

Early regeneration response to aggregated overstory and harvest residue retention in *Populus tremuloides* (Michx.)-dominated forests

Miranda T. Curzon¹ · Anthony W. D'Amato² ·
Brian J. Palik³

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Abstract Recent emphasis on increasing structural complexity and species diversity reflective of natural ecosystems through the use of retention harvesting approaches is coinciding with increased demand for forest-derived bioenergy feedstocks, largely sourced through the removal of harvest residues associated with whole-tree harvest. Uncertainties about the consequences of such approaches prompted us to examine the combined impacts of aggregated overstory retention and harvest residue retention on the composition and density of regeneration following biomass harvests on four operational-scale (40 ha) study areas dominated by *Populus tremuloides* Michx. in northern Minnesota. Whole-tree harvest had no statistically significant effects on initial (2-year) regeneration densities, including root suckers, sprouts, and seedlings relative to conventional, stem-only harvest. The density of shrub stems was also unaffected by harvest residue retention. Despite having a lower mean leaf area index than intact forest controls, aggregates maintained comparable densities of the four most common tree species, individually, as well as all tree species combined. The composition of regeneration within aggregates differed from surrounding harvested areas as expected, but this increase in complexity at the stand scale was achieved without diminishing *P. tremuloides* densities in the edge area (0–5 m) surrounding aggregates 2 years after harvest. These initial findings suggest even small aggregates of overstory reserves may achieve basic objectives related to structural complexity and sustaining shade-tolerant tree species in harvested units without compromising regeneration objectives for less tolerant species.

✉ Miranda T. Curzon
mcurzon@umn.edu

¹ Department of Forest Resources, University of Minnesota, 1530 Cleveland Avenue North, Saint Paul, MN 55108, USA

² Rubenstein School of Environment and Natural Resources, University of Vermont, 81 Carrigan Drive, Burlington, VT 05405, USA

³ USDA Forest Service, Northern Research Station, 1831 Hwy 169 E., Grand Rapids, MN 55744, USA

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Introduction

In recent decades, a paradigm shift in forest management has led to greater emphasis on practices that restore and sustain structural complexity and compositional diversity. This serves to both maintain ecosystem services under current conditions, as well as to better ensure ecosystem resilience given uncertainty about future disturbance regimes and climate (Franklin et al. 1997, 2007; Lindenmayer et al. 2012). Retention of mature trees during harvest is one method for sustaining structural complexity in managed forests by creating conditions that reflect, to varying degrees, the structural outcomes of natural disturbance (Franklin et al. 2007). Such practices are particularly important in areas like the Lake States region of the United States and Canada where traditional even-aged forest management has simplified forest structure and altered forest species composition, specifically increasing the abundance of *Populus tremuloides*-dominated forests across the landscape (Mladenoff and Pastor 1993; Franklin et al. 2007; Guay-Picard et al. 2015). Aggregated retention of mature trees has been promoted because of its potential value for ‘lifeboating’ interior forest species in areas managed with clearcutting systems (Franklin et al. 1997), so that surrounding areas can be recolonized (Tabor et al. 2007; Baker et al. 2013). Aggregates also influence surrounding disturbed areas by altering the adjacent microclimate, providing habitat for both flora and fauna, supplying seed, and enriching fine and coarse woody debris pools, key components for maintaining forest structural complexity and species diversity (Bradshaw 1992; Baker et al. 2013).

While ecological benefits of retention trees have been demonstrated for multiple ecosystems (Aubrey et al. 2009; Baker et al. 2013; Fedrowitz et al. 2014; Palik et al. 2014), important tradeoffs may exist in the growth of developing regeneration due to the influence of retained trees on resource availability (Bradshaw 1992; Mitchell et al. 2007; Bose et al. 2014b). For example, application of retention forestry methods (c.f. Lindenmayer et al. 2012) can reduce the abundance of species reliant on early-successional, post-disturbance conditions relative to clearcuts as has been observed across both boreal and temperate ecosystems globally (Fedrowitz et al. 2014). Understanding potential trade-offs for regeneration of early successional tree species may be particularly important in forests dominated by clonal species, such as *P. tremuloides*, where retained mature trees create a hormonal environment that may impede (above resource limitations alone) root suckering (Frey et al. 2003; Brais et al. 2004; Gradowski et al. 2010).

