Long-Term Influence of Retained Forest Aggregates on Conifer Regeneration in Harvest Units of the Pacific Northwest

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Abstract

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Aggregated retention, in which undisturbed patches of forest are retained within harvest units, is increasingly used in forests managed for multiple objectives. Retained aggregates can serve as refugia for disturbance-sensitive species and as sources for dispersal into adjacent harvested areas. However, it less clear how they shape natural regeneration processes, including the recruitment and growth of early- and late-seral tree species. I modeled the effects of distance from edge (0-70 m), edge type (1-ha aggregate vs. harvest-unit boundary), and edge exposure (a proxy for heat/moisture stress) on the recruitment and height growth of early- and late-seral conifers nearly two decades after aggregated-retention harvest at four sites in the Cascade Mountains of Oregon and Washington. Aggregates effectively mimicked the influences of harvest-unit (intact-forest) boundaries on recruitment and growth. For both seral groups, recruitment density declined similarly with distance from edge. Distance-related trends in growth were generally similar between edge types but varied among sites. Height tended to increase with distance but peaked closer to edge for late-seral advanced regeneration than for early-seral recruitment. Late-seral recruits—common in the two Washington sites—were shorter than survivors and unresponsive to distance from edge. Edge exposure had no consistent effect on recruitment or height growth. My results suggest that 1-ha aggregates are functionally equivalent to larger blocks of intact forests in their influences on conifer recruitment and growth. By distributing aggregates across harvest units, managers can accelerate rates of recruitment and promote heterogeneity in the seral composition and height structure of the regenerating forest. Additional research is needed on the sensitivity of regeneration processes to aggregate size, shape, and spatial distribution.

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1. Introduction

Historically, forest management has prioritized wood production and rapid regeneration of crop trees over the ecological values of forests, while undisturbed reserves have been set aside to conserve biological diversity (Baker et al., 2013). There has been growing recognition, however, that forests can be managed both for their commodity and ecological values. “Retention forestry” has emerged globally as a strategy for balancing timber production and maintaining or enhancing recovery of biodiversity in managed forests (Gustafsson et al., 2012; Fedrowitz et al., 2014; Franklin et al., 1997). The approach leaves individual trees or, more commonly, undisturbed groups of trees (aggregates), within harvest units to provide habitats, substrates, or refugia for disturbance-sensitive species. A primary objective of aggregates is to serve a “lifeboating” function through disturbance, providing areas of relatively undisturbed habitat from which species can repopulate harvested areas (Franklin et al., 1997; Halpern et al., 2012; Nelson and Halpern, 2005a, 2005b). In addition to serving as refugia, aggregates can promote recovery of biodiversity in the adjacent harvested area through effects of “forest influence” (*sensu* Baker et al., 2013, 2015, 2016a, 2016b).

Habitat fragmentation resulting from timber harvest has spurred an abundance of research on edge effects, including the depth and extent to which remnant forest has been altered (Chen et al., 1995; Harper et al., 2015; Laurance et al., 2007; Murcia, 1995; Saunders et al., 1991; Turner, 1996). By comparison, the potential for forest remnants to shape the recovery of adjacent clearings has received little attention. Recent research has demonstrated both “positive” and “negative” effects of residual forest edge on biodiversity, with the nature of the effect dependent on species’ affinities for early-seral (open) or late-seral (closed) habitats (Baker et al., 2013, 2015, 2016a; Huggard and Vyse, 2002). For example, environments close to the edge are more likely to favor late-seral, but to suppress early-seral plant species (Baker et al., 2015; Dynesius et al., 2008; Nelson and Halpern, 2005b).

There are two principal mechanisms by which forest aggregates can influence biological processes in adjacent harvest areas: by tempering the microclimate and dispersing seeds. Through shading, residual forest edges produce gradients of light, temperature, and humidity (Baker et al., 2014, 2016b; Dovčiak and Brown, 2014; Heithecker and Halpern, 2007) that can shape the post-harvest establishment, growth, and survival of regenerating trees (Coates, 2000; Hughes and Bechtel, 1997; York et al., 2003). However, responses are likely to vary with species' resource requirements and tolerance of shade (Bazzaz, 1979; Minore, 1979). For example, recruitment of early-seral, shade-intolerant, species may be inhibited close to the edge, but recruitment or survival of late-seral, shade-tolerant species may be enhanced.

Forest aggregates may also serve as local sources of seed within harvest units. For species with wind-dispersed seeds, density of seed rain declines steeply with distance from the source (Carkin et al., 1978; Clark et al., 1999; Dovčiak et al., 2007; Huggard and Vyse, 2002) resulting in greater potential for establishment near the forest edge (Dovčiak et al., 2005; Kremer et al., 2014). The distance to which seeds are carried can also vary with the orientation of the edge if the timing of dispersal coincides with seasonal winds (e.g., winter storms).

Although aggregated retention offers the opportunity to distribute forest influence over a greater portion of the harvest unit, it is not clear that aggregates are as effective as the longer, deeper edges of intact forests. The small size and isolation of aggregates makes them susceptible to internal edge effects (e.g., stem breakage, windthrow, and abiotic stressors) that may compromise these functions (Esseen, 1994; Jönsson et al., 2007; Lovejoy et al., 1986; but see Urgenson et al., 2013a). Nevertheless, in a mature *Eucalyptus* forest in Tasmania, Baker et al.

(2016b) found few differences in microclimate adjacent to aggregate (1-6.5 ha) and intact-forest edges. Similarly, in a global (four-continent) comparison of plant compositional responses, Baker et al. (2016a) reported generally comparable effects of forest influence associated with aggregate and intact-forest edges. In a companion study of edge types at one of these sites, Curzon et al. (2017) detected few differences in the regeneration of *Populus tremuloides* 12 years after harvest.

In this study, I explore edge-related gradients in the recruitment and height growth of naturally regenerating conifers nearly two decades after aggregated-retention harvests of mature western Cascade forests of Oregon and Washington, USA. I hypothesized the following relationships with distance from edge, edge type (aggregate vs. intact forest), and edge exposure (cool/moist vs. warm/dry) for early- and late-seral species consistent with their differing tolerance of shade and heat/drought stress (Minore, 1979) (Fig. 1):

H1. Distance from edge. Post-harvest recruitment of early- and late-seral species will decline with distance from edge (Fig. 1a and b), consistent with a decline in seed rain. Height growth, irrespective of origin (post-harvest recruitment or advanced regeneration), will increase with distance from edge in light-demanding, early-seral species (Fig. 1c); however, it will decrease in less stress-tolerant, late-seral species (contingent on exposure, Fig. 1d).

H2. Edge type (aggregate vs. intact forest). Post-harvest recruitment will be greater adjacent to intact-forest than to aggregate edges (Fig. 1a and b), assuming greater availability of seed along the longer, deeper, edges of harvest units. However, edge type will not affect the relationship with distance (parallel negative slopes). In contrast, height growth will not vary with edge type (Fig. 1c and d), assuming comparable shading along aggregate and intact-forest edges.

H3. Edge exposure. Relationships with distance from edge will differ between warmer/drier, south/west-facing edges (S/W exposures) and cooler/moister, north/east-facing edges (N/E exposures). Specifically, recruitment of early-seral species will be greater, but will decline more steeply with distance from edges with S/W vs. N/E exposures (Fig. 1a); for late-seral species, the pattern will be reversed (Fig. 1b). Height growth of early-seral species will increase with distance from edges with N/E exposures but will change minimally for edges with S/W exposures (Fig. 1c). In contrast, height growth of late-seral species (including post-harvest recruitment and advanced regeneration) will decline with distance from edges with N/E exposures but will change minimally for edges with S/W exposures (Fig. 1d).

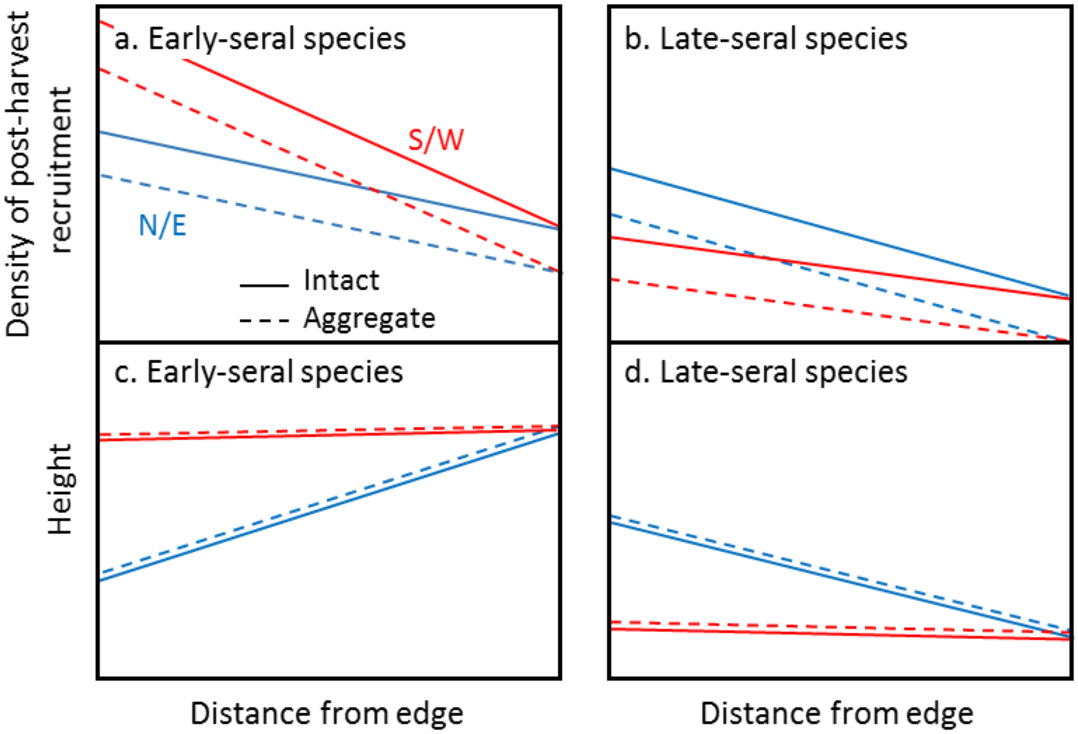

Fig. 1. Hypothesized relationships for density of post-harvest recruitment and height growth to distance from edge, edge type (intact forest vs. aggregate) and edge exposure (S/W vs. N/E) for (a, b) early-seral and (c, d) late-seral species.

2. Methods

2.1. Study area and experimental design

I conducted my research within the context of a long-term, regional-scale experiment in variable retention, The Demonstration of Ecosystem Management Options (DEMO) Study (Aubry et al., 1999, 2009). The experiment was established in 1994 to explore how level and pattern of overstory retention shape ecological responses to harvest of mature coniferous forests in the Pacific Northwest. The experimental treatments were replicated at six sites—three in the southern Cascades of Washington, one in the Black Hills of coastal Washington, and two in the southern Cascades of Oregon. Of these, I selected two Cascade sites in each state: Butte, (BU) and Paradise Hills (PH) in Washington; Dog Prairie (DP) and Watson Falls (WF) in Oregon (Fig. 2)—sites representing a range of physical environments and forest structures (Aubry et al., 2009). The full experimental design includes a control (100%), 75% aggregated retention (75%A), and four treatments comprising a factorial combination of dispersed (D) and aggregated (A) retention at 40 or 15% of the original basal area (i.e., 40%D, 40%A, 15%D, and 15%A). I limited my sampling to the 15%A treatment where it was easier to isolate the influences of individual aggregates.

