of these gap areas may become stronger barriers to dispersal over time as vegetation fills in at the edge (Harper et al., 2005). The initial conditions presented here will be highly influential on development of forest structure associated with gap closure (Royo and Carson, 2006) and may, therefore, have strong implications for long-term gap development. Further study may be warranted to investigate long-term effects of gap creation on understorey plant communities.

4.3. Measurement of gap influence using understorey vegetation

The use of understorey species as a metric for delineating gap influence has a number of advantages: the response is easily measurable, can be used as indicator of wildlife habitat (Carey, 2003), and can be an integrative indicator of ecosystem response (Nilsson and Wardle, 2005). Disadvantages in relying on understorey vegetation communities to illustrate gap influence include effects of stand history and initial condition on vegetation response (Palik and Murphy, 1990; Hughes and Fahey, 1991), a high degree of variability in the response (Halpern et al., 2005), and the temporally dynamic nature of the response (Halpern, 1989; Roberts and Gilliam, 1995).

In this study, understorey vegetation community composition proved useful as a measure of the extent of gap influence into surrounding thinned forest. However, in less-disturbed, natural gaps the dominant influence of initial vegetation distributions on post-disturbance communities will make compositional changes less useful in this capacity (Moore and Vankat, 1986; Hughes and Fahey, 1991). In the absence of harvest disturbance to the forest surrounding the gap (such as an unthinned forest matrix), effects of gap creation on understorey species distributions may be even less pronounced. Understorey vegetation composition may be most useful as a measure of gap extent in large gaps with relatively high levels of ground-layer disturbance (Fahey and Puettmann, 2007). In natural gaps, measurement of growth and flowering responses in understorey vegetation may be a more effective method of obtaining information about gap influence, as gap effects on these

responses would likely occur even in smaller, less-disturbed gaps (St. Pierre, 2000; Lindh, 2005).

The complex patterns observed here suggest that utilizing the response of a single understorey plant species to delineate gap extent may be difficult. This is especially true in study systems for which no pre-treatment data exist, effectively precluding any solid conclusions based on distributions of individual species (Nelson and Halpern, 2005). One valid approach in systems with pre-treatment data may be to designate the greatest DGI found on any gap-indicator species as the effective DGI. A relatively ubiquitous species would be required for determination of DGI; however, many understorey species have patchy distributions (Beatty, 2003) and would therefore be of little use in such an analysis. Functional groups, such as plant strategy groups, may be more informative as their use reduces problems with patchy distributions and could be more easily compared between stands with differing species composition and site characteristics. However, great differences appear to exist in gap influence depending on the functional group of interest, and the choice of functional group will depend on the specific question of interest.

5. Conclusions and management implications

Extent of gap influence, as defined by understorey vegetation, appears to be highly variable, and will depend greatly on the measures used to delineate this influence and the nature of the gaps investigated. Gap influence on composition of understorey vegetation communities was limited primarily to the physical area of canopy tree removal in young Douglas-fir forests in western Oregon. The lack of a large gap influence on surrounding thinned forests may have implications for the ability of these types of treatments to influence forest ecosystems on stand and landscape scales (Coates and Burton, 1997). This limited influence could play a role in the lack of a statistically significant response in understorey plant diversity or composition to gap creation on a stand scale (Beggs, 2004; Berryman et al., 2005). However, even if gap influence on understorey plants is limited primarily to physical gap areas, gap creation may nonetheless have impacts on forest ecosystems (Menard et al., 2002; Carey, 2003).

Area of gap influence, and likely the influence of gaps on stand level processes, does not appear to scale linearly with gap size. The small extent of gap influence may signal a limited efficiency of gaps in general, and small gaps in particular, as a tool for management of understorey layer diversity on a stand or landscape level. This finding suggests that to influence some ecosystem processes and functions, managers may be better served with few, large rather than multiple, smaller gaps. On the contrary, the limited gap influence observed in small gaps may also help mitigate potential negative effects related to gap creation, such as invasion opportunities for exotic species (Beggs, 2004). The gap-size relationship demonstrated here suggests a tradeoff between creation of gaps large enough to influence stand processes but small enough to limit potential negative impacts. In designing treatments, managers would do well to weigh the potential for negative impacts versus possible

benefits to biodiversity objectives, and the results presented here may help inform such decisions.

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