The retention of woody debris following harvests is also recognized as an important component of prescriptions aimed at achieving complexity-based objectives because of influences on the microenvironment, stored nutrients, and habitat provision for a wide variety of species (Harmon 2001). One source of woody debris, harvest residues, is increasingly viewed as a source for bioenergy feedstocks (Duchesne and Wetzel 2003; Berger et al. 2013; Börjesson et al. 2017). In ecosystems dominated by trees relying primarily on vegetative reproduction where nutrients are not limiting, the removal of residues may provide at least initial benefit to tree regeneration by improving microsite conditions for root sucker growth (Bella 1986; Fraser et al. 2002; Palik and Kastendick 2009; Curzon et al. 2014). On the other hand, many studies indicate negative effects on

nutrient availability and tree growth (Walmsley et al. 2009; Helmisaari et al. 2011; Wall 2012), and any initial reductions in stocking or growth caused by post-harvest declines in nutrient availability may persist even if site productivity recovers over time (Egnell 2011).

Guidelines specific to ‘biomass harvests’ are being developed globally in response to higher demand for bioenergy feedstocks with the potential for utilization of harvest residues to reduce post-harvest woody debris (Stupak et al. 2007; Evans et al. 2010). These guidelines generally include recommendations for minimum levels of overstory tree and harvest residue retention (e.g. MFRC 2007; Herrick et al. 2007; MI DNRE 2010) based on the best scientific data available, but in many cases those data have been limited (Janowiak and Webster 2010; Berger et al. 2013). How these legacies, or a lack thereof, influence regeneration and other processes across forest ecosystems is not fully understood (Berger et al. 2013).

We investigated how patches of aggregated retention of mature trees (“aggregates”) in *P. tremuloides*-dominated forests, implemented following guidelines for the state of Minnesota, USA, influenced species composition and stem densities in the understory of aggregates, surrounding harvested areas (c.f. Bradshaw 1992; Baker et al. 2013), and intact forest controls. Response to aggregated retention was examined in combination with different levels of harvest residue (slash) retention associated with the procurement of bioenergy feedstocks. We hypothesized that aggregates would support similar tree species in the understory as intact forest, but that changes to the light environment would increase overall stem densities. We also expected *P. tremuloides*, a shade-intolerant species that produces prolific root suckers after harvest (Frey et al. 2003; Guay-Picard et al. 2015), to dominate regeneration in harvested areas, but with lower densities near aggregates (within 5 m) compared to open plots at least 20 m from aggregate edges because of shading and maintenance of apical dominance by retained *P. tremuloides* stems (Frey et al. 2003). Lastly, we expected reduced *P. tremuloides* densities with greater retention of harvest residues due to potential for woody debris to lower soil temperatures and to physically inhibit *P. tremuloides* suckering (Bella 1986; Fraser et al. 2002).

Methods

Study sites

This study included four sites in northern Minnesota, USA: Independence (IN; 47.01N, 92.59W), Melrude (MR; 47.25N, 92.32W), Pelican Lake (PL; 48.01N, 92.98W), and Lost River (LR; 48.14N, 92.97W). Forests at each site were classified as northern wet-mesic boreal hardwood-conifer forests (MHn44) using the Minnesota Department of Natural Resources ecological classification system (MNDNR 2003). *P. tremuloides* dominated at all locations, having regenerated following clearcut harvests in the 1940s and 1950s (stand age at time of harvest in 2010 was 55–68 years; Kurth et al. 2014). Site index for *P. tremuloides* ranged from 22 to 24 m at 50 years across the sites (Klockow et al. 2013). Other important species included *Fraxinus nigra* Marsh. (black ash), *Acer rubrum* L. (red maple), *Abies balsamea* L. (balsam fir), and *Betula papyrifera* Marshall (paper birch) with minor components of *Pinus strobus* L. (eastern white pine), *Picea glauca* Moench. (white spruce), *A. saccharum* Marsh. (sugar maple), and *Tilia americana* L. (American basswood). Common understory shrub species included *Corylus cornuta* Marsh. (beaked hazelnut) and *A. spicatum* Lam. (mountain maple). The four sites ranged in elevation

between 395 and 428 m above sea level with slopes less than 8%. At IN soils were predominantly Inceptisols, belonging to the Brimson soil series and with a fine sandy loam texture. Otherwise, soils belonged to the Alfisol order, ranging in texture from loam-silty clay (PL and LR, Ashlake, Effie, and Suomi soil series) to silt loam (MR, Dusler and Ellsburg soil series; Slesak 2013). Mean annual precipitation of the study region encompassing the sites is approximately 66 cm. Each stand (nine harvested and one unharvested control) was 4 ha in size. This meant each sale included at least 36 ha (90 acres) of forest, an area greater than the average (13.7 ha) and within the range (1.2–61.9 ha) reported for harvested sites monitored by the Minnesota Forest Resources Council in 2011 (Rossman 2012), ensuring the experiment was operational in scale. Each site was harvested in February, 2010 on frozen soil conditions and over snowpack (Klockow et al. 2013) using a tracked feller-buncher and grapple skidder. Harvest residues were redistributed across stands following harvest except where treatments called for removal (“[Experimental design](#)” section, see below).