The climate of this region is maritime: summers are warm and dry; winters are cool and wet. Most precipitation falls between October and April (Franklin and Dyrness, 1988). Soils are moderately deep and well-drained loams to loamy sands originating from andesite, breccia, or basalt parent material or pumice deposits (Radtke and Edwards, 1976; Wade et al., 1992). Sites vary in elevation (942 to 1536 m), topography (flat to steep), and local climate (warmer, drier *Abies concolor* zone to cooler, moister *Abies amabilis* zone; Franklin and Dyrness, 1988). At the time of harvest (1997 or 1998) stand ages ranged from 70 to 165 years. *Pseudotsuga menziesii*

(Douglas-fir) was the dominant canopy species at all sites, but overstory structure and composition varied (Table 1; Maguire et al., 2007; Urgenson et al., 2013a). Intact forests adjacent to each experimental unit were of similar age and structure as the forests within each unit prior to harvest.

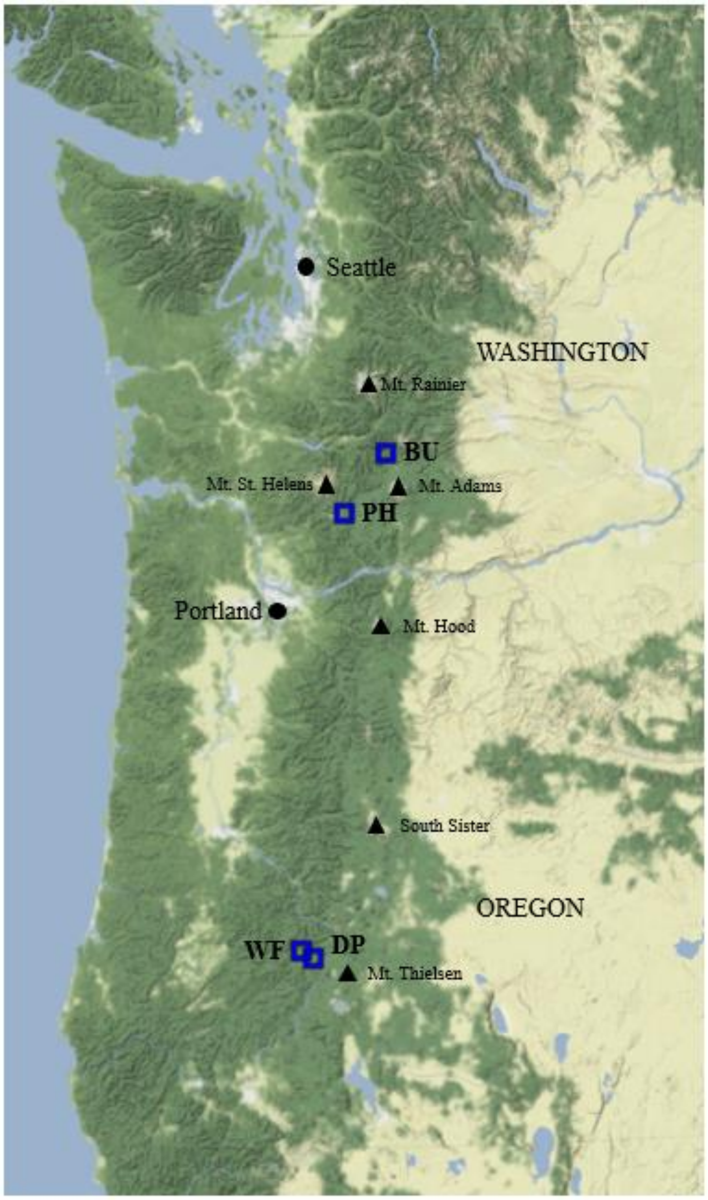

Fig. 2. Locations of the four study sites in Washington (BU, PH) and Oregon (WF, DP) (base layer from Stamen Design and OpenStreetmap, 2018).

Table 1. Environmental characteristics, pre-harvest overstory structure, and treatment history of the four experimental units.

	Butte (BU)	Paradise Hills (PH)	Dog Prairie (DP)	Watson Falls (WF)
Environmental characteristics				
Latitude, longitude	46.37 N, 121.59 W	46.01 N, 121.99 W	43.20 N, 122.20 W	43.27 N, 122.34 W
Elevation (m)	961 - 1121	959 - 1018	1356 - 1536	942 - 957
Slope (%)	14 - 42	3 - 15	20 - 28	0 - 4
Aspect	E-SE	S-SE	SW	flat
Precipitation (mm)[a]	1860	2968	1683	1443
Temperature (min, max) (°C)[b]	-5.5, 21.5	-4.0, 22.1	-6.4, 22.3	-3.7, 26.2
Pre-harvest overstory structure				
Stand age (years)	70 - 80	110 - 140	165	110 - 130
Basal area (m^2/ha)[c]	64.8	79.1	105.6	45.4
Density (trees/ha)[c]	928	732	460	445
Previous management history	none	none	thinned (1986)	salvaged dead trees (1970 - 1978)
Treatment history				
Date of harvest	May - Sep 1997	Jun - Oct 1997	Jul - Sep 1998	Jun - Oct 1998
Yarding method	helicopter	shovel loader and skidder	helicopter	shovel loader
Non-merchantable trees[d]	retained	felled	absent	felled if damaged
Date of planting	Apr - May 1998	Jun 1999	May - Jun 1999	Apr - Jun 1999
Planting density (seedlings/ha)	825	468	698[e]	466

[a] Estimated mean annual precipitation, derived from DAYMET (Thornton et al., 1997), a set of 1-km GIS raster coverages generated from meteorological records (1980–1997) and digital elevation data.

[b] Estimated monthly means, derived from DAYMET; min is the January minimum temperature and max is the August maximum.

[c] Trees ≥5.0 cm dbh

[d] Trees <18 cm dbh

[e] Replanted in Apr 2001 (405 seedlings/ha) following significant gopher-related mortality of the original cohort.

Experimental units are ~13 ha in area (320 × 400 m) with two circular, 1-ha (~56-m radius) aggregates retained in diagonally opposite corners (Fig. A1). All merchantable trees (>18 cm diameter at breast height, dbh) were cut in the remainder of each unit. Yarding methods varied among sites and included helicopter or ground-based systems (Table 1). Treatment of non-merchantable (subcanopy) stems also varied: stems were retained at BU, felled at PH, and felled if damaged at WF. Sub-canopy stems were largely absent at DP. Slash was left untouched at all sites except WF, where fuel loadings were deemed excessive and partly reduced by pile burning. Additional details on treatment implementation are reported in Halpern and McKenzie (2001).

Conifer seedlings were planted in the harvested portions of each unit in the spring or early-summer after harvest. The species mix (mostly early-seral species) and density varied among sites (Table 1), but densities were considerably lower than typical of operational units to limit interaction with natural regeneration. Survival and growth of planted trees were examined in an earlier paper (Urgenson et al., 2013b) and are not considered here.

2.2. Sampling design

To capture the range of edge exposures in each harvest unit, I established multiple 70-m transects perpendicular to aggregate and harvest-unit boundaries (bordering intact forest) (Fig. 3). Where possible, I established two perpendicular transects per aggregate (four in total) and four additional transects from the harvest-unit boundaries (one per edge). Several combinations of edge type and exposure were not sampled at PH, DP, and WF due to the presence of roads, adjacent treatments, or windthrow damage. Transect locations along harvest-unit boundaries were determined randomly with the restriction that they not fall within 70 m of another edge (aggregate or intact forest) to reduce the potential for confounding (Heithecker and Halpern, 2007; Baker et al., 2016b). At each site, additional transects were established to increase sampling intensity. Those associated with aggregates were oriented 11 degrees from an existing transect to sample a comparable exposure without overlap. Those associated with intact forest were established randomly, with the same restrictions, but were at least 10 m from an existing transect. In adding transects, priority was given to aggregate edges (the focus of this study) and to sites in which the density of advanced regeneration was relatively low (to increase sampling intensity). In total, I sampled 47 transects (10 - 14 per site; Figs. A2-A5, Table A1, Appendix A).

Each transect began at the forest edge, defined by the line connecting the outer (harvest-unit facing) edges of the two nearest mature trees. From the edge, I established 15 rectangular plots (1 × 6 or 1 × 10 m), with the long axis perpendicular to the transect. Plots were spaced at 4-m intervals to 40 m, then at 45, 50, 60 and 70 m (horizontal distances). Plot length was 6 m where regeneration was denser (PH) and 10 m where it was sparser (BU, DP, and WF).

