New cohort growth and survival in variable retention harvests of a pine ecosystem in Minnesota, USA

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ABSTRACT

There is significant interest in silvicultural systems such as variable retention harvesting (VRH) that emulate natural disturbance and increase structural complexity, spatial heterogeneity, and biological diversity in managed forests. However, the consequences of variable retention harvesting for new cohort growth and survival are not well characterized in many forest ecosystems. Moreover, the relative importance of resource preemption by existing ground layer vegetation after variable retention harvests is unclear. We addressed both in a VRH experiment implemented as a randomized block design replicated four times in red pine forest in Minnesota, USA. Treatments included a thinning with residual trees dispersed evenly throughout the stand (dispersed) and two patch cuts that left 0.1 ha gaps (small gap) or 0.3 ha gaps (large gap) in a forest matrix. Residual basal area was held near constant in the three harvest treatments. We planted seedlings of three common pines (*Pinus banksiana*, *P. strobus* and *P. resinosa*) and measured light, soil nutrients and growth over seven growing seasons. We hypothesized that forests with equivalent average structures (e.g., basal area) would have higher stand-level seedling growth and survival in aggregated retention versus dispersed retention stands. However, variable retention harvest resulted in relatively small differences in growth and survival across the three retention treatments (although all differed as expected from uncut controls). Species specific responses to overstory treatments were partially related to shade tolerance. Tolerant white pine had high survival across all overstory treatments whereas intolerant red and jack pine had lower survival in uncut controls. In general, jack pine had the strongest growth response to reduction of overstory density. However, both white and jack pine achieved highest growth in the dispersed treatment despite differences in shade tolerance. Regardless of species, shrubs had a strong impact on seedling growth. Indeed, differences in growth were often larger across shrub treatments than among retention treatments. Our results support the hypothesis that shrubs preempt resources and dampen the impacts of different overstory retention patterns on new cohort growth and survival. Our results imply that managers have considerable flexibility to employ various types of retention patterns coupled with planting in red pine ecosystems at least at the levels of retention studied here.

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1. Introduction

In managed forests, practices that increase structural complexity have emerged as a key approach for restoring spatial heterogeneity and sustaining species diversity and ecological function. Retention harvesting, where some large trees are retained during harvest (Franklin et al., 1997; Mitchell et al., 2007), has become a widely used tool for sustaining or restoring complexity in forest stands managed for timber (Gustafsson et al., 2012; Lindenmayer et al., 2012). The approach is based on observations that natural disturbances, even those that are stand replacing, leave a spatially heterogeneous landscape that includes living trees, dead wood, and undisturbed patches of understory, providing the context for new regeneration and continuity of ecological functions in the developing stand (Franklin and MacMahon, 2000; Franklin et al., 2000). Retention harvesting prescriptions are designed to create residual stand structures that more closely resemble the structural outcomes of natural canopy disturbance, compared to clearcutting (Franklin et al., 1997; Lindenmayer et al., 1991; Seymour and Hunter, 1999). Like trees surviving natural disturbance, retained trees may be important for "life-boating" organisms and functions from the old stand to the new and for increasing connectivity across the

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landscape (Franklin et al., 1997; Halpern et al., 2005; Hansen et al., 1995). However, the ecological benefits of retention may come at a cost to productivity of tree regeneration because of resource competition with residual trees (Acker et al., 1998; Birch and Johnson, 1992; Seymour and Hunter, 1999). This may be true particularly for species intolerant of competition (Dignan et al., 1998; Huffman et al., 1999; Palik et al., 1997; Zenner et al., 1998).