Experimental design

We examined the combined impacts of aggregated overstory retention and harvest residue retention on stem densities (vegetative, seedling, and advance regeneration) in the understory by examining the effects of three harvest treatments replicated at four sites: unharvested controls, stem-only harvest (SOH), and whole-tree harvest (WTH). SOH entailed removal of merchantable boles with all other woody materials retained on site, whereas WTH removed entire trees with no intentional retention of residues. Within stands (4 ha) receiving the SOH and WTH treatments, two patches (“aggregates”) of mature overstory trees were retained per site-level guidelines for Minnesota that recommend 5% of canopy trees (determined by area) be reserved in aggregates ≥ 0.1 ha in size (MFRC 2007). Aggregates in this study were approximately 0.1 ha in size, meeting the minimum suggested by voluntary guidelines. Foresters marked the experimental treatments selecting trees and aggregates for retention using the same criteria (i.e. containing desirable species for regeneration such as *P. strobus*, located surrounding ephemeral ponds, etc.) that characterize operational harvests.

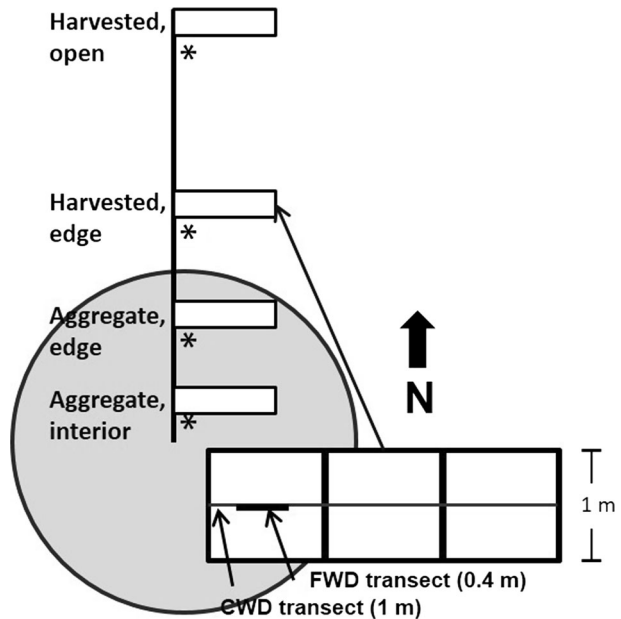
Field sampling

Transects, used to locate vegetation sampling plots in each treatment unit, were oriented north–south and centered on one randomly selected aggregate within each harvested stand and in the center of control stands (Fig. 1). The north and south portions of each transect were treated as replicates within each stand, thus 16 transects were analyzed. Paired t-tests were used to confirm no differences in any of the response variables between the two aspects ($p > 0.1$ in all cases). Rectangular plots (1 × 3 m) were placed to capture interior aggregate conditions (2 m from center), aggregate edge conditions (7 m from center), harvest edge conditions (22 m from center), and open conditions approximately one tree height in distance from aggregates (42 m from center, Fig. 1). None of the plots were directly impacted by skid trails.

Within each plot, all shrub and tree stems < 2.5 cm diameter at breast height (1.37 m) were identified to species and counted during the 2011 and 2012 growing seasons, respectively. A smaller diameter size threshold would have excluded some fast-growing *P. tremuloides* suckers. Volume of downed coarse woody debris (CWD) and fine woody

Fig. 1 Sampling design.

Transects like that pictured were placed so that they extended north and south from the center of retained overstory aggregates in harvested stands. Identical transects were also established in the center of control stands (intact forest). *Asterisks* indicate where LAI and soil moisture were sampled for each plot



debris (FWD) was estimated using the line-intercept method (Brown 1974). Where CWD intersected a transect dividing each rectangular plot, diameter at the point of intersection (if > 7.5 cm) was recorded. In a similar fashion, FWD (7.5 cm $>$ diameter $>$ 0.5 cm) was tallied and measured in three randomly selected 0.4 m subsections of each woody debris transect.