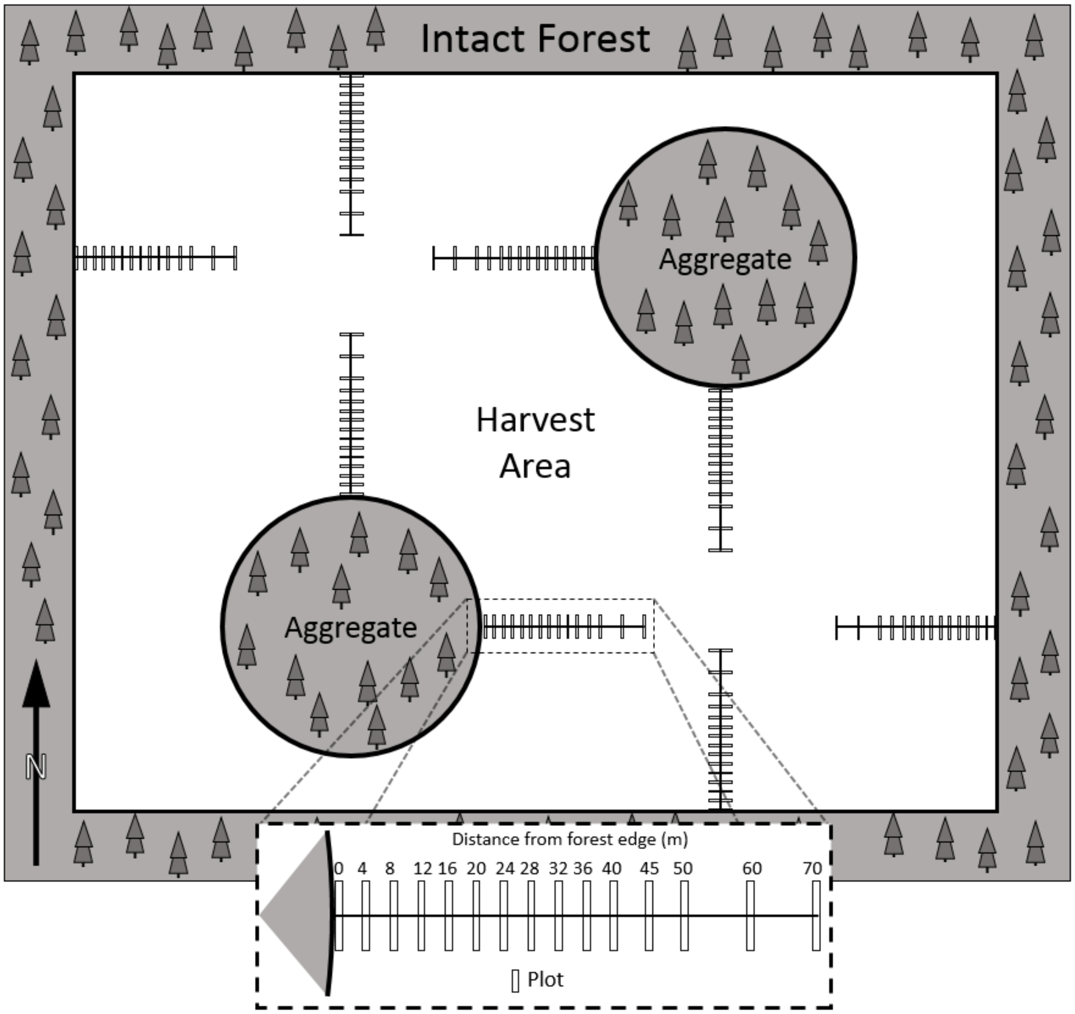

Fig. 3. Schematic layout of transects used to sample contrasting edge types (aggregate vs. intact forest) and edge exposures (N vs. S and W vs. E in this example). Harvest unit dimensions are 320 × 400 m; aggregates have a radius of ~56 m.

2.3. Data collection

Data were collected between 17 June and 29 August 2016. For each tree in each plot I determined the species, height (nearest 1 cm, or 10 cm for trees taller than 2 m), age, and origin (advanced regeneration, post-harvest recruitment, or planted). Origin provided the basis for distinguishing between post-harvest recruitment (hereafter ‘recruitment’) and surviving trees (advanced regeneration) and for assessing differences in their height growth. Origin was inferred from age as determined from a count of bud-scale scars, branch whorls or, for individuals that originated close to the time of harvest, ring counts from an increment core or basal cross-section of the tree. Basal sections were also taken for species that do not produce distinctive bud-scale scars or branch whorls (*Thuja plicata*, *Tsuga heterophylla*, and *Calocedrus decurrens*). It was not possible to determine origin (recruitment vs. planted) for a small percentage (2.2%) of stems. However, I treated these as recruitment because densities of naturally establishing trees were much greater than those of planted trees (Urgenson et al., 2013b).

I recorded several additional transect- and plot-scale descriptors. For each transect I recorded edge exposure (bearing perpendicular to the forest edge) and heights of 4 to 8 mature trees to characterize canopy height at the edge (Table A1, Appendix A). For each plot I recorded aspect and slope.

2.4. Data manipulation and species details

Edge exposure was converted to a continuous index of “northeastness” using a cosine transformation (range of -1 at 225 deg [S/W] to +1 at 45 deg [N/E]). At each site, the pre-harvest height distributions of advanced regeneration (surviving stems) were assumed to be comparable among and within transects, thus any trends with distance, edge type, or edge exposure were assumed to reflect variation in growth after harvest.

I treated *Abies grandis* and *A. concolor* as a single taxon in the Oregon sites (DP and WF), equivalent to *Abies grandis* in Washington. Distinguishing between these species in this region of the southern Cascades is difficult due to the blending of morphological traits (indicative of introgressive hybridization; Zobel, 1973). The few individuals of *Taxus brevifolia* encountered were not included in the analyses due to frequent physical damage and/or poor growth form. All species were assigned a seral status (early or late) based on descriptions in Burns and Honkala (1990), consistent with previous studies of these sites (Urgenson et al., 2013a, 2013b). Seral status coincides with species' relative tolerance of shade (ability to persist in the understory of mature, closed-canopy forest; Minore, 1979). For each plot I computed density of recruitment of each species and seral group.

2.5. Statistical analyses

To explore the hypothesized relationships with distance from edge, edge type, and edge exposure (Fig. 1), I used a series of generalized linear mixed-effects models (GLMMs). Response variables included density and height of recruitment, as well as height of advanced regeneration for both early-seral and late-seral species (six responses in total but see exceptions below). Potential predictors (fixed effects) in each model included distance from edge, edge type (aggregate vs. intact forest), edge exposure (-1 to 1), and all two-way interactions. Height models also included a quadratic distance term after exploratory analyses suggested a hump-shaped relationship with distance. Site and transect (nested within site) were treated as random effects; height models also included plot (nested with transect) as a random effect.

For many response variables, preliminary analyses indicated substantial variation among sites in the relationship with distance and edge type. To explore this variation, I ran site-specific models in addition to an 'all-sites' model. For one or more sites, density of post-harvest recruitment or advanced regeneration was sparse (Table 2), thus site-specific models could not be developed. In these instances, the all-site model was based on a reduced number of sites. Finally, whereas a single species typically dominated the late-seral group, *Tsuga heterophylla* and *Abies amabilis* were both common at PH as advanced regeneration and recruitment (Table 2). Because their growth forms differed as advanced regeneration, separate height models were run to assess the consistency of species' response. This was not the case for the growth forms of recruits, thus species were combined in the late-seral model.

Table 2. Total numbers of post-harvest recruitment and advanced regeneration sampled in the transects at each site. The total number of transects varies by site: BU = 13, PH = 10, DP = 10, and WF = 14. The seral classification of species follows Urgenson et al. (2013a). Beneath the early- and late-seral totals, species are listed in descending order of abundance.

		Post-harvest recruitment				Advanced regeneration			
Species	Common name	BU	PH	DP	WF	BU	PH	DP	WF
Early-seral species (total)		195	184	101	392	26	27	7	259
Pseudotsuga menziesii	Douglas-fir	184	179	98	350	25	27	7	255
Pinus ponderosa	ponderosa pine	0	0	0	36	0	0	0	2
Abies procera	noble fir	10	2	0	0	0	0	0	0
Pinus monticola	western white pine	2	3	3	6	0	0	0	2
Pinus contorta	lodgepole pine	0	0	0	0	1	0	0	0
Late-seral species (total)		184	394	68	54	62	768	12	213
Abies amabilis	Pacific silver fir	3	84	0	0	1	700	0	0
Tsuga heterophylla	western hemlock	160	295	0	2	56	67	4	5
Abies concolor	white fir	1	0	14	49	0	0	6	207
Calocedrus decurrens	incense cedar	0	0	50	3	0	0	2	1
Thuja plicata	western redcedar	20	15	0	0	5	1	0	0
Abies magnifica var. *shastensis*	Shasta red fir	0	0	4	0	0	0	0	0

For all models, I used a process of stepwise forward selection, retaining model terms based on the Akaike information criterion (AIC$_c$; Akaike, 1974). The base model included distance, edge type, and edge exposure. I then tested a quadratic distance term (height models only) and all two-way interactions among terms in the base model or the quadratic distance term (if significant), in a stepwise fashion. Significance of model terms was based on Wald Z scores and was confirmed using likelihood ratio tests (LRT; Neyman and Pearson, 1928) when *P*-values were > 0.001. Density models assumed a negative binomial distribution with a log link. Height models assumed a gamma distribution with a log or inverse link, based on the AIC_c of the base model. All models were developed using the R library *lme4* (Bates et al., 2015; R Core Team, 2016).

3. Results

3.1. Variation in density and seral-group composition among sites

Across all sites I recorded 1,596 post-harvest recruits and 1,381 advanced regeneration (Table 2). The former included both early- and late-seral species, but at varying proportions among sites (e.g., from comparable numbers at WF, to three times as many late- as early-seral recruits at PH). Among early-seral recruits, *Pseudotsuga menziesii* accounted for 93% of stems.

Late-seral species dominated the advanced-regeneration pool, but the density and species composition varied among sites (*Tsuga heterophylla* at BU, *Abies amabilis* at PH, and *Abies concolor* at WF; Table 2). Early-seral *Pseudotsuga* was also common as advanced regeneration at WF due to the presence of root-rot gaps in the original forest canopy. DP was distinctive in its very low density of advanced regeneration.

Advanced regeneration tended to be taller than post-harvest recruitment. Among the four sites, height of advanced regeneration averaged 2.2 m (PH) to 7.5 m (BU), whereas height of recruitment averaged 0.8 m (PH) to 1.2 m (WF).

3.2. Distance from edge (Hypothesis 1)

Density of post-harvest recruitment. As predicted, density of early- and late-seral recruitment generally declined with distance from edge (Table 3, Fig. 4), with several exceptions. Specifically, early-seral species showed only a marginally significant decline at PH (Fig. 4c) and the decline was contingent on edge type at WF (significant for aggregate edges only; Fig. 4e). For late-seral species, density did not show a decline at BU (Fig. 5b) and the decline was contingent on edge type at PH (significant for intact-forest edges only; Fig. 5c). Generally, early-seral species recruited to a distance of at least 70 m from the edge (most distant sample); late-seral recruits tended to decline more steeply from greater densities near the edge, resulting in few or no individuals beyond 50-60 m (Fig. 5).

Table 3. *P*-values and signs of predictors (+ or –) from GLMMs of post-harvest recruitment as a function of distance, edge type, and edge exposure. Separate models were run for early- and late-seral species at each site and all sites combined. Significant ($P \leq 0.05$) predictors are noted by bold font, non-significant predictors by blanks. Late-seral recruitment was too sparse to model at Dog Prairie (DP). Main effects and two-way interactions that were never significant are not shown. A negative sign for distance × edge type indicates a steeper decline in recruitment density with distance from intact-forest than from aggregate edges.

