

Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington

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Abstract

Aggregated retention is now a common method of regeneration harvest in forest ecosystems managed for both timber and ecological objectives. If residual forest aggregates are to serve as temporary refugia for species sensitive to disturbance or environmental stress, microclimatic conditions must be sufficiently buffered to allow for their persistence. In 1-ha aggregates at three experimental sites in western Washington, we quantified spatial gradients in microclimate (light, air and soil temperature, and soil moisture), effects of aspect on these gradients, and how microclimate compared to conditions in adjacent harvest areas and larger tracts of undisturbed forest (controls). Light availability and temperature, were greatest at the edge, but declined sharply inside the aggregate, with most change occurring within 20 m of the edge. Beyond this distance, light generally declined to levels observed in the controls. Soil temperatures exhibited greater spatial variation and stabilized further from the edge (10-30 m), but air temperatures were generally higher than those in controls. Soil moisture exhibited no spatial trends and was comparable among aggregates, harvest areas, and controls. Aspect exerted strong effects on light and temperature, particularly within 15 m of the edge, as did forest structure. Where tree density was low, microclimatic gradients were less steep and aspect-related differences were small. Comparisons with previous studies of ground vegetation indicate that microclimatic effects were consistent, in part, with declines among some groups of vascular and non-vascular plants; however, these declines were restricted to edge environments (5-10 m) and were unaffected by aspect. Our results suggest that 1-ha aggregates are sufficiently large to contain areas with light, temperature, and soil moisture that are comparable to those in undisturbed forest and suitable, in the short-term, for persistence of forest-dependent species.

Keywords: Aggregated retention; Edge-effects; Forest microclimate; Light; Temperature; Variable-retention

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1. Introduction

Increasingly, forest managers are designing silvicultural systems to meet multiple objectives (e.g., maintaining biodiversity, producing timber, and enhancing wildlife habitat). Structural retention harvests that retain elements of the original forest (live trees, snags, and logs)

have been adopted as one method to achieve these objectives (Franklin et al., 1997; Deal, 2001; Drever and Lertzman, 2003). On federal lands in the Pacific Northwest, the current policy for regeneration harvests within the range of the northern spotted owl requires that live trees are retained over at least 15% of the harvest unit, with 70% of this retention as 0.2- to 1.0-ha aggregates of undisturbed forest (USDA and USDI, 1994). Among other functions, aggregates are intended to provide refugia for disturbance-sensitive species and dispersal sources for recolonization of adjacent harvest areas (Franklin et al., 1997). However, this requires that microclimatic conditions within forest aggregates are sufficiently buffered to maintain species sensitive to environmental

changes. Patches that are too small or permeable may be vulnerable to microclimatic changes that diminish their ecological integrity. Thus, understanding the potential for edge effects is critical to designing variable-retention systems that employ aggregates to maintain and facilitate recovery of biological diversity after harvest.

Studies of clearcut-forest boundaries provide the empirical basis for much of our understanding of edge effects. Radiation, temperature, and other physical processes can differ substantially between forest-edge and interior environments. Steep gradients in microclimate are typical along the boundary between recently cut and intact forest. Most change appears to occur within 40-50 m of the edge (e.g., Chen et al., 1993; 1995), however, stabilization may occur at considerably shorter distances for variables that are less sensitive to ambient conditions (e.g., soil temperature; Williams-Linera, 1990; Young and Mitchell, 1994; Camargo and Kapos, 1995; Davies-Colley et al., 2000). In contrast, some microclimatic variables (e.g., humidity, wind speed) are highly sensitive to forest edges and effects can be detected at distances >200 m (e.g., Chen et al., 1995). Topography and latitude can diminish or amplify the depth and magnitude of these effects through changes in solar angle or heat load (e.g., Camargo and Kapos, 1995; Chen et al., 1995; Turton and Freiburger, 1997). Forest structure can also affect these gradients. Edge contrast, the difference in canopy height between cleared and intact forest, and edge closure, the density and vertical distribution of foliage along the edge, can affect light penetration and air movement and thus gradients in temperature and humidity (Canham et al., 1990; Matlack, 1993; Chen et al., 1995). Moreover, both can change over time with growth of the regenerating forest and in-filling along the edge (e.g., Denyer et al., 2006).

In this study, we explore edge-related gradients in microclimate (light, temperature, and soil moisture) within residual forest patches resulting from aggregated-retention harvest of mature, coniferous forests in the southern Cascade Range of western Washington. To our knowledge, this is the first such study of forest

aggregates and one of the few studies that have explored the microclimatic effects of structural retention (e.g., Barg and Edmonds, 1999; Chen et al., 1999; Zheng et al., 2000; Heithecker and Halpern, 2006). We utilize a subset of the aggregated retention and control treatments, from the Demonstration of Ecosystem Management Options (DEMO) Study, a large-scale experiment that examines ecological responses to variable-retention harvest (Aubry et al., 1999). We address the following questions: (1) Do forest aggregates show consistently greater light availability, greater summer temperature, and lower soil moisture than larger blocks of undisturbed forest? Conversely, do they support microclimatic conditions that differ significantly from those in adjacent harvest areas? (2) How do light, temperature, and soil moisture vary with distance from forest edge? (3) How do these gradients vary with aspect? These characteristics represent important mechanistic links between the manipulation of forest structure and the responses of forest organisms to resulting changes in microclimate. We conclude by discussing the relevance of microclimatic patterns for biological responses at these sites using data on the edge-related responses of vascular and non-vascular plants (Nelson and Halpern, 2005a, b).

2. Methods

2.1. Study sites

Studies were conducted at three sites in the southern Cascade Range, Washington, within the framework of the DEMO study (Aubry et al., 1999; Halpern et al., 1999, 2005). The sites — Butte (BU), Paradise Hills (PH), and Little White Salmon (LWS) — occur at elevations between ~800 and 1158 m and vary in slope and aspect (Table 1). Soils are moderately deep and well-drained loams to loamy sands derived from andesite, basalt, or breccia parent materials, or from aerial deposits of pumice (Wade et al., 1992). The climate is characterized by warm, dry summers and cool, wet winters. Most precipitation falls between October and April resulting in a long period of summer drought (Franklin and Dyrness, 1988). Additional details on the physical environments of these

sites are contained in Halpern et al. (2005).