Soil moisture was measured at the corner of each plot closest to the aggregate center using a TDR probe (ML2x ThetaProbe Soil Moisture Sensor; Dynamax, Houston, TX; Fig. 1). Three moisture readings were collected around each point (within 30 cm) and averaged. All soil moisture measurements were recorded at least 48 h after rainfall on one of two consecutive days in mid-August, 2012 so only late season moisture is represented. Leaf area index (LAI), a dimensionless index approximating the ratio of foliage area to ground area, was estimated with FV2200 (Li-COR Biosciences, Inc. 2010) using light readings collected with a Licor LAI-2000 Plant Canopy Analyzer (LiCor, Inc., Lincoln Nebraska) during late July and August, also at the point where each plot intersected the transect (Fig. 1). If understory shrubs obscured readings taken at 1.0 m above the ground, an additional reading was taken at a higher level to better capture overstory conditions and prevent overestimation of LAI. Readings were collected under consistent sky conditions. This was accomplished by sampling plots once at dawn or dusk or by combining two readings collected for each plot on a clear day in the morning and in the afternoon with the unit facing east or west, respectively, and using a 180° view restrictor to block the sun (Comeau et al. 2006). Calculation of LAI required “above-canopy” readings of light interceptance sampled at the same time as understory readings. These were collected every 15 s using a second unit stationed in a nearby clearing.

Analysis of treatment effects

We estimated aggregate influence on tree and shrub densities and environmental variables using the following equation adapted from methods for assessing magnitude of edge influence (MEI; Harper et al. 2005):

$$\text{MEI} = (e-r)/(e+r) \quad (1)$$

where e represents the mean responses for plots located at some location relative to aggregate center and r represents the mean of observations from a reference condition located in interior forest (Fig. 1). This approach yields values that range between -1 and 1 with a value of 0 indicating no influence and allows for comparison of response variables within this study as well as to other studies (Harper et al. 2005). Reference values were quantified by averaging observations from intact forest controls located at the same site (Fig. 1; Harper and Macdonald 2011). We then tested the null hypothesis that aggregates had no influence ($\text{MEI} = 0$) using the randomized test of edge influence (RTEI) approach (Harper and Macdonald 2011; i.e. Dodonov et al. 2013; Dupuch and Fortin 2013), a method demonstrated to produce consistent estimates, even with variability in reference conditions (Harper and Macdonald 2011). This entailed comparing observed MEI to 95% confidence intervals derived from a distribution of randomized MEI values for each response variable at each distance, individually (i.e. Harper et al. 2015; Dupuch and Fortin 2013). The randomized distributions were generated using blocking for each site with 5000 permutations as described by Harper and Macdonald (2011).

We tested whether treatment effects on tree and shrub densities and environmental variables differed from one another using mixed effects analysis of variance (ANOVA) with the SAS MIXED procedure (SAS Institute, Inc. 2012). Treatment condition (aggregate interior, aggregate edge, SOH edge, WTH edge, SOH open, WTH open) was treated as a fixed effect, and a random effect allowing the intercept to vary by site was included to account for between-site variability. Initially, LAI was included as a covariate to account for variability and overstory loss in the aggregate canopy since harvest, but model fit as evaluated using AICc (Burhnam and Anderson 2002, 2013) was not improved and no difference was observed in results, so we used the simpler model. Some response variables required a natural log- or power-transformation to meet ANOVA assumptions for homoscedasticity.

Given the variability observed across sites and the likelihood of windthrow or other damage to overstory trees retained in aggregates, we also used LAI and CWD volume, measured continuously, to approximate the categorical treatment conditions associated with overstory retention and harvest residue removal, respectively. The effect of these conditions on tree and shrub regeneration densities was assessed using multilevel linear models. Each model included non-nested random effects that allowed the intercept to vary by site (to account for variability occurring naturally among sites) as well as by harvest treatment (WTH, SOH, or unharvested aggregate). LAI and CWD were treated as fixed effects and were centered (mean = 0, standard deviation = 1). The response variables, tree and shrub stem densities, were natural log-transformed when necessary to meet assumptions for linear regression.

Results

Relationships between treatments and environmental variables

Environmental conditions (soil moisture, LAI, CWD, and FWD) varied widely across the study (Figs. 2, 3). Soil moisture, CWD, and FWD were indistinguishable between aggregates and intact forest controls (MEI not different from 0, Fig. 2), and no differences in any environmental variables occurred between SOH and WTH (Fig. 3).