	All sites		Butte (BU)		Paradise Hills (PH)		Dog Prairie (DP)	Watson Falls (WF)	
Predictor	Early	Late	Early	Late	Early	Late	Early	Early	Late
Distance	**<0.0001** **–**	**<0.0001** **–**	**<0.0001** **–**		0.09 –		**0.001** **–**	**<0.0001** **–**	**0.003** **–**
Distance × Edge type						**0.005** **–**		**0.01** +	

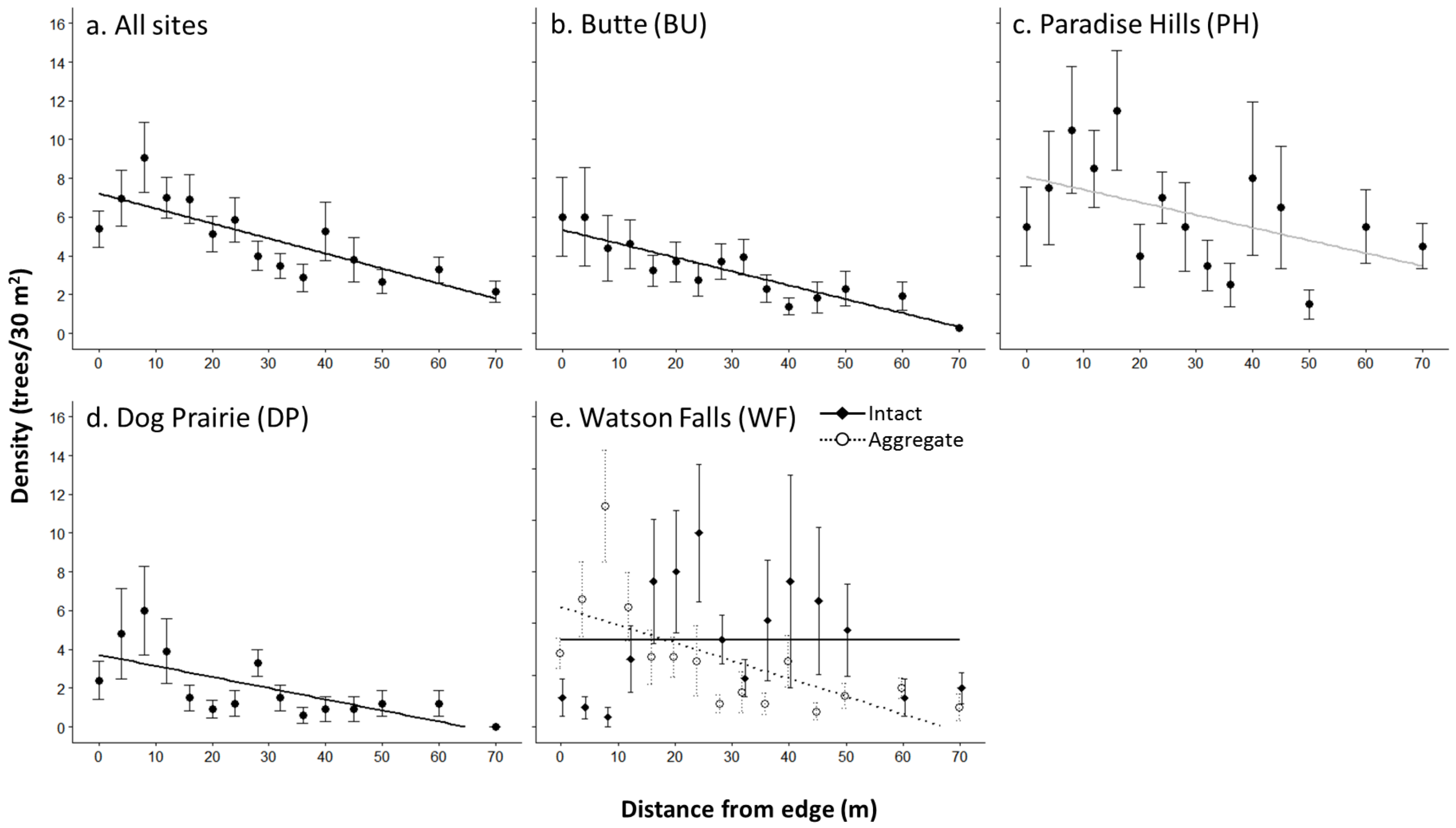

Fig. 4. Density (mean ±1 SE) of **early-seral** recruitment as a function of distance from edge for (a) all sites combined and (b-e) individual sites. Density was modeled as number of trees/30 m^2, to enable the use of discrete negative binomial distributions while modelling density data originating from both 10-m and 6-m plots. The fitted relationships shown were developed using simple linear models. Single black lines represent significant linear relationships with distance. The solid grey line for PH indicates a marginally significant ($P = 0.09$) relationship. At WF, there was a significant interaction between distance and edge type (non-significant slope for intact forest). All interactions with edge exposure were non-significant. For the significance of model terms see Table 3.

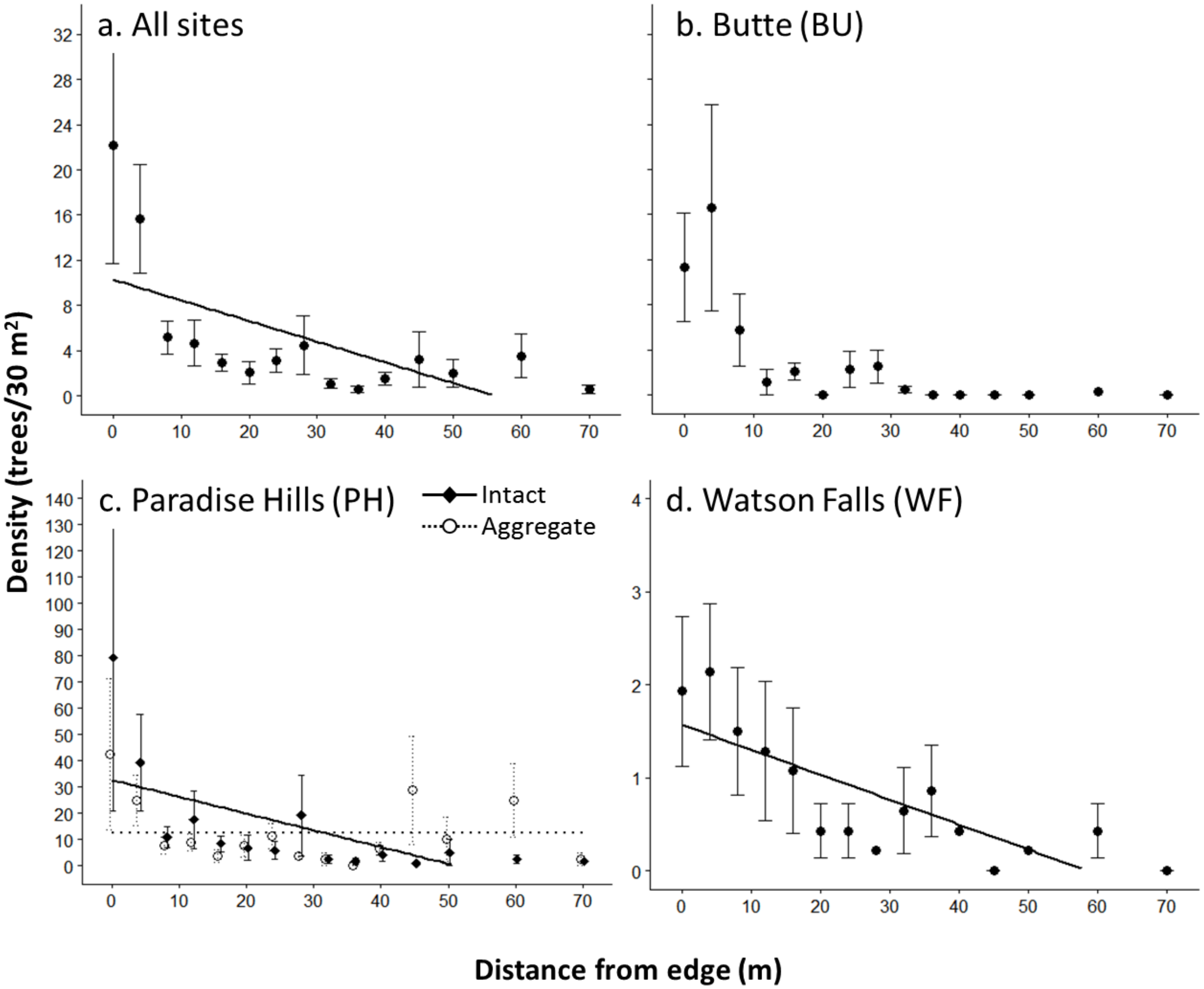

Fig. 5. Density (mean ±1 SE) of **late-seral** recruitment as a function of distance from edge for (a) all sites combined and (b-d) individual sites. The relationship was non-significant at BU. Late-seral recruitment was too sparse to model at DP. See Fig. 4 for other details.

Height of early-seral species. Although I predicted that height growth of early-seral species would increase with distance from edge, height tended to peak at intermediate distances (significant or marginally significant quadratic terms in most height models; Table 4, Fig. 6). At two sites, however, trends were consistent with the prediction. At BU, height of recruitment increased with distance from intact (but not aggregate) forest edges (Table 4, Fig. 6c) and at WF, height showed a marginally significant increase (Table 4, Fig. 6d).

Height of late-seral species. For late-seral species, I predicted that height growth would either decline or not vary with distance from edge (depending on edge exposure). Results varied among sites. For late-seral recruitment, height did not vary with distance from edge, except at WF, where it declined (Table 4, Fig. 7d). Similarly, for late-seral advanced regeneration, height did not vary with distance at BU or WF (Fig. 7g and i). In contrast, at PH, it peaked at intermediate distances, with a more distant peak for *Tsuga heterophylla* than for *Abies amabilis* (Table 4, Fig. 7h and j).

3.3. Edge type (Hypothesis 2)

Density of post-harvest recruitment. Density of recruitment was not greater next to intact-forest than to aggregate edges, counter to expectation (Table 3). However, consistent with expectation, distance relationships did not vary with edge type, with two exceptions. At WF, density of early-seral recruitment declined with distance from aggregate but not intact-forest edges (significant distance × edge-type interaction; Table 3, Fig. 4e). At PH, the nature of the interaction was reversed for late-seral recruitment (Table 3, Fig. 5c).

Table 4. *P*-values and signs of predictors (+ or –) from GLMMs of height as a function of distance, edge type, and edge exposure. Separate models were run for post-harvest recruitment (Rec.) and advanced regeneration (Adv.) of early- and late-seral species at each site and all sites combined (if there were sufficient numbers of stems). At Paradise Hills, (PH) advanced regeneration models were also run for the two common late-seral species, *Abies amabilis* and *Tsuga heterophylla*. Significant ($P \leq 0.05$) predictors are noted by bold font, non-significant predictors by blanks. A positive sign for edge type indicates greater height adjacent to aggregate than intact-forest edges. A positive sign for edge exposure indicates greater height on edges with N/E than with S/W exposures. A negative sign for distance × edge type indicates a steeper decline in height with distance from intact-forest than from aggregate edges. A positive sign for distance × edge exposure indicates a steeper decline in height with distance from edges with S/W than with N/E exposures.