All forests were dominated by Douglas-fir (*Pseudotsuga menziesii*), but stand age, structure, and species composition varied markedly (Table 2; see also Halpern et al., 1999, 2005; Maguire et al., 2007). Forests at BU were relatively young (70-80 yr) and dense (830-1,000 stems ha⁻¹) with a significant component of western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*) in the subcanopy; canopy height averaged 28-33 m. Forests at PH were mature (110-140 yr), moderately dense (590-1,000 stems ha⁻¹), and structurally and compositionally more diverse than at BU or LWS. *Tsuga heterophylla* comprised a significant proportion of canopy stems and Pacific silver fir (*Abies amabilis*) was common in the understory; canopy height averaged 27-32 m. Forests at LWS were the oldest (140-170 yr) and very open (230-300 stems ha⁻¹), comprised of large *Pseudotsuga menziesii* with a well-developed shrub layer of vine maple (*Acer circinatum*) (~70% cover); canopy height averaged 49 m. Additional information on understory composition is contained in Halpern et al. (1999, 2005).

2.2. Sampling design

At each site we used two of the six, 13-ha experimental treatments that comprise the DEMO study: 15% aggregated retention (15%A; 15% of the original basal area) and an undisturbed control (100%, no harvest). In 15%A, two 1-ha circular patches (56.4 m radius) were retained, separated by a distance of ~115 m (Fig. 1). All merchantable trees (>18 cm dbh) were cut and yarded from the surrounding harvest area. Smaller non-merchantable trees were left standing at BU, but were felled at PH (similar-sized stems were uncommon at LWS). Logging was completed in 1997 (BU and PH) or 1998 (LWS) (for details see Halpern and McKenzie, 2001; Halpern et al., 2005). Microclimatic measurements were made during summer 2004, 6 or 7 yr after harvest.

To characterize microclimatic gradients within and adjacent to forest aggregates, we established two perpendicular transects extending from the center of each aggregate, across the edge, to a distance of 63 m into the

harvest area (Fig. 1). Microclimatic conditions were sampled at 15 points (stations) along each transect: eight within the aggregate (0, 5, 10, 15, 20, 30, 40 and 56.4 m from the edge) and seven in the harvest area (5, 10, 15, 20, 30, 40, and 63 m from the edge). Edge was defined as a fixed distance from the aggregate center — 56.4 m, the radius of a 1-ha circle.

In addition to these transects, microclimatic conditions were sampled in two reference environments at each site: 11 ha of harvested area surrounding the aggregates and 13 ha of undisturbed forest comprising the control treatment (henceforth, control). In each environment, microclimatic stations were established at 20 (in one case 19) locations randomly selected from permanent grid points evenly spaced on a 40 x 40 m sampling grid (Fig. 1) (Aubry et al., 1999). Each station was located in a random direction, 1.5 m from the selected grid point.

2.3. Measurements of topography and overstory structure

To evaluate potential differences in microclimate due to variation in topography or overstory structure, we collected additional data at each station. At each point we measured slope and aspect; from these and latitude we derived an index of heat load (McCune and Keon, 2002). Data on overstory structure were obtained from measurements of permanent tree plots associated with the systematic grid in each experimental unit. For reference environments (harvest area and control), these corresponded to the randomly selected grid points ($n = 19-20$). For forest aggregates, they corresponded to the five grid points within each aggregate ($n = 10$ per site). Within each tree plot, all stems ≥ 5 cm diameter at breast height (dbh) were identified by species, assigned to one of four canopy classes (suppressed, intermediate, codominant or dominant), and measured for diameter. Heights of all dominant and codominant trees were estimated from species- and site-specific height:diameter equations (D. Maguire, unpublished data).

2.4. Microclimatic measurements

At each microclimatic station we sampled four variables — light, air temperature, soil temperature, and soil moisture. An index of light availability was obtained from hemispherical photography of the forest canopy (Lieffers et al., 1999). A Nikon Coolpix 990 digital camera with a Nikon FC-E8 fisheye converter was placed on a monopod 2 m above the ground surface (above most understory vegetation) and leveled, with the top of the camera oriented north. Photographs were taken under overcast sky conditions between June and November 2004. Images were analyzed with the software, Gap Light Analyzer 2.0 (GLA; Frazer et al., 1999), employing the standard overcast sky model (UOC). Total transmitted light or photosynthetic photon flux density (PPFD; mol m⁻² day⁻¹) was calculated for the growing season (June through September) (Frazer et al., 1999; Drever and Lertzman, 2003).

Air and soil temperature were measured using temperature data loggers (Model DS1921G, iButton ThermoChron, Maxim/Dallas Semiconductor Corp., Dallas, Texas). Two loggers were installed at each station: the first, on a wooden stake 1 m above the ground surface (air), the second at 15 cm beneath the mineral soil surface (soil). For measurements of air temperature, loggers were placed on the inside of a small (10 cm long) plastic shield covered with aluminum foil to prevent direct radiation and perforated to allow airflow to minimize heat accumulation. Plastic containers were attached to a wooden arm extending perpendicular from the top of each stake. Temperature was recorded hourly at each point over a 2-3 wk period between late July and late September to sample the most stressful portion of the growing season. Measurements were taken synchronously within each site, but were staggered in time among sites (LWS = 19 July-5 August, BU = 10-31 August, and PH = 1-23 September).