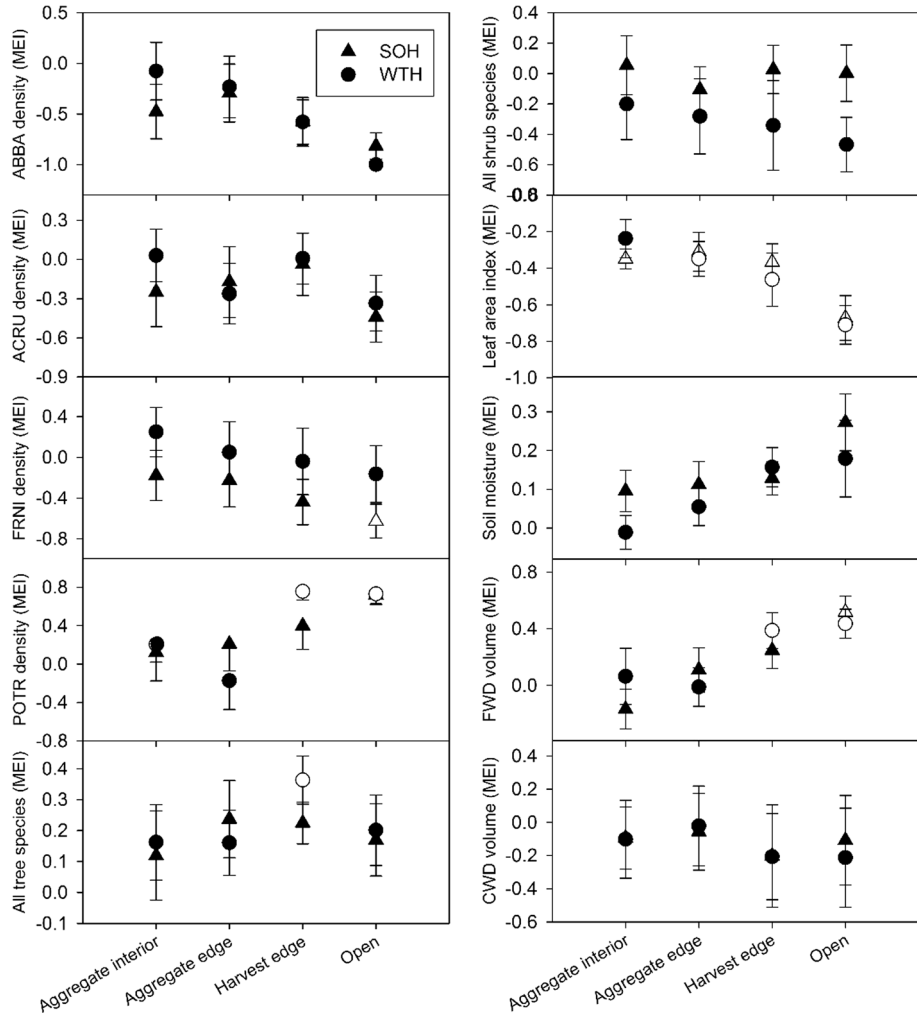


Fig. 2 Response of environmental characteristics and regeneration densities relative to nearby unharvested areas as they differed between stem-only (SOH) and whole-tree (WTH) harvest. *Hollow symbols* indicate distances where the magnitude of edge influence (MEI) for a given variable differed significantly from zero ($p < 0.05$), indicative of change from reference conditions. Only those species making up $>1\%$ of all seedlings are shown. *ABBA* *A. balsamea*, *FRNI* *F. nigra*, *ACRU* *A. rubrum*, *POTR* *P. tremuloides*, *FWD* fine woody debris volume, *CWD* coarse woody debris volume. *Error bars* indicate standard error