	All sites			Butte (BU)			Paradise Hills (PH)					Dog Prairie (DP)	Watson Falls (WF)			
	Early	Late		Early	Late		Early	Late		*Abies*	*Tsuga*	Early	Early		Late	
Predictor	Rec.	Rec.	Adv.	Rec.	Rec.	Adv.	Rec.	Rec.	Adv.	Adv.	Adv.	Rec.	Rec.	Adv.	Rec.	Adv.
Distance	**0.002** +		**<0.0001** +	**0.02** **+**			**0.0003** +		**<0.0001** +	**<0.0001** +	**0.02** +	**0.02** **+**	0.1 +	**0.0001** +	**0.005** –	
Distance^2	**0.02** **–**		**0.0005** –	**0.02** –			**0.004** –		**<0.0001** –	**<0.0001** –	**0.04** –	0.08 –		**0.0006** –		
Edge type		**0.04** **–**		**0.01** –			**0.001** +	**0.05** –	**0.01** +					**0.0005** +		
Edge exposure							**0.03** +							0.09 +		
Distance × Edge type							**0.004** –		**0.007** –							
Distance^2 × Edge type				**0.05** **+**										**0.02** **–**		
Distance × Edge exposure			0.09 +													
Distance^2 × Edge exposure									0.06 +							

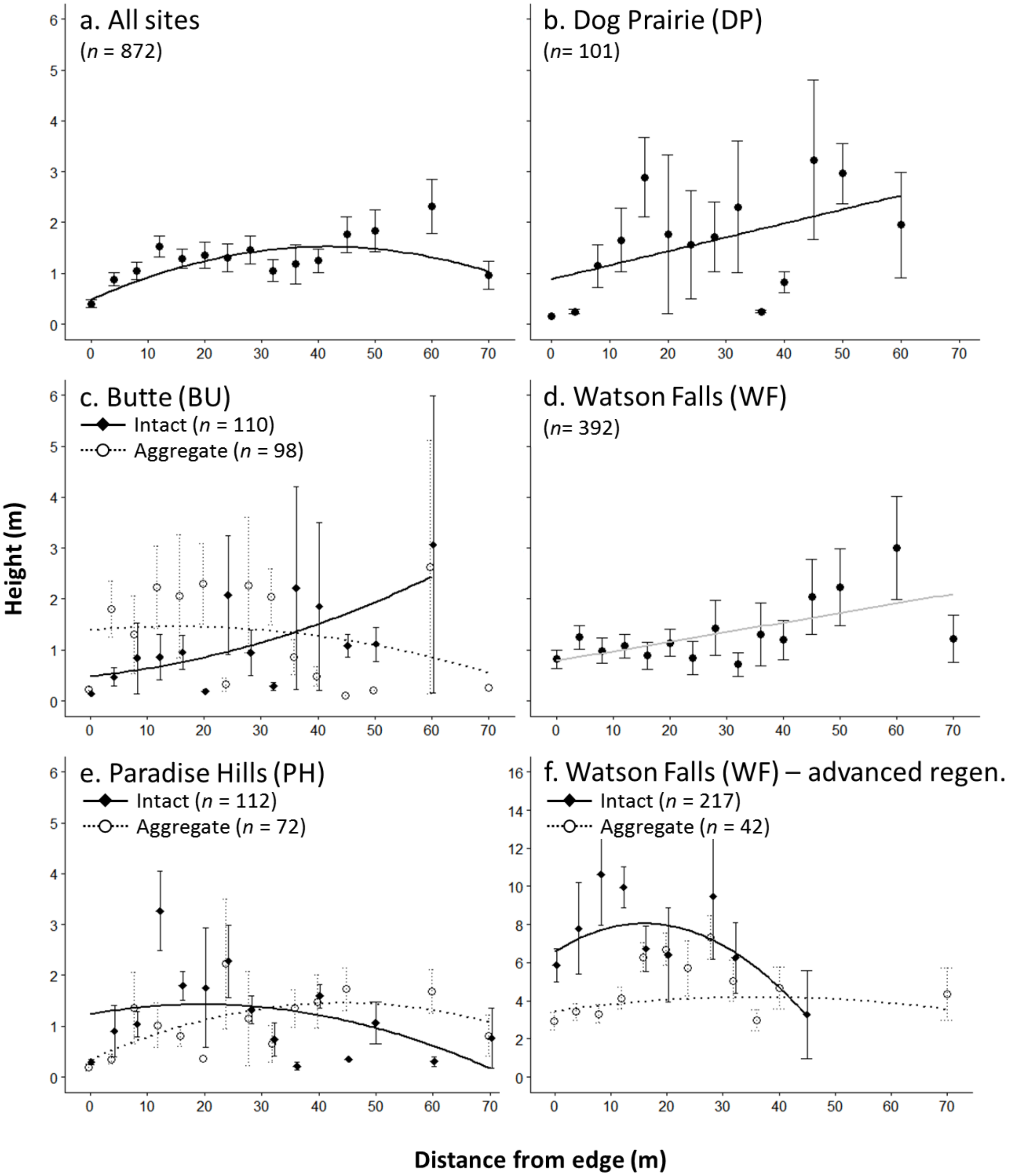

Fig. 6. Height (mean ±1 SE) of (a-e) **early-seral recruitment** and (f) **early-seral advanced regeneration** (present only at WF) as a function of distance from edge. *n* = number of trees sampled. The fitted relationships shown were developed using simple or quadratic linear models. Single black lines indicate significant linear (DP) or quadratic (All sites) relationships with distance. The solid grey line for WF indicates a marginally significant (*P* = 0.10) relationship. At BU, PH, and WF (advanced regeneration) there were significant interactions between distance and edge type. For the significance of model terms, see Table 4.

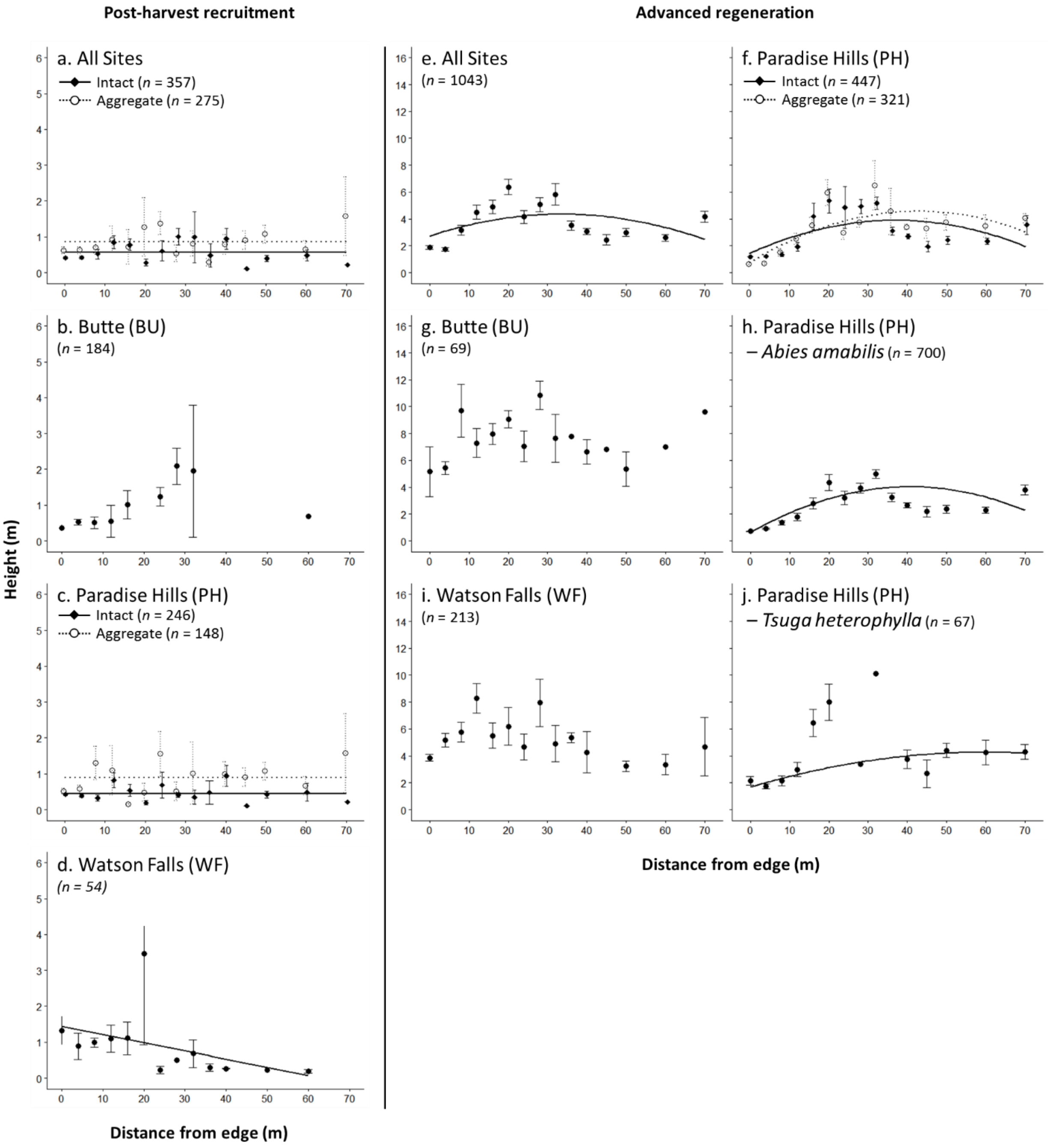

Fig. 7. Height (mean ±1 SE) of (a-d) **late-seral recruitment** (left column) and (e-j) **late-seral advanced regeneration** (center and right columns) as a function of distance from edge. The fitted relationships shown were developed using simple or quadratic linear regressions. Single black lines indicate significant linear or quadratic relationships with distance. Parallel horizontal lines indicate significant effects of edge type (but no relationship to distance). No line indicates a non-significant model. At PH (advanced regeneration) there was a significant interaction between distance and edge type. For relationships with edge exposure and the significance of all model terms, see Table 4.

Height growth. I hypothesized that height growth would not vary with edge type. Trends in height for early-seral recruitment were consistent with this prediction in Oregon (WF and DP) but not in Washington (BU and PH; Table 4, Fig. 6). Specifically, at BU, height increased with distance from intact-forest edges but peaked at intermediate distances from aggregate edges (Fig. 6c). In contrast, at PH, height peaked closer to the edges of intact forest than to aggregates (Fig. 6e). Where early-seral species were present as advanced regeneration (WF), height also peaked closer to intact-forest than to aggregate edges (Fig. 6f).

For late-seral species, edge type generally had no effect on height growth, as predicted. PH was an exception, however. Mean height of recruitment was slightly, but significantly, greater along aggregate than intact-forest edges (Table 4, Fig. 7c) and height of advanced regeneration peaked somewhat further from aggregate than from intact-forest edges (Table 4, Fig. 7f).

3.4. Edge exposure (Hypothesis 3)

I hypothesized that edge exposure would mediate distance-related trends in density of recruitment and height growth, resulting in contrasting responses for early- and late-seral species. There was no support for these predictions among density models (Table 3) and very little support among height models (Table 4). Among the latter, only one of 12 site-specific models yielded a marginally significant interaction between distance and exposure and these patterns were not easily interpreted.

4. Discussion

Forest managers in many regions of the world are adopting retention forestry as a means of balancing timber production with maintenance of biodiversity (Baker et al., 2016a; Fedrowitz et al., 2014; Gustafsson et al., 2012; Lindenmayer et al., 2012). Previous studies of aggregated-retention harvests have focused on the internal stability of retained forest patches and their roles as refugia for forest-dependent species. Conversely, few studies have examined the extent to which aggregates influence ecological (including regeneration) processes in adjacent clearings (but see Baker et al., 2013, 2015, 2016a; Curzon et al., 2017). My research begins to fill these gaps in knowledge by characterizing the nature and strength of aggregate edge influence on the post-harvest recruitment and height growth of regenerating trees. Across a diversity of western Cascade sites, I observed strong and consistent effects of aggregate edge in promoting recruitment of both early- and late-seral species. Moreover, effects were comparable to those of the longer, deeper edges of harvest units. In contrast, I did not observe consistent patterns of height growth: height tended to be suppressed by proximity to edge but showed varying relationships with distance and edge type. Finally, although I expected edge-related gradients in recruitment and height growth to vary with exposure, there was little evidence for these effects for either seral group.