Volumetric soil moisture was measured using time domain reflectometry (TDR; see Gray and Spies, 1995 for details). Stainless steel probes (30 cm) were inserted at an angle of 30° from the soil surface to sample the upper 15 cm of mineral soil. Measurements were taken multiple times during the growing season. At each measurement, all points within a site were sampled over a 1-2 day period of dry weather

(no precipitation in the previous 48 hr); all sites were visited within the same 1-wk period. At the time of sampling, probes were attached to the TDR monitor with alligator clips soldered to coaxial wire; data were collected on a palmtop computer. Volumetric soil moisture was calculated using the calibration curves of Gray and Spies (1995).

2.5. Data reduction

From the continuous measurements of air and soil temperature at each site, five days were selected to represent physiologically stressful summer conditions (hot, sunny days). We focus on these rather than average conditions over the growing season because they are more likely to limit persistence of species associated with forest-interior environments. From hourly readings for each of these days, we calculated a daytime mean and maximum temperature at each microclimatic station for air (06:00 - 20:00 hr) and soil (09:00 - 23:00 hr, displaced 3 hr to capture the heating lag between air and soil; e.g., Heithecker and Halpern 2006). We then computed an average mean and maximum for the five-day sample. For analysis of soil moisture, the driest measurement during the growing season (4-12 August) was selected from the set of periodic samples at each station. Although soil moisture often declines into September (Gray and Spies, 1997; Gray et al., 2002), several extended periods of precipitation precluded use of the September measurements.

For the aggregates, data representing distance from edge were averaged for pairs of transects within each site: south- and west-facing transects representing warmer exposures (S/W; >135° and <315°) and north- and east-facing transects representing cooler exposures (N/E; >315° and <135°).

2.6. Comparability of physical environments and overstory structure

Comparisons between forest aggregates and reference environments (harvest area and control) were conducted separately for each site because of marked differences in climate among locations. However, even within sites, there was variation in topography and overstory structure,

which can affect light availability and temperature. To test for systematic differences in topography among the control, harvest area, and forest aggregates at each site, we used one-way analysis of variance (ANOVA) to compare predicted values of heat load ($n = 19$ -26 stations per environment). If environments differed significantly ($P \leq 0.05$), individual means were compared with a Tukey HSD test (Zar, 1999). To test for significant differences ($P \leq 0.05$) in overstory structure between controls and aggregates, two sample t -tests ($n = 20$ and 10 plots, respectively) were used to compare tree density, basal area, and canopy height (average height of dominant and codominant trees).

2.7 Microclimatic gradients within aggregates and comparisons to reference environments

For aggregates at each site, microclimatic means (and SEs) were plotted relative to distance from the edge for each aspect group (S/W and N/E). To compare these values to those in the harvest area and control, we used a simple and conservative approach that accounted for microclimate variation within these reference areas (see Laurance et al., 1998). From the 20 (or 19) microclimatic stations representing each reference environment, we generated a 95% confidence interval around the mean for each microclimatic variable. Means of aspect groups at each distance that fell outside the confidence interval were considered to differ from the reference environment. Formal statistical tests were not conducted due to the small sample size at each distance ($n = 2$). Instead, our primary objective was to document spatial trends and the range of distances over which means differed from the two reference areas.

3. Results

3.1. Comparability of topography and overstory structure between aggregates and reference environments

Heat load (predicted from slope and aspect) was comparable between forest aggregates and reference environments at BU and PH (Table 2). At LWS, however, heat load was significantly greater in the control than in the aggregates,

reflecting its more westerly aspect (Table 1). As a result, reference temperatures were higher than expected in the control.

Overstory structure showed significant variation in two of the three sites (Table 2). At BU, where differences were fairly small, basal area was ~25% greater and canopy height 18% greater in the aggregates than in the control. However, at PH, density and basal area were 25% and 70% greater in the control; thus, reference values for light and daytime temperature were likely to be lower than expected.

3.2. Transmitted light

Transmitted light (PPFD) declined steeply inside the edges of aggregates at each site (Fig. 2). Patterns of decline were similar at BU and PH: PPFD dropped more rapidly along N/E than S/W transects, with the greatest reduction within 10-15 m of the edge (Fig. 2). At these distances, PPFD was 1.5 to nearly 3 times higher along S/W exposures. Beyond 15 m, PPFD generally declined to levels observed in the controls (except for S/W transects at PH).

Declines in PPFD were not as steep at LWS (Fig. 2) where tree density was markedly lower and the edges of aggregates were less continuous. As a result, differences between aspects were small and PPFD remained elevated above that in the control at nearly all distances from the edge.

At all sites, light levels within aggregates were consistently lower than those in the harvest area (Fig. 2). In addition, aggregates significantly reduced PPFD in the adjacent harvest area to distances of 10-30 m. For four of six aspect groups, PPFD was significantly reduced to a distance of 20 m in the harvest area; distance effects were greatest at LWS where tree heights were greatest (49 m vs. 32-33 m at BU and PH).

3.3. Air temperature

Gradients in air temperature within aggregates were similar to those of transmitted light, but were less steep across the edge (Fig. 3). Aspect had a large effect on maximum temperature at all sites and on mean temperature

at BU and PH. At the aggregate edge (and occasionally to a distance of 5-10 m), temperatures along S/W exposures did not differ from those in the harvest area. In contrast, at similar distances along N/E exposures, temperatures (maxima in particular) were significantly lower than in the harvest area and dropped steeply, stabilizing within 20 m of the edge. Differences in maximum temperature between N/E and S/W exposures were as large as 6°C.

In contrast to PPF, temperatures within the aggregates were significantly higher than those in the controls (except at BU; Fig. 3). As with light, aggregates significantly reduced mean and maximum temperatures in the adjacent harvest area, but only to distances of 5-20 m and more so on N/E than on S/W exposures.

3.4. Soil temperature

Gradients in soil temperature within aggregates were similar to those of air temperature, declining with distance from the edge, with temperatures greater on S/W than N/E exposures (except at LWS) (Fig. 4). Mean and maximum temperatures also showed high spatial coherence. However, soil temperatures differed from air temperatures in several respects. Means were ~2 to 9 °C lower and maxima ~6 to 13°C lower than air temperatures. Soil temperatures also exhibited greater spatial variation within 15 m of the forest edge and greater variability between points at the same distance within each aspect group (larger SEs; Fig. 4). In addition, temperatures within 15 m of the edge were often as high as those in the harvest area. However, further from the edge (beyond 10-30 m), and typically on N/E exposures, soil temperatures were often comparable to those in the control (e.g., BU and PH).