Canopy disturbance, whether natural or anthropogenic, alters resource availability, generally freeing resources for a new cohort of trees, for canopy trees that survive the disturbance, or for other forest vegetation. In variable retention harvesting (VRH) systems, residual trees can be left in either dispersed or aggregated (i.e., leaving trees in clumps with gaps or openings between clumps) spatial patterns (Franklin et al., 1997, 2007). Differences in the spatial pattern of retention alter individual tree and stand scale resource availability (Boyden et al., 2012; Palik et al., 2003). Specifically, stand scale resource availability may increase from dispersed to aggregated retention because of non-linear relationships between competitor abundance and resource availability at the scale of individual trees (Boyden et al., 2012; Palik et al., 1997, 2003). Under this model, resources are low across a wide range of competitor abundance, increasing rapidly below a threshold level of competitor abundance. Thus, with dispersed retention uniform tree densities across the stand result in most competitive neighborhoods falling above the threshold level of competitor abundance and few seedlings experience a low enough level of competition to have high resource availability. With aggregated retention, areas within residual patches will be highly competitive, but openings between patches will have low levels of competition from the overstory and will experience higher resource availability.

The neighborhood-scale effect of overstory competitors on resource availability should translate into analogous responses in growth of understory plants, including regenerating tree seedlings. At whole-stand scales, with dispersed retention, most regeneration neighborhoods should be in close proximity to overstory competitors where growth of target plants will be restricted. In contrast, with aggregated retention, a larger proportion of regeneration neighborhoods should be farther away from overstory competitors leading to increases in growth due to reduced competition. The degree to which a residual overstory leads to productivity reductions of the new cohort of trees may depend on the level of tolerance for shade and low soil resources of regenerating species (Dovciak et al., 2001; Montgomery et al., 2010; Peck et al., 2012). Species tolerant of low resource may be less negatively impacted by proximity to residual overstory trees than intolerant species.

Following a disturbance, productivity of a new cohort of trees can also be influenced by competition with already established understory plants that preempt resources liberated by overstory removal (e. g. Bush and Van Auken, 1995; Lorimer et al., 1994; Montgomery et al., 2010). The strength of this response may be a function of spatial pattern of retention and its effects on resource availability and heterogeneity. For example, in longleaf pine (*Pinus palustris*) systems, retention harvests create persistent light gaps (Battaglia et al., 2002), but root gaps, having increased N availability, are formed only when overstory trees and understory plants are removed (Palik et al., 1997, 2003). Overstory disturbances, even up to 0.3 ha is size, that have an intact understory, result in belowground gaps that are indistinct and ephemeral, with existing understory plants quickly filling the void (Jones et al., 2003).

Here we report on results of a VRH experiment implemented in a *Pinus resinosa* (red pine) ecosystem in north-central Minnesota, USA (Palik and Zasada, 2003). There is a long-held view in the managerial community that *P. resinosa* ecosystems, and more broadly Great Lakes mixed-pine ecosystems, largely had even-aged structure as result of stand-replacing fire (Benzie, 1977). While such a disturbance dynamic and structure likely did occur historically,

there is accumulating evidence that these forests also occurred as two or even three age cohort stands, as a result of mixed-severity fire disturbance (and perhaps even wind disturbance) that were less than stand replacing (Drobyshev et al., 2008; Fraver and Palik, 2012). This evidence provides some ecological justification for VRH approaches in this ecosystem; that is, natural disturbance left more than a trivial amount of residual live tree legacies. Moreover, results from spatial reconstructions of tree establishment in old-growth multiple cohort *P. resinosa* stands demonstrate examples of both intermixed and spatially distinct cohort spatial patterns (Fraver and Palik, 2012), providing justification for emulating natural disturbance using both dispersed and aggregated retention harvesting.

Our experiment included three overstory harvest treatments consisting of dispersed retention and two levels of aggregated retention, as well as an unharvested control. Spatial pattern of overstory retention varied, while residual tree abundance remained relatively constant. We measured resource availability and tree seedling growth of three native pine species that differ in shade tolerance. We hypothesized that forests with equivalent average structures (e.g., basal area) will have higher stand-level seedling growth in aggregated retention versus dispersed retention stands due to differences in the distribution (types and abundances) of competitive neighborhoods and the subsequent effects on resource availability (Boyden et al., 2012). In addition, we hypothesized that responses to retention pattern will vary among species, with greatest new cohort seedling growth of mid-tolerant species occurring with dispersed retention and greatest seedling growth of intolerant species occurring with aggregated retention. Further, we hypothesized that if resource preemption by shrubs occurs, growth of the new cohort of trees will be significantly lowered, even with aggregated retention, relative to that which occurs when competition from the shrub layer is reduced.