4.1. Aggregate influences on recruitment

Post-harvest recruitment declined with distance from edge for both early- and late-seral species. Moreover, these relationships were unaffected by edge type, suggesting that inputs of seed, and the conditions that promote or inhibit germination and establishment, are comparable along the edges of isolated aggregates and the longer, deeper edges of harvest units. This result is consistent with those of a global study of forest influence, demonstrating comparable effects of aggregate and intact-forest edges on the vegetation of adjacent regenerating forests (Baker et al., 2016a). It is also consistent with a study of edge-related microclimatic effects demonstrating that the largest differences in shading between edge types occur at times of day when sun angles and heat stress are lowest (Baker et al., 2016b). Clearly, the ability to demonstrate differences in edge effects may hinge on the relative lengths or depths of edge. The aggregates in this experiment are relatively large (1-ha), exceeding the minimum patch size (0.2 ha) required for regeneration harvests on ‘matrix’ lands in the Pacific Northwest (USDA and USDI, 1994; Tuchmann et al., 1996). Smaller aggregates are likely to produce fewer seeds and less intense shading and, at the same time, to be more susceptible to wind damage (Esseen, 1994; Jönsson et al., 2007). For these smaller patches to be as effective for regeneration as large aggregates would likely require greater levels of retention (e.g., closer inter-patch spacing).

In general, my models of post-harvest recruitment suggest linear declines in the density of early-seral species to a distance of 70 m from the edge (the furthest distance sampled), and somewhat steeper declines from initially greater densities for late-seral species, resulting little recruitment beyond 50-60 m. I am unable to quantify the relative contributions of seed rain, shading, or competitive interactions to these gradients, but knowledge of seed dispersal patterns and edge-related gradients in microclimate offer some insights. First, differences in seed flight distances are not likely to explain the steeper decline or truncated recruitment of late-seral *Tsuga* and *Abies*, which are capable of dispersing well beyond 70 m (Carkin et al., 1978; McCaughey et al., 1985; Minore, 1979). Moreover, studies of microclimatic gradients at these sites suggest that any moderating effects of edge on solar radiation or air and soil temperatures extend no further than 10-40 m into the harvested area (Heithecker and Halpern, 2007). For late-seral species that typically establish in the shade of the understory (Bazzaz, 1979; Loucks, 1970), the steeper decline and reduced density of recruitment beyond these distances, suggest strong abiotic controls on regeneration. On the other hand, edge exposure, which can affect the amount and timing of direct radiation—thus the effective heat load—had no effect on the relationship between recruitment and distance from edge. Although the absence of an interaction with exposure runs counter to expectation (*H3*), it is consistent with the observation that understory light and temperature are reduced to a greater degree by small changes in distance from edge than by changes in edge exposure (Heithecker and Halpern, 2007). The more subtle effects of exposure may also be masked or confounded by within-site variation in other factors that affect recruitment success (e.g., harvest-related soil disturbance, topography, or competing vegetation).

4.2. Aggregate influences on height growth

Aggregate effects on height growth were considerably more complex than the effects on recruitment. Relationships with distance from edge (*H1*), edge type (*H2*), and exposure (*H3*) varied markedly among sites and seral groups, producing patterns that were often at odds with my expectations. For example, I hypothesized that height growth would increase with distance from edge in light-demanding early-seral species but decrease in shade-tolerant late-seral species. Instead, in all-site models, I found that height peaked at intermediate distances both for early-seral recruits and late-seral advanced regeneration and did not vary with distance for late-seral recruits. At individual sites, distance relationships differed from these. Similarly, I hypothesized that edge type would not influence patterns of height growth, but I observed contrasting interactions of edge type with distance among some sites (Fig. 6).

Several factors are likely to contribute to the non-linear and contrasting patterns of height growth among sites. First, the general hump-shaped response to distance suggests that growth is constrained by different processes (abiotic and biotic) near to vs. far from the edge. Moreover, the relative importance of these factors is likely to vary among sites with differing physical environments and densities of competing vegetation, and for species with differing tolerance of shade and heat or drought stress. For example, close to the edge height growth may be reduced by shading or root competition from residual trees (Coomes and Grubb, 2000; Drever and

Lertzman, 2001) or by the greater density of recruitment near the edge. Effects of shading may be particularly important for light-demanding early-seral species (Bazzaz, 1979; Minore, 1979). In contrast, distant from the edge, growth may be constrained by competition with taller early-seral shrubs (Erickson and Harrington, 2006; Sharma et al., 2010) or by increasing drought or heat stress—the latter more likely to influence late-seral species (Bazzaz, 1979; Minore, 1979). My growth models did not account for variation in the cover or height of competing vegetation, which may explain some of the variability in response to distance both within sites (between edge types) and among them. Moreover, heights at greater distance from edge represent many fewer individuals, thus model predictions are more susceptible to the distinct growing environments or growth histories of “outliers.” Finally, variation in model performance may relate to underlying assumptions of my sampling and modeling approach. Given the difficulty of reconstructing cumulative height growth in advanced regeneration, I assumed that pre-treatment height distributions were similar among and within transects. Any trends with distance, edge type, or exposure would thus be attributable to differences in post-harvest growth. Significant spatial variation in height prior to treatment could mask these trends in growth. Similarly, for post-harvest recruitment, height models implicitly assume that timing of establishment (i.e., tree-age distributions) did not vary among or within transects. However, if age distributions vary with distance from edge (e.g., due to temporal lags in establishment), variation in height may be more indicative of edge-related effects on recruitment than of growth responses to the local environment. Despite these uncertainties, consistent reductions in height close to the edge suggest that effects of shading are strong and generalizable.

Among late-seral species, patterns of height growth differed markedly between post-harvest recruitment and surviving stems. Recruits were substantially shorter than advanced regeneration and, for the most part, unresponsive to edge (distance or type). Advanced regeneration appeared more responsive to edge at most sites, although the humped-shaped trend in growth was significant only at PH. Although late-seral *Tsuga* and *Abies* spp. are highly shade tolerant, they are also capable of release following the creation of canopy gaps or full or partial canopy removal (Gray et al., 2012; Maranto et al., 2008; Seidel, 1985) provided that apical growth is not inhibited by age, physical damage, or poor vigor (Metslaid et al., 2005; Renninger et al., 2007; Stan and Daniels, 2014). That height growth tended to decline at greater distance from edge suggests, however, that there are tradeoffs for growth at higher levels of light (e.g., increasing physiological stress or competition; Lakshmi et al., 2003; Tilman, 1985).

The differing growth patterns of late-seral recruitment and survivors may have important implications for the structural development of these regenerating forests. For example, vertical stratification and structural complexity should be much slower to develop in forests lacking an advanced regeneration component prior to harvest. In contrast, the variable growth response of surviving subcanopy *Tsuga* and *Abies* should lead to more rapid horizontal and vertical diversification of the canopy. In fact, post-harvest felling of larger, non-merchantable stems at PH, may have reduced the diversity of late-seral tree heights, and with it, the potential for early structural diversification. In the longer term it is less clear to what extent late-seral recruitment will contribute structural diversification. This is likely to depend on their rates of establishment, the relative density of advanced regeneration, and the extent to which aggregates continue to influence patterns of height growth as the regenerating forest matures.

4.3. Management implications and conclusions

Retention forestry is used globally as means of balancing timber production and ecological values of managed forests. Retention of undisturbed patches of forest, or aggregates, was initially conceived as means of ‘life-boating’ disturbance sensitive, forest-dependent species through harvest into the early-regeneration phase (Franklin et al., 1997). This function has been confirmed in the short-term for a diversity of temperate and boreal systems (Aubry et al., 2009; Baker et al., 2013, 2015, 2016a; Fedrowitz et al., 2014; Nelson and Halpern, 2005a and b). My research contributes to a growing body of literature that addresses another important function of aggregates: shaping post-harvest recovery through the direct and indirect effects of edge (Baker et al., 2013, 2015, 2016a; Scott et al., 2015; Curzon et al., 2017). For managers, retaining undisturbed aggregates within harvest units has clear tradeoffs for timber production, logging-system design, and maintenance of biodiversity. My research highlights some of the benefits and tradeoffs for regeneration, including effects on recruitment and growth.

Where rapid regeneration of forest cover is a goal, the most obvious benefit of aggregates is an increase in the recruitment of both early- and late-seral species. My distance models indicate that for early-seral species (mainly *Pseudotsuga menziesii*), recruitment can be enhanced to at least 70 m from the aggregate edge, at levels comparable to the edges of larger, intact forests. For late-seral (shade-tolerant) species, the benefit of edge appears to decline more quickly. However, there are complex tradeoffs to edge influence. Close to the edge, increased recruitment is accompanied by reduced height growth; further from edge, recruitment is reduced but growth is enhanced; and distant from edge, neither recruitment nor growth benefit.

In general, edge-related patterns of height growth appear less predictable than those of recruitment. This likely reflects small-scale variation in the many factors (biotic and abiotic) that influence tree growth. Moreover, distinct differences in the growth rates and responses to edge of late-seral survivors and post-harvest recruits suggest that the presence of advanced regeneration can have important consequences for the structural development of these forests. Moreover, as the forest matures, the benefits of edge for late-seral recruitment may be enhanced, creating understory conditions more conducive to late-seral species. In sum, managers can incorporate patches of intact forest within harvest units to promote recruitment of both early- and late-seral species and, in some situations, capitalize on variation in the growth of advanced regeneration to increase horizontal and vertical complexity.

Functionally, the circular, 1-ha sized aggregates in this study appear to effectively mimic the longer deeper edges of forest that bound these harvest units. Baker et al. (2015, 2016b) have come to similar conclusions regarding their benefits for biodiversity and amelioration of microclimate. However, the functionality of smaller-sized or irregularly shaped aggregates characterized by fewer trees, larger edge-to-area ratios, and greater susceptibility to wind damage, remains unclear. Managers who seek flexibility in the design of retention harvests for multiple objectives would benefit from further study of the sensitivity of ecological and regeneration responses to aggregate size, shape, and distribution.