Effects of aggregates on soil temperatures in the harvest area were difficult to discern. Only at PH were temperatures adjacent to the aggregates consistently cooler than those at reference stations in the harvest area; a similar pattern was observed at BU, but only for the N/E exposure. At BU and LWS, temperatures fluctuated widely among adjacent stations in the

harvest area and between points at the same distance within each aspect group.

3.5. Volumetric soil moisture

Soil moisture was generally low at the time of sampling, ranging from ~8 to 14% within forest aggregates. Unlike light and temperature, however, it was highly variable over relatively short distances, showing no detectable gradients with proximity to edge (data not shown). Variation between pairs of transects comprising each aspect group was high and there were few consistent differences between these groups. Moreover, 95% confidence intervals for mean soil moisture in the controls and harvest areas showed near (LWS), partial (PH) or complete overlap (BU). As a result, there were few discernable differences in soil moisture between aggregates and reference areas.

4. Discussion

4.1. Microclimatic conditions within 1-ha forest aggregates

Do microclimatic conditions within forest aggregates differ from those of larger tracts of undisturbed forest? Our measurements within these 1-ha patches during hot summer days indicate that most variables were altered significantly at or near the forest edge, but to varying degrees at greater distance depending on topography and overstory structure. We detected increases in light to distances ranging from <5 m along N/E exposures at BU (where forests were most dense) to >40 m at LWS (where aggregate edges were not continuous and stands were open). At all sites, however, most of the change in transmitted light occurred within 20 m of the edge, and it was within this relatively narrow ecotonal area that differences between N/E and S/W exposures were greatest. In old-growth coniferous forests in southern Washington, Chen et al. (1995) documented elevated light to distances of 30-60 m from a forest-clearcut edge. In contrast, in temperate and tropical broadleaved forests, others have documented increases in light to distances of ~15 m (Williams-Linera et al., 1998; Davies-Colley et al., 2000).

Gradients in temperature within the aggregates were driven, in part, by changes in solar radiation (Chen et al., 1995; Davies-Colley et al., 2000), but also by advective heating as wind moved warm air masses from the harvest area across the forest edge (e.g., Chen et al. 1995). As a result, mean and maximum air temperatures were typically elevated to greater depths in the aggregates than were levels of light. Many factors may contribute to this effect, including topography, forest structure, and speed and direction of wind (Chen et al., 1995 and references therein). We lack data on wind and thus, are unable to assess its contribution to patterns of elevated temperature. However, variation in the depth to which temperature was elevated was consistent with differences in overstory structure among sites. At BU, where the aggregates and control shared similar topography and forest structure and where stem density was highest, air and soil temperatures showed very similar sensitivity to edge as did light: effects were limited to the edge (0 m) on N/E exposures and to 20 m (occasionally to 30 m) on S/W exposures. At PH, comparisons were confounded, in part, by the inherently lower temperatures in the control resulting from its greater stem density. Had forest structure been more similar between experimental units, it is likely that temperatures would have been more comparable. Nevertheless, edge effects were limited in spatial extent: air temperatures stabilized within 10 m on N/E exposures and within 30-40 m on S/W exposures. In contrast to these sites, patterns at LWS clearly illustrate the susceptibility to edge effects of forests with low stem density and an open canopy structure. Forest edge, defined as a fixed distance from the aggregate center, was often several to as many as ten meters from the nearest tree. Consequently, at essentially all points within the aggregates, air and soil temperatures were higher than reference temperatures in the control; this may reflect both greater penetration of solar radiation and greater wind speed through a more open forest (Fons, 1940; Raynor, 1971; Chen et al., 1995). Differences would have been even greater had the control and aggregates occupied more comparable aspects with similar heat loads (Table 2).

Soil moisture at 0-15 cm depth in mid-August was generally low at all sites, consistent with a pattern of prolonged summer drought in this region (Gray and Spies, 1997). However, unlike light and temperature, soil moisture did not exhibit a monotonic relationship with distance from edge, nor did it differ significantly between the strongly contrasting environments of the control and harvest area. We observed similar insensitivity to overstory structure in comparing soil moisture across a broad range (0-100%) of dispersed retention (Heithecker and Halpern, 2006), as did Barg and Edmonds (1999). Despite major differences in solar radiation and heating, greater evaporation in harvest areas may be balanced by greater transpiration in the forest where tree roots are more abundant (e.g., Morecroft et al., 1998; Chen et al., 1999). High spatial variation along the aggregate transects suggests that heterogeneity in understory cover, microtopography, and edaphic properties (e.g., organic matter) is likely to be more important than overstory structure in determining soil moisture availability (Joffre and Rambal, 1993; Breshears et al., 1998; Xu et al., 2002).

4.2. *Effects of aspect*

To what extent are edge effects mediated by aspect? Our comparisons of transects representing distinct aspect groups indicate strong effects of edge orientation. This is consistent with the findings of Chen et al. (1995) in old-growth Douglas-fir forests (depth-of-edge influence of 30 vs. 60 m for NE- and SW-facing edges), and with many others (Wales, 1972; Palik and Murphy, 1990; Matlack, 1993; Young and Mitchell, 1994; Chen et al., 1995; Cadenasso et al., 1997; Dignan and Bren, 2003). In our aggregates, differences in light and temperature between aspect groups were greatest at the edge and to distances of up to 10 m. Beyond this, however, microclimatic conditions tended to stabilize rapidly along N/E exposures at levels comparable to, or somewhat above those in the controls, but showed gradual and continuous change along S/W exposures, often to the center of the aggregate, 56 m from the edge. Hence, effects of aspect were manifested both in the magnitude of change and its spatial

extent (distance). Clearly, in the northern hemisphere, south-facing edges experience greater heat load than do north-facing edges because they receive greater direct radiation. To what extent variation in the depth of elevated temperature can also be attributed to aspect-related differences in wind direction remains unclear.