This study builds on prior work in this experimental system (Atwell et al., 2008; Ostry et al., 2012; Peck et al., 2012; Powers et al., 2008, 2009a,b, 2010, 2011). We examine the consequences of increased resource availability with aggregated retention compared to dispersed retention (Boyden et al., 2012) for tree seedling growth and survival as well as explore the relative importance of overstory versus shrubs for resource availability, seedling growth and survival. Further, we extend our understanding of the influence of shrubs to the scale of the stand building on prior work that examined the relative importance of above-versus belowground effects of shrubs on tree seedlings in gap centers and closed canopy sites (Montgomery et al., 2010).

2. Methods

2.1. Study area

We conducted the experiment in largely single-cohort monotypic red pine forests in the Chippewa National Forest in north central Minnesota, USA. The site has a cold temperate climate with mean annual temperatures of 3.9 °C and mean annual precipitation of 70 cm. The study area contains outwash and ice contact landforms characterized by deep sand parent materials. Soils are excessively to well-drained nutrient poor loamy sands. Soil analysis of the 0–20 cm mineral horizon of an adjacent experimental forest indicated a pH of 5.5, total soil N of 1.12 Mg ha^{-1} and total soil P of 0.64 Mg ha^{-1} (Bray's extraction; Alban, 1974). The forest overstory is dominated by red pine (90% of total basal area) with smaller amounts of *Pinus strobus* (eastern white pine), *Acer rubrum* (red maple), *Populus tremuloides* (trembling aspen), *Populus grandidentata* (big tooth aspen), *Betula papyrifera* (paper birch), *Abies balsamea* (balsam fir), *Picea glauca* (white spruce), *Quercus rubra* (northern red oak) and *Q. macrocarpa* (bur oak). The understory

is dominated by *Corylus cornuta* (beaked hazel) and *Amelanchier* spp. (serviceberry).

Forests in the study area were estimated to be ~85 years old, broadly even-aged and naturally regenerated after early 20th century logging and wildfire. Stands have a moderately open canopy with an average basal area of trees >10 cm DBH of 36 m^2 ha^{-1} (Atwell et al., 2008) and canopy light transmittance of 10–14% (Boyden et al., 2012). The forests are classified as "Red Pine-White Pine Woodland" (FDn33a) according to the Native Plant Community Classification for the State of Minnesota (MNDNR, 2003). Historically, these ecosystems were dominated in the overstory by *P. resinosa*, with lesser and varying amounts of *P. strobus* and *Pinus banksiana* and canopy covers ranging from 50% to 75%. Basal areas were likely less than typically occurs in contemporary stands where fire has been excluded.

2.2. Experimental design

The study was implemented as a randomized block split-plot design replicated four times. It included three retention harvest treatments and an unharvested control split by two understory removal treatments (woody shrubs reduced by brush cutting, ambient levels of woody shrubs). Each block was ~65 ha with four ~16 ha treatment stands. A block design was used for the study because the four treatment areas were separated geographically by 1–8 km and varied somewhat in local topographic relief. Stands were logged on snow in winter 2002/2003 (Palik and Zasada 2003). Crowns were left on-site as slash. The overstory treatments included a partial harvest with residual trees dispersed evenly throughout the stand (dispersed) and two aggregated treatments created through patch cutting of 0.1 ha gaps (small gap) or 0.3 ha gaps (large gap) in a forest matrix. Residual basal area was held near constant (~15 m^2 ha^{-1}) in the three harvest treatments, with the intent that treatments differ only in spatial pattern of retained canopy trees. In the aggregated retention treatments, there was