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Appendix A

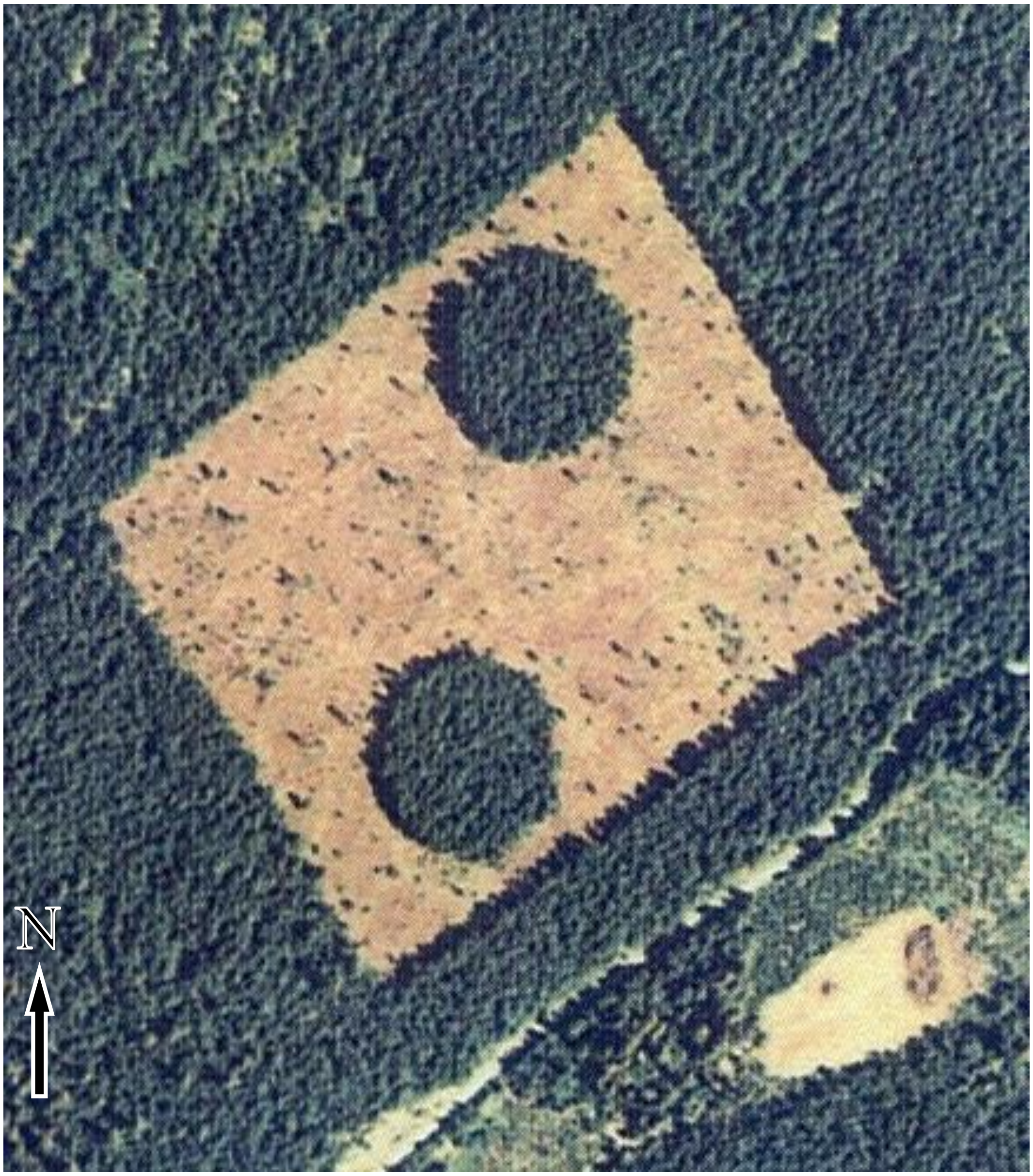

Fig. A1. Aerial photograph of the 15% aggregated-retention harvest unit at Butte (BU) shortly after harvest. The two 1-ha (~56 m radius) aggregates are evident in the N/E and S/W corners of the 320 × 400 m unit.

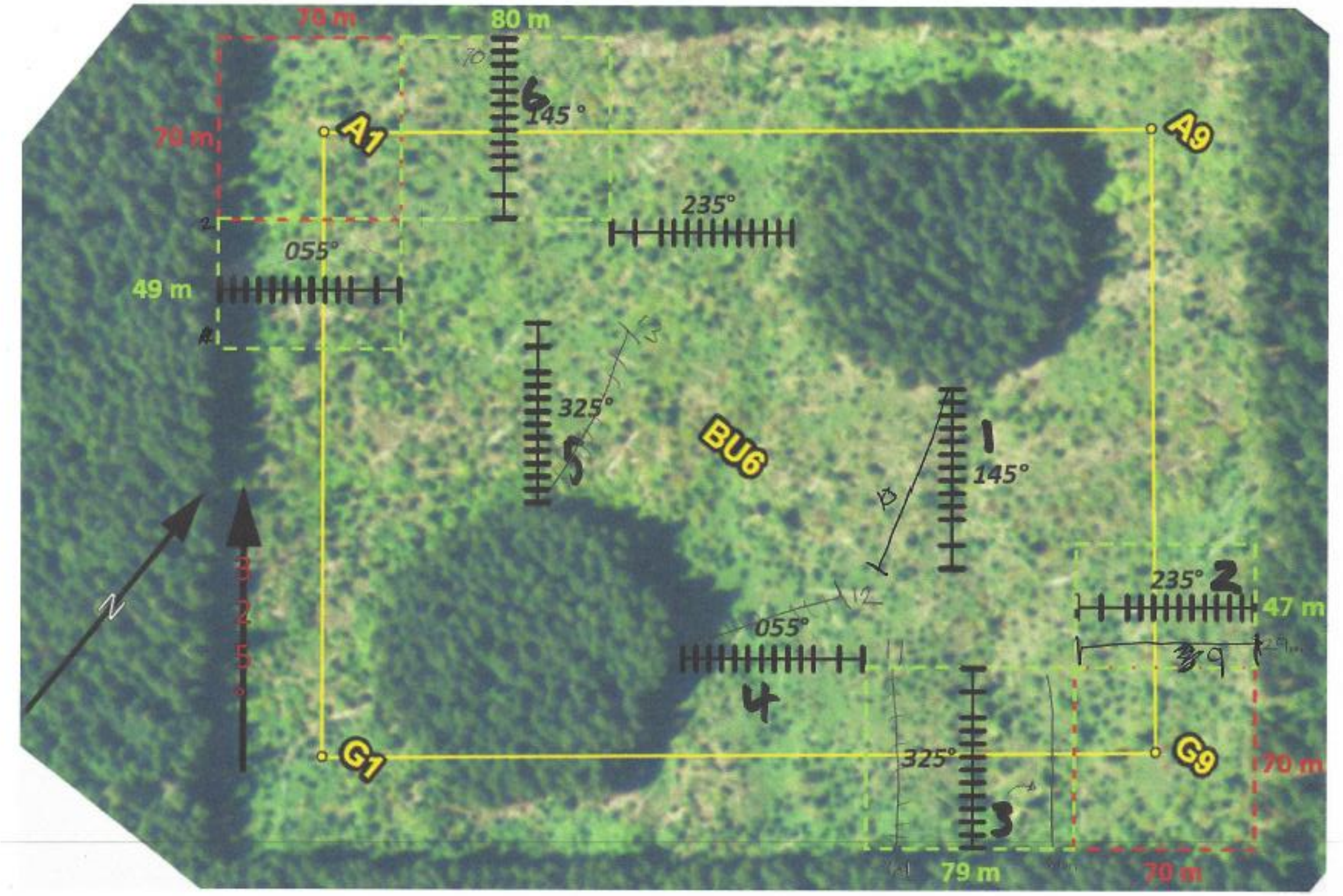

Fig. A2. Field sketch indicating the 13 transect locations at Butte (BU). Transects added to increase sampling intensity are shown with finer lines.

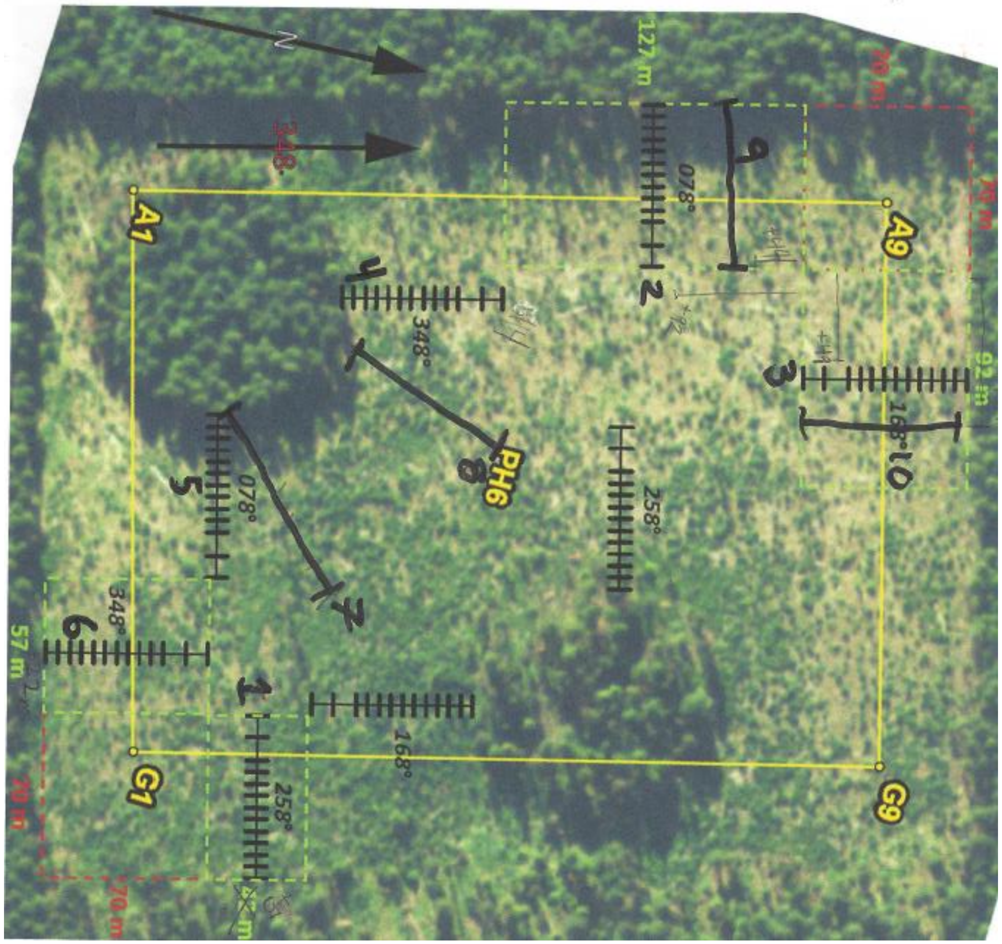

Fig. A3. Field sketch indicating the 10 transect locations at Paradise Hills (PH). Transects added to increase sampling intensity are shown without plot locations. The two transects associated with the lower right aggregate were not sampled due to significant wind damage in the aggregate.