4.3. Effects of aggregates on adjacent harvest areas

In studies of edge effects, emphasis is typically placed on the depth and magnitude of effects within intact forest (e.g., Chen et al., 1993; Matlack, 1993; Chen et al., 1995). Although our primary objective was to understand microclimatic variation within the aggregates, we were also able to document the extent to which forest patches reduced light and temperature stress in the harvest areas, which may be important for recolonization by forest species. As expected, solar radiation was significantly reduced to distances of 20-30 m from the edge—somewhat less than the heights of dominant/codominant trees. However, moderation of air temperature was less apparent, extending no further than 20 m from the edge (and typically less for temperature maxima). Greater mixing of air masses in the harvest area may reduce the distance to which edge-related shading lowers local air temperatures (Chen et al., 1993). Interestingly, we did not observe similar effects on soil temperature: mean and maximum temperatures were highly variable adjacent to the edge (and beyond), suggesting that local variation in other factors, including cover of understory vegetation or residual logging slash may exert greater controls on soil temperature than shading by neighboring trees (e.g., Chen et al., 1993; Heithecker and Halpern, 2006).

4.4. Correspondence between microclimatic and biological gradients within aggregates

Are gradients in microclimate consistent with biological responses within these forest aggregates? Previous studies of forest aggregates at BU and PH suggest that initial (first- and second-year) responses of vascular

plants and bryophytes were consistent, in part, with the gradients in microclimate documented in the current study. However, the spatial coherence of biological and environmental changes was often relatively poor. For example, the abundance of one-third of the more common herbaceous species declined with proximity to the edge, as did species richness (Nelson and Halpern, 2005b). However, these declines occurred largely within 5 m of the edge—comparable to the distances over which light was elevated (5-10 m), but significantly less than the distances over which air temperatures remained elevated. Similarly, ruderal species, absent prior to harvest, established infrequently within the aggregates and only to a distance of 10 m from the edge, consistent with trends in transmitted light. Responses of ground-layer bryophytes were mixed. Mosses did not show detectable responses to edge, but liverworts, which are thought to be more sensitive to temperature, humidity, and substrate quality (Söderström, 1988; Frisvoll and Prestø, 1997; Fenton et al., 2003), showed significant declines in cover and richness (Nelson and Halpern, 2005a). Similar to vascular plants, however, declines were limited to a distance of 10 m, consistent with trends in light, but truncated with respect to air temperature. Finally, despite strong contrasts in light and temperature along N/E and S/W exposures, aspect did not affect responses of vascular plants or bryophytes.

Considered together, these studies highlight the potential disparity between environmental and biological responses to edge, which has been observed elsewhere (Matlack, 1993, 1994). In this system, forest understory plants appear to exhibit threshold responses to more continuous changes in microclimate and these thresholds are typically exceeded only near the edge. It is important to acknowledge, however, that our inferences are based on short-term observations of a limited set of forest organisms. If responses to environmental stress are lagged, the magnitude or depth of edge effects may increase over time (e.g., Nelson and Halpern, 2005b). Conversely, if closure of the forest edge occurs rapidly, light and temperature stress may be reduced (e.g., Didham and Lawton, 1999; Matlack 1994), allowing for recovery (although this may also exhibit a temporal lag; Matlack,

1994). Other groups of organisms may be more or less sensitive to these microclimatic gradients or to other aspects of habitat isolation that limit population persistence or reproduction (Simberloff 1988; Turner, 1999).

4.5. Implications for management

Although the Northwest Forest Plan mandates use of aggregated retention within the range of the northern spotted owl, the ecological benefits of small (0.2-1.0 ha) patches of undisturbed forest are not well understood. In the absence of empirical data, it has been assumed that microclimates within forest aggregates differ substantially from those of larger tracts of undisturbed forest (e.g., Franklin et al., 1997). However, our results suggest that levels of light and temperatures at the forest floor can be surprisingly similar to those of interior forests. Although edge environments were markedly altered, for five of the six variables sampled (all but mean air temperature), portions of each aggregate supported microclimates similar to those found in undisturbed forest. Moreover, short-term responses of vascular and non-vascular plants suggest that adverse ecological effects may be limited to a relatively narrow region of the edge. Thus, for some species, remnant patches of 1 ha in size may, in fact, provide habitats with a microclimate that is indistinguishable from that in interior forest. However, current retention standards allow for aggregates as small as 0.2 ha (~25 m in radius). Our results suggest that even if the depths of edge effects were not affected by patch size (Brothers and Spingarn, 1992; Young and Merriam, 1994; Burke and Nol, 1998), microclimatic conditions in aggregates this small would be severely compromised. Moreover, as forest fragments are reduced in size, they become increasingly susceptible to tree damage or mortality (e.g., Essen, 1994; Laurance et al. 1998) and thus, to greater incursion of edge effects.

The strong effects of aspect on microclimatic variation suggest that patch shape and orientation can be used to advantage in temperate regions to reduce the area susceptible to elevated light and temperature. Although a circular shape minimizes the ratio of edge to

area, the strong directionality of solar radiation and associated increases in temperature suggest that an ellipsoid, with its long axis oriented SW-NE would minimize the area subjected to edge effects, and thus the area in which adverse biological effects are more likely to occur.

Finally, comparisons among forests of differing density and canopy openness highlight the importance of stand structure in mediating edge effects. At LWS, characterized by large, widely spaced trees, light and temperature were elevated over a much larger portion of the aggregate, and effects of aspect were more subtle than at BU and PH. Stand structure should be an important consideration when selecting the size of aggregates; where canopy cover is less continuous, patches will need to be larger to provide at least some areas with microclimates that are comparable to undisturbed forest. However, barriers to plant or animal dispersal over greater distances of edge environment may reduce the functionality of these larger patches.