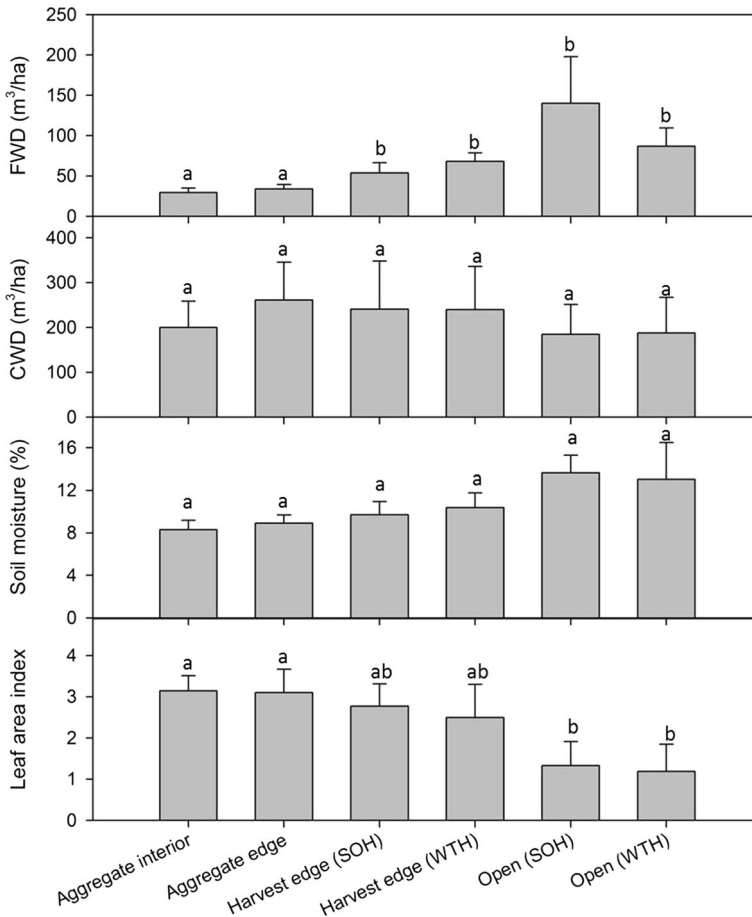


Fig. 3 Mean leaf area index, soil moisture, coarse woody debris volume, and fine woody debris volume as they differ among treatment conditions. Lower-case letters indicate significant differences between conditions as determined using post hoc Tukey-adjusted pairwise comparisons ($p < 0.05$). Error bars indicate standard error. SOH stem-only harvest, WTH whole-tree harvest, CWD coarse woody debris, FWD fine woody debris

Stem densities

The density of individual species and the combined densities of seedlings and sucker sprouts were comparable between aggregates and intact forest controls (MEI not different from 0, Fig. 2), but aggregates did positively influence the combined stem density of all tree species near harvested edges for the WTH treatment where the highest densities occurred (Fig. 2). Although comparison with controls suggests a positive influence of WTH on total regeneration densities near aggregate edge, no direct effect of CWD levels on total densities was observed (Table 1). As with all tree species combined, densities of *F. nigra* were comparable to controls within and near aggregates, but the abundance of this species was significantly different (lower) in the open, SOH plots located 42 m from aggregate center (Fig. 2). The density of *P. tremuloides* suckers was also similar between aggregates and controls (Fig. 2), but *P. tremuloides* abundance was not diminished by

Table 1 Estimates from multilevel linear models predicting total seedling and sapling stem densities (n = 64)

	Model 1	Model 2	Model 3	Model 4	Model 5
<i>Fixed effects</i>					
Intercept	2.42 (0.12)*	2.42 (0.12)*	2.43 (0.13)*	2.45 (0.15)*	2.45 (0.16)*
LAI	–	–	–	–0.01 (0.04)	–0.01 (0.04)
CWD	–	–	–	–	–0.00 (0.00)
<i>Error variance</i>					
Level-1 (plots)	0.29 (0.05)*	0.22 (0.05)*	0.22 (0.05)*	0.22 (0.05)*	0.22 (0.05)*
Level-2 intercept (site)	0.04 (0.05)	0.02 (0.05)	0.02 (0.05)	0.02 (0.05)	0.02 (0.05)
Level-2 intercept (transect)	–	0.09 (0.06)	0.08 (0.05)	0.09 (0.06)	0.09 (0.07)
Level-2 intercept (harvest treatment)	–	–	0.003 (0.01)	–0.002 (0.05)	–0.002 (0.05)
<i>Model fit</i>					
AICc	113.1	110.5	112.7	117.5	132.2

Standard error for each estimate is given in parentheses

LAI leaf area index, CWD coarse woody debris volume (m³/ha)

* $p < 0.05$

close proximity to the aggregates, contrary to expectations (Fig. 4). *P. tremuloides* densities did not differ between SOH and WTH nor were any differences attributed directly to CWD loads (Table 2). No differences in total shrub densities or *C. cornuta*, specifically (means not shown), occurred between aggregates and controls (Fig. 2), between aggregates and harvested areas (Fig. 4; Table 3), or between SOH and WTH (Fig. 4; Table 3). Based on the interclass correlation coefficient, site accounted for only 2% of the variability in *P. tremuloides* densities and 12% in all seedling and sapling stem densities, regardless of species (Tables 2, 3). Site was a more important factor for shrub densities, explaining 61% of the variability (Table 4).

Discussion

This study assessed the combined short-term effects of aggregated overstory retention and the retention of harvest residues on regeneration densities at an operational scale. The former was done to increase structural complexity in managed forests and the latter to assess potential impacts of removing residues to meet rising demand for bioenergy feedstocks. While larger aggregates may be desirable, our results show that small aggregates