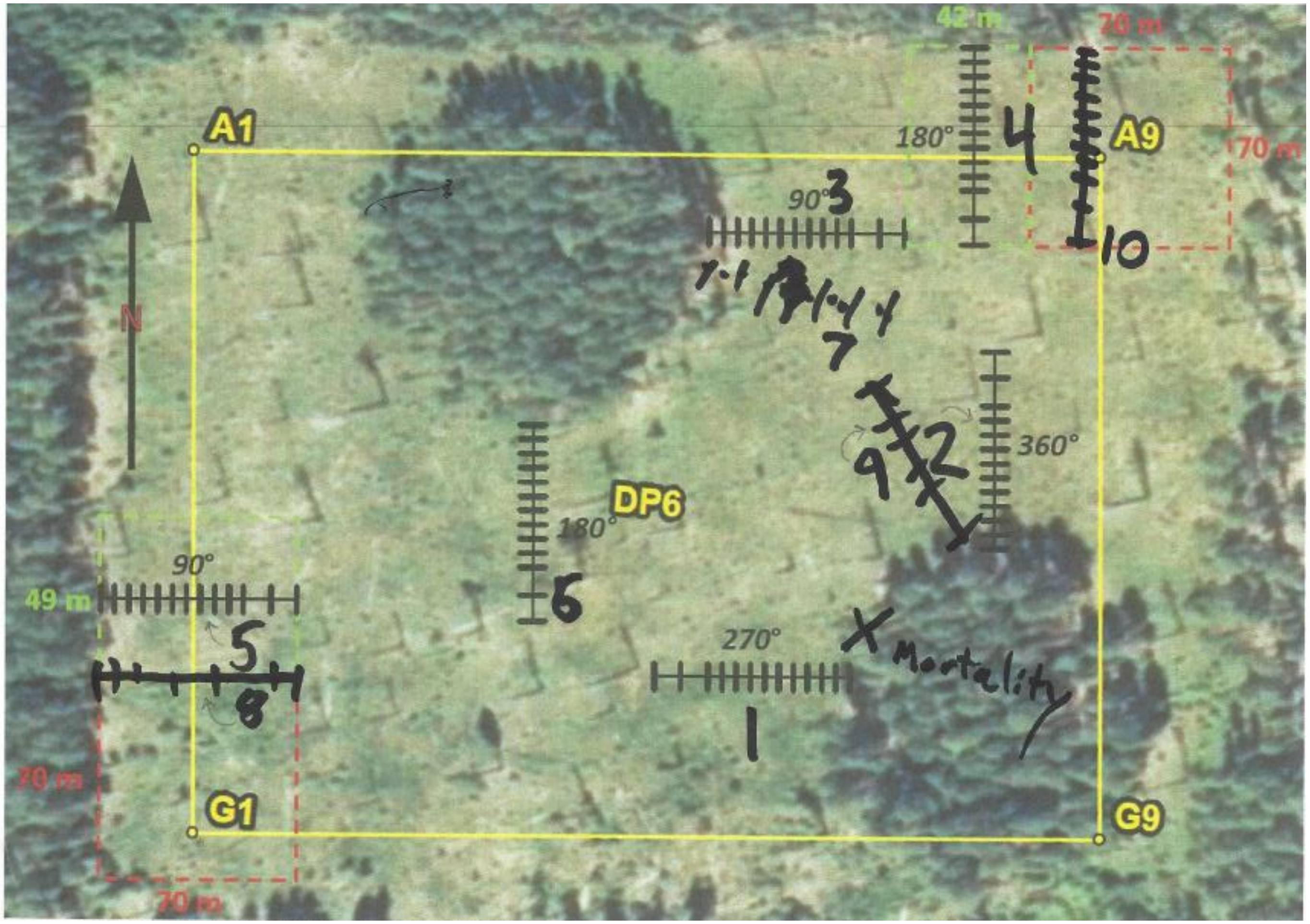

Fig. A4. Field sketch indicating the 10 transect locations at Dog Prairie (DP). Transects added to increase sampling intensity are shown with thicker lines.

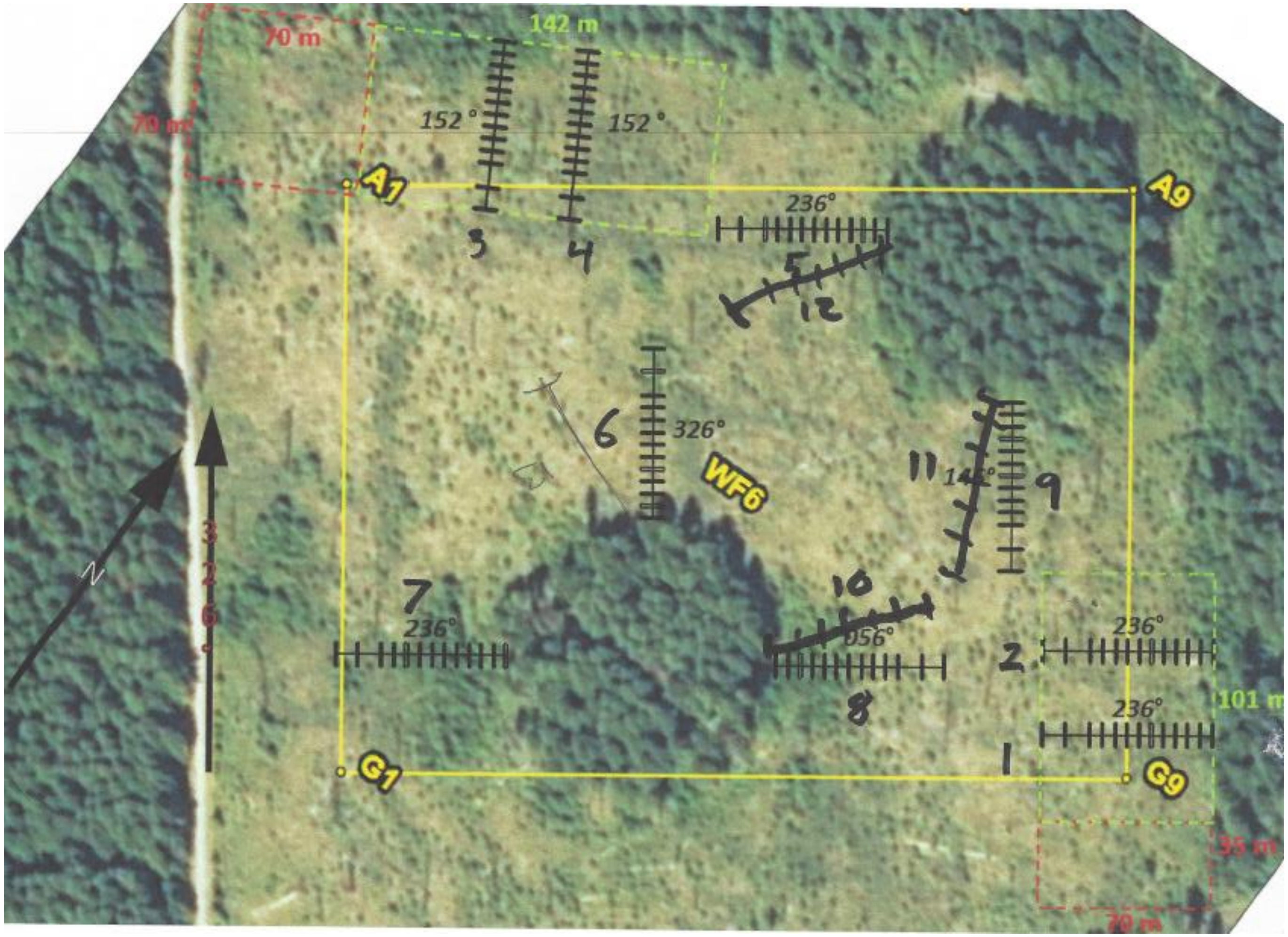

Fig. A5. Field sketch indicating 13 of the 14 transect locations at Watson Falls (WF) (the final transect was located at 281° from the southern aggregate). Transects added to increase sampling intensity are shown with thicker or thinner lines.

Table A1. Characteristics of the 47 transects and their adjacent edges. Slope and aspect are the means of 15 plots per transect. Edge height is the mean of four to eight dominant trees. Tree density and basal area were sampled in both aggregates at each site, but not in the adjacent intact forest. Primary tree species apply to all transects within a site; Rec. = post-harvest recruitment, Adv. = Advanced regeneration.

						Aggregate		Primary tree species (all transects)			
Site	Edge type	Edge exposure (°)	Slope (°)	Aspect (°)	Edge height (m)	Tree density (trees/ha)	Basal area (m^2/ha)	Species*	Overstory	Rec.	Adv.
Butte (BU)	Aggregate	44	27	138	34	935	85.4	Abpr	×	×	
		55	27	142	32	935	85.4	Psme	×	×	×
		145	32	116	33	720	69.8	Thpl	×		×
		156	32	137	31	720	69.8	Tshe	×	×	×
		235	17	156	31	720	69.8				
		325	23	136	33	935	85.4				
		336	27	145	32	935	85.4				
	Intact forest	55	20	146	38						
		145	30	135	37						
		235	26	148	36						
		235	29	150	30						
		325	27	154	39						
		325	26	135	35						
Paradise Hills (PH)	Aggregate	67	8	206	32	560	67.5	Abam	×	×	×
		78	8	203	29	560	67.5	Psme	×	×	×
		348	8	211	34	560	67.5	Thpl	×	×	
		359	5	226	35	560	67.5	Tshe	×	×	×
	Intact forest	78	6	152	32						
		78	10	163	32						
		168	8	138	39						
		168	6	142	36						
		258	6	146	34						
		348	7	159	32						

Table A1. Continued.

Site	Edge type	Edge exposure (°)	Slope (°)	Aspect (°)	Edge height (m)	Aggregate		Primary tree species (all transects)			
						Tree density (trees/ha)	Basal area (m^2/ha)	Species*	Overstory	Rec.	Adv.
Dog Prairie (DP)	Aggregate	0	27	218	43	420	112.8	Abmas	×		
		90	27	201	41	460	104.0	Abco		×	×
		180	23	186	43	460	104.0	Cade	×	×	
		270	25	200	46	420	112.8	Psme	×	×	×
		281	26	198	37	460	104.0	Tshe	×		×
		349	26	212	43	420	112.8				
	Intact forest	90	23	183	36						
		90	25	185	32						
		180	25	212	46						
		180	25	206	47						
Watson Falls (WF)	Aggregate	45	2	242	39	1610	67.5	Abco		×	×
		56	3	290	40	1610	67.5	Cade	×		
		146	2	294	41	690	62.6	Pipo	×	×	
		157	2	244	44	690	62.6	Psme	×	×	×
		225	2	316	43	690	62.6	Tshe	×		×
		236	4	336	42	690	62.6				
		236	0	0	41	1610	67.5				
		281	0	0	37	1610	67.5				
		315	2	246	38	1610	67.5				
		326	2	214	38	1610	67.5				
	Intact forest	152	2	261	38						
		152	2	346	39						
		236	2	240	35						
		236	2	240	44						

*Species codes: Abam = *Abies amabilis*, Abco = *Abies concolor*, Abmas = *Abies magnifica* var. *shastensis*, Abpr = *Abies procera*, Cade = *Calocedrus decurrens*, Pipo = *Pinus ponderosa*, Psme = *Pseudotsuga menziesii*, Thpl = *Thuja plicata*, Tshe = *Tsuga heterophylla*.