Both microclimatic and vegetation studies provide strong evidence that 1-ha sized aggregates are sufficiently large to provide microclimatic conditions that enable persistence, at least in the short term, of shade-dependent plant species at our study sites. In addition, they ameliorate microclimatic conditions in the adjacent harvest area, which may facilitate recolonization of species extirpated by timber harvest (Halpern et al., 2005; Nelson and Halpern, 2005a, b; Dovčiak et al., 2006). Successful reestablishment of such species is likely to depend as much on dispersal ability and how rapidly microclimatic conditions improve in the harvest area, as on the microclimatic suitability of forest aggregates.

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Table 1

Environmental attributes of forest aggregates and reference environments at each site.

Site	Lat., long. (deg)	Environment	Elevation (m)	Slope (deg)	Aspect (deg)
Butte (BU)	46.37N, 122.20W	Harvest area	988-1134	30	138
		Forest aggregates	988-1134	31	145
		Control	963-1158	28	146
Paradise Hills (PH)	46.01N, 121.99W	Harvest area	985-1027	6	157
		Forest aggregates	985-1027	6	155
		Control	853-902	6	133
Little White Salmon (LWS)	45.86N, 121.59W	Harvest area	792-939	29	74
		Forest aggregates	792-939	28	74
		Control	841-1000	23	316

Table 2

Variation in predicted heat load and overstory structure among forest aggregates and reference environments at each site.

Site	Variable	Harvest area		Forest aggregates		Control		<i>P</i>
		Mean	(SE)	Mean	(SE)	Mean	(SE)	
Butte (BU)	Heat load ^a	0.77	(0.02)	0.78	(0.02)	0.81	(0.02)	0.261
	Basal area (m ² ha ⁻¹) ^b	—	—	67	(3.6)	58	(2.2)	0.026
	Tree density (no. ha ⁻¹) ^b	—	—	830	(69.0)	1014	(111.9)	0.280
	Canopy height (m) ^c	—	—	33	(0.5)	28	(0.7)	<0.001
Paradise Hills (PH)	Heat load	0.90	(0.01)	0.91	(0.01)	0.89	(0.01)	0.101
	Basal area (m ² ha ⁻¹)	—	—	61	(3.5)	77	(1.8)	<0.001
	Tree density (no. ha ⁻¹)	—	—	585	(40.0)	1001	(47.2)	<0.001
	Canopy height (m)	—	—	32	(0.8)	27	(0.3)	<0.001
Little White Salmon (LWS)	Heat load	0.55 ^a	(0.02)	0.58 ^a	(0.02)	0.79 ^b	(0.02)	<0.001
	Basal area (m ² ha ⁻¹)	—	—	72	(11.8)	69	(7.9)	0.804
	Tree density (no. ha ⁻¹)	—	—	305	(55.3)	233	(29.6)	0.216
	Canopy height (m)	—	—	49	(1.1)	49	(0.6)	0.632

P values for heat load are from one-way ANOVA ($n = 19-26$ microclimatic stations per environment); means followed by different letters differ significantly based on a Tukey HSD test. *P* values for basal area, tree density, and tree height are from two-sample t-tests ($n = 10$ plots for forest aggregates and 19 or 20 plots for harvest area and undisturbed forest).

^a Heat load (unitless) based on (McCune and Keon, 2002)

^b Trees ≥ 5 cm dbh

^c Mean height of dominant and codominant trees

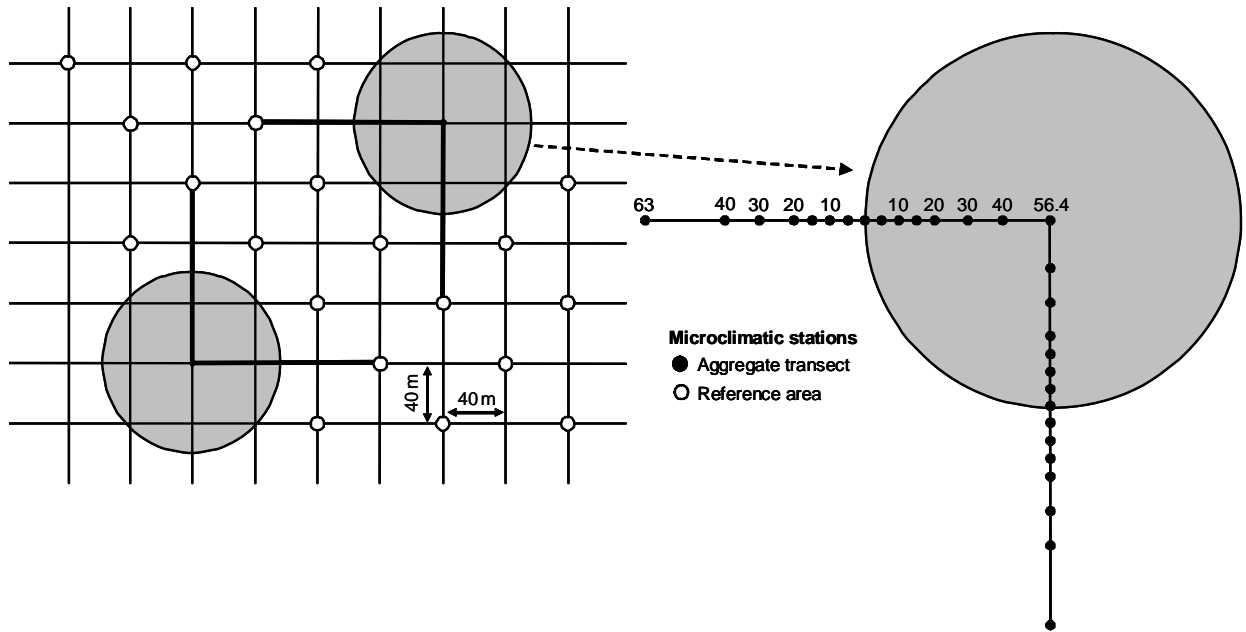


Fig. 1. Sampling design illustrating the distribution of microclimatic stations. For aggregates, stations were placed at 15 points spaced 5-23 m apart extending from the aggregate center 63 m into the harvest area. Reference stations in the harvest area (or undisturbed forest [control]; not shown) were established at 20 (in one case 19) points randomly selected from permanent plots on a systematic grid (40 x 40 m spacing).