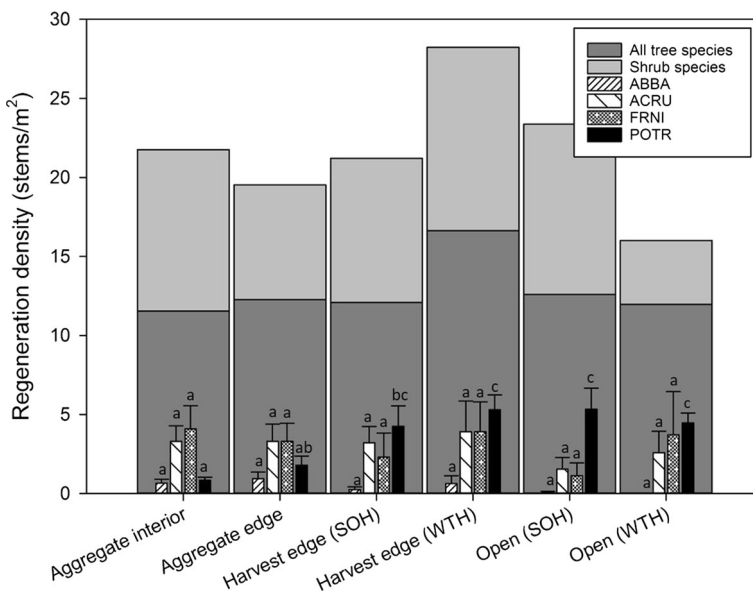


Fig. 4 The effect of aggregated overstory reserves (“aggregates”) on understory tree and shrub densities at different locations relative to the boundary between aggregates and harvested areas. The wide, stacked bars show total densities of trees on bottom (dark grey) and shrubs on top (light grey). Means for neither group differed among conditions ($p > 0.05$). The narrower bars indicate densities for individual tree species. Only those species making up $>1\%$ of all tree seedlings are shown, individually. ABBA *A. balsamea*, FRNI *F. nigra*, ACRU *A. rubrum*, POTR *P. tremuloides*, SOH stem-only harvest, WTH whole-tree harvest. Lower-case letters indicate significant differences in densities within individual species between conditions based on post hoc Tukey-adjusted pairwise comparisons ($p < 0.05$). Error bars indicate standard error

Table 2 Estimates from multilevel linear models predicting *P. tremuloides* stem densities (n = 64)

	Model 1	Model 2	Model 3	Model 4
<i>Fixed effects</i>				
Intercept	0.89 (0.14)*	1.08 (0.43)	1.17 (0.43)	1.24 (0.44)
LAI	–	–	–0.04 (0.05)	–0.03 (0.05)
CWD	–	–	–	–0.00 (0.0004)
<i>Error variance</i>				
Level-1 (plots)	0.87 (0.16)*	0.49 (0.09)*	0.49 (0.48)*	0.49 (0.48)*
Level-2 intercept (site)	0.02 (0.07)	0.05 (0.07)	0.05 (0.06)	0.07 (0.08)
Level-2 intercept (harvest treatment)	–	0.49 (0.51)	0.45 (0.48)	0.46 (0.48)
<i>Model fit</i>				
AICc	179.8	152.9	156.5	169.3

Standard error for each estimate is given in parentheses

LAI leaf area index, CWD coarse woody debris volume (m³/ha)

* *p* < 0.05

Table 3 Summary of ANOVA results

Response variable	Fixed effect	<i>df</i>	F	<i>P</i> value
<i>Abies balsamea</i> density	Condition	5	2.52	0.040
<i>Acer rubrum</i> density			0.62	0.687
<i>Fraxinus nigra</i> density			1.06	0.394
<i>Populus tremuloides</i> density			10.42	<0.0001
<i>Corylus cornuta</i> density			1.49	0.211
Density, all tree species, combined			0.88	0.500
Density, all shrub species, combined			1.1	0.372

Bold text indicates significance (*p* < 0.05). Means shown in Fig. 4

Table 4 Estimates from multilevel linear models predicting shrub stem densities (n = 64)

	Model 1	Model 2	Model 3	Model 4
<i>Fixed effects</i>				
Intercept	1.62 (0.56)	1.60 (0.56)	1.62 (0.56)	1.63 (0.56)
LAI	–	–	0.15 (0.12)	0.12 (0.12)
CWD	–	–	–	0.12 (0.12)
<i>Error variance</i>				
Level-1 (plots)	0.75 (0.15)*	0.73 (0.15)*	0.74 (0.15)*	0.74 (0.15)*
Level-2 intercept (site)	1.18 (1.00)	1.15 (0.98)	1.19 (1.02)	1.19 (1.02)
Level-2 intercept (harvest treatment)	–	0.03 (0.09)	–	–
<i>Model fit</i>				
AICc	157.6	159.6	158.4	159.8

Standard error for each estimate is given in parentheses

LAI leaf area index, CWD coarse woody debris volume (m³/ha)

* *p* < 0.05

(0.1 ha) create conditions intermediate between harvested areas and intact forest by protecting regeneration of shade tolerant species that might otherwise be less abundant at the stand-scale without reducing initial regeneration densities of shade-intolerant species in surrounding harvested areas. Effects of residue removal are less clear and reflect the variability of harvest effects that might be expected at an operational scale, particularly when harvest occurs during winter.

Relationships between treatments and environmental variables

Canopy cover varied widely across the study and within treatments as indicated by LAI. Severe storms during the first and second growing season following harvested snapped and uprooted many retained trees in the aggregates, contributing to lower LAI than expected within those reserves. This mortality was not surprising given other reports of mortality in retained *P. tremuloides* stems within 1–3 years of harvest (Bose et al. 2014a). Also, whereas other studies have reported comparable understory light environments between the interior of aggregates and intact forest based on LAI estimates, the radii of the aggregates studied here (approximately 18 m) are well within the range of expected edge effects reported elsewhere (Fraver 1994; Heithecker and Halpern 2007), and would likely have lower LAI than interior forest. Trends in our one-time measure of soil moisture are consistent with those collected continuously over the growing season in another study conducted as part of the larger research project, with no differences observed between residue retention treatments (Kurth et al. 2014). Our failure to detect any ameliorating effects from retained woody debris that might be expected with SOH (Zabowski et al. 2000; Heithecker and Halpern 2006) is likely due to the variability in woody debris associated with both harvest treatments (Fig. 3). Significant breakage occurred during the winter harvest, resulting in up to 50% of available residues persisting across sites even in those stands treated with WTH (Klockow et al. 2013). Woody debris levels also likely varied spatially, potentially leading to less distinction between residue removal treatments.

Regeneration

Although other studies have reported potential for reduced sucker growth and biomass production in association with more abundant woody debris (Bella 1986; Curzon et al. 2014), stem densities did not differ between SOH and WTH in the present study. This may partially be due to the variability in woody debris levels that occurred across the study regardless of the residue retention treatment assigned to a given area (Fig. 3; Klockow et al. 2013). We also suspect that FWD levels may influence the presence and abundance of competitive species, including *P. pratensis* and *P. aquilinum*, and thus provide a potential release effect for aspen regeneration in SOH-treated stands (Curzon 2014) as dense herbaceous vegetation has been shown to negatively impact aspen sucker growth (Lieffers 1995; Landhausser and Lieffers 1998). Even where differences in initial *P. tremuloides* densities have been observed in response to soil disturbance or harvest residue removal (i.e. Bella 1986; Stone 2001), those densities and the differences among them may change over extended periods (Bella 1986; Curzon et al. 2014). So, while no difference in 2-year regeneration densities occurred between SOH and WTH in this study, repeated sampling in the future will be necessary to determine long-term impacts.

Overstory retention may present a trade-off between achieving ecological objectives related to structural complexity and biodiversity and maximizing regeneration in surrounding harvested areas (Gradowski et al. 2010; Bose et al. 2014b; Palik et al. 2014). *P.*

tremuloides is highly intolerant of shade (Burns and Honkala 1990), and root sucker initiation (Maini and Horton 1966) and density are sensitive to soil surface temperatures (Landhausser and Loeffers 1998; Frey et al. 2003), carbohydrate stores in the parent root system, and hormonal control from nearby mature stems (Frey et al. 2003). Our initial, short-term findings indicate that aggregated retention did not reduce *P. tremuloides* sucker densities in the harvested areas adjacent to aggregates, contrary to expectations. Considering the distance of “open” condition plots from aggregates (about 20 m), these results align with reported sucker densities in “large gaps” in northern British Columbia (Coates 2002). Moreover, the combined density of seedlings and suckers of all species did not differ significantly between aggregates and harvested areas although species composition and associated shade tolerances for plant cover varied as expected. This supports the notion that aggregates provide some level of interior forest conditions for maintenance of tree species diversity even if it is primarily edge habitat.

Conclusions

We examined the impacts of aggregated overstory retention, a method promoted to enhance structural complexity in harvested forest, combined with WTH, a practice expected to increase with demand for bioenergy feedstocks on initial regeneration in *P. tremuloides*-dominated forests. Our results suggest that aggregated retention achieved ecological objectives for this forest with no apparent trade-off in initial regeneration densities in harvested areas adjacent to aggregates. These findings also demonstrated no significant effect of SOH versus WTH on initial regeneration densities, regardless of species, but this may be a reflection of the variability in levels of harvest residues that occurs in practice, despite greater emphasis on complete removals with WTH. Removing harvest residues for use as bioenergy feedstocks has potential to influence tree survival, growth, and composition over time given its influence on microclimatic conditions, nutrient dynamics, and the abundance of competing vegetation. Assessing the impact of WTH and retention on biodiversity objectives will require repeated assessment of these communities over time. In the meantime, these results inform silvicultural decisions in terms of establishing initial composition and regeneration densities.

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