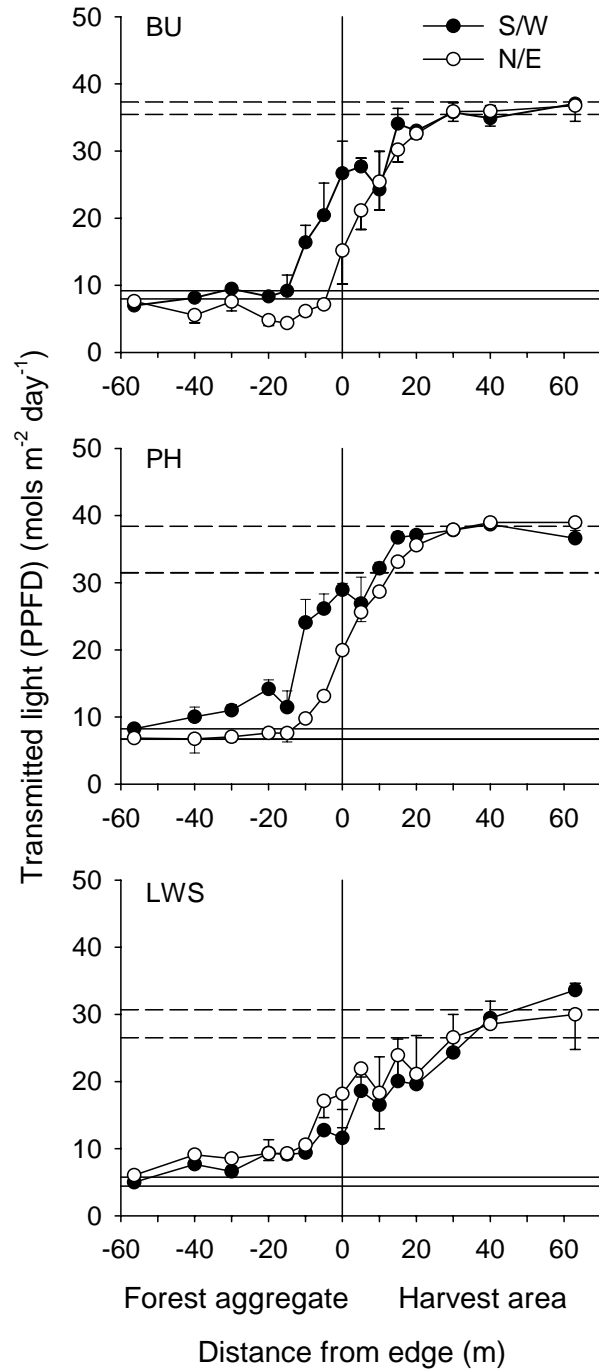


Fig. 2. Gradients in transmitted light (PPFD) with distance from the aggregate edge at each of the three study locations (BU = Butte, PH = Paradise Hills, LWS = Little White Salmon). Values are the means (± 1 SE) at each distance of two transects representing south- and west-facing aspects (S/W) or north- and east-facing aspects (N/E). Solid and dashed lines are 95% confidence intervals of the mean ($n = 20$ [or 19]) for reference stations in the control (undisturbed forest) and harvest area, respectively.

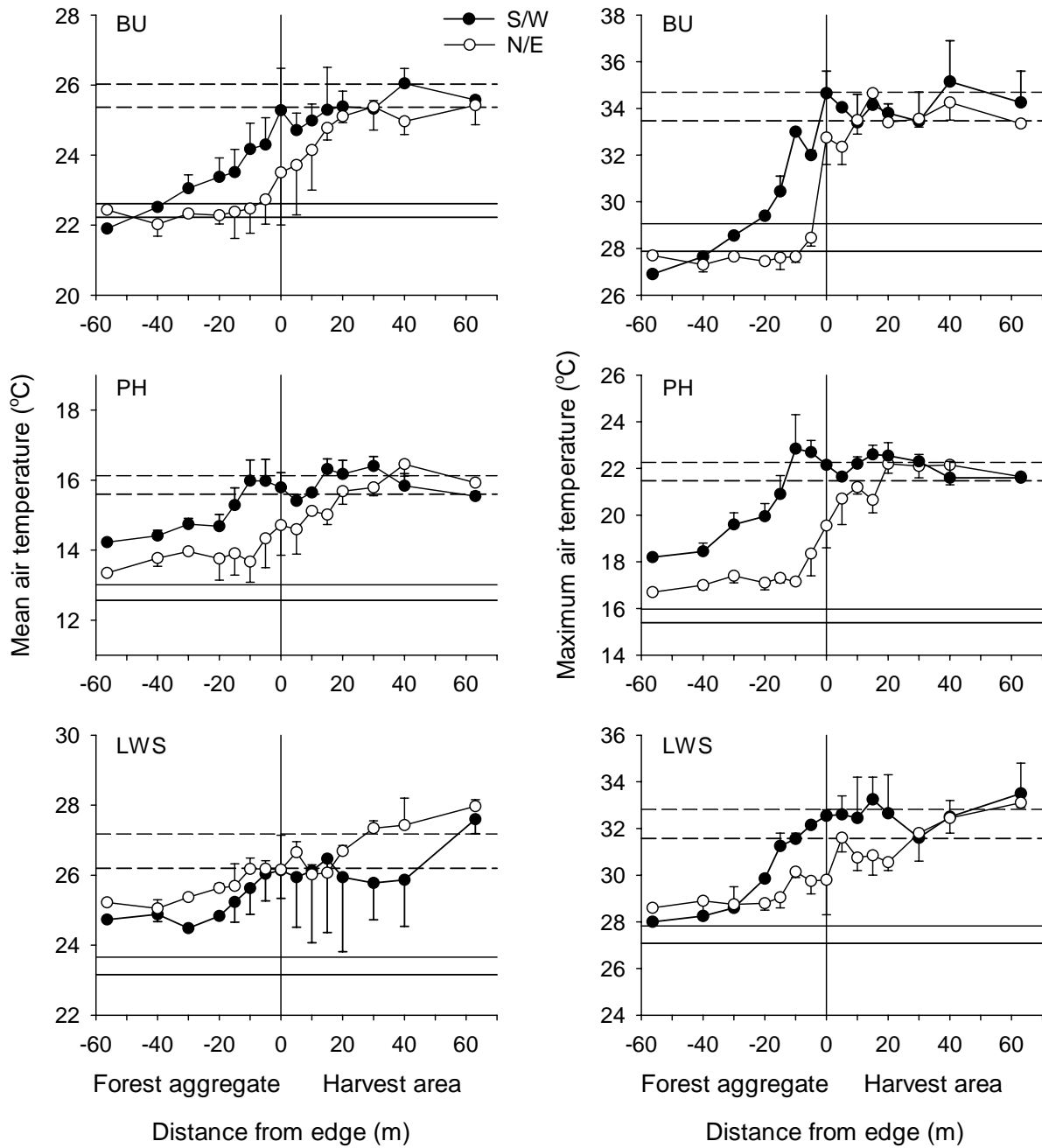


Fig. 3. Gradients in mean and maximum air temperature (1 m above the ground surface) with distance from the aggregate edge at each of the study locations (see section 2.4. *Microclimatic measurements*, for details). See Fig. 2 for other details.

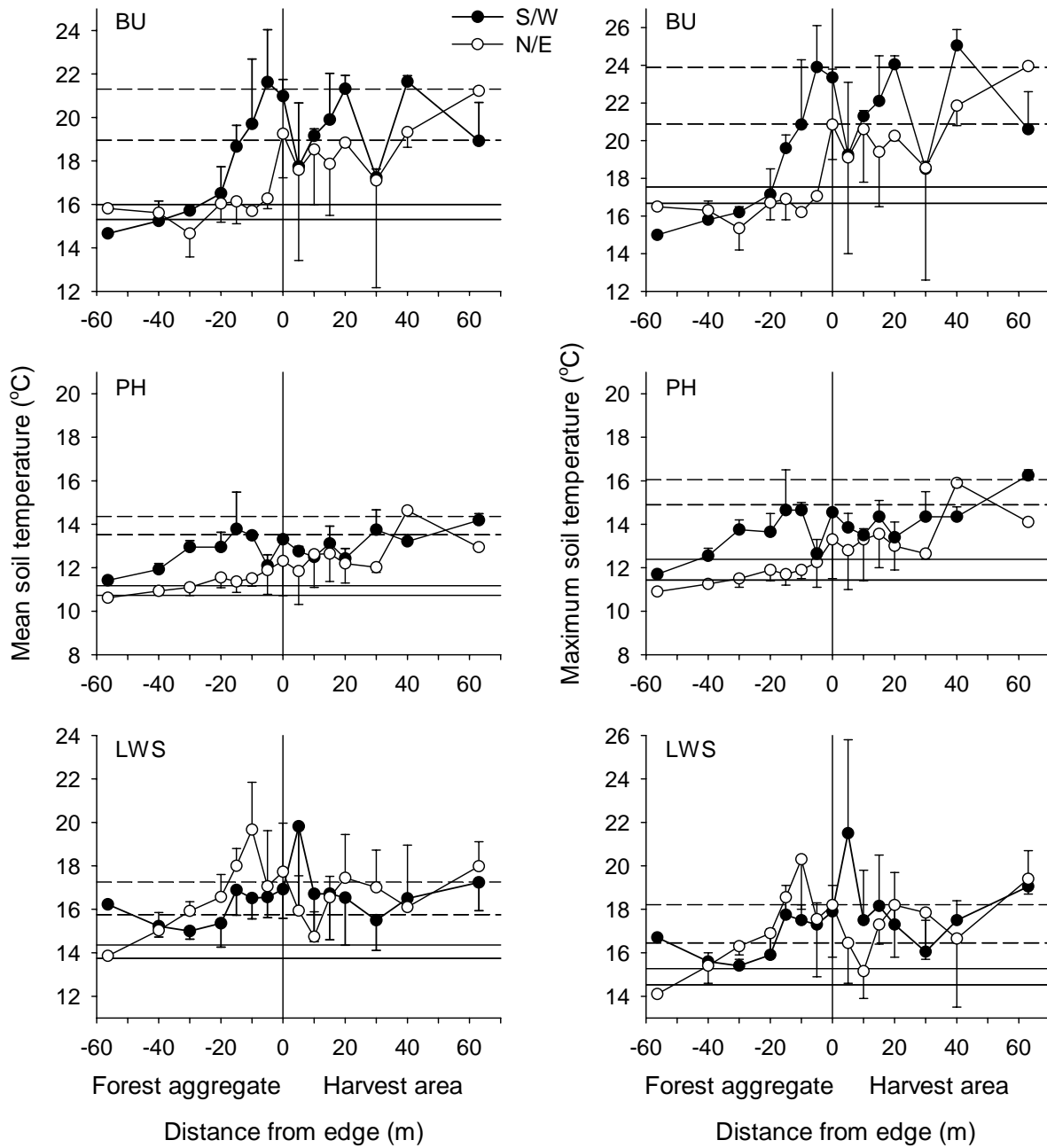


Fig. 4. Gradients in mean and maximum soil temperature (15 cm depth) with distance from the aggregate edge at each of the study locations (see section 2.4. *Microclimatic measurements*, for details). See Fig. 2 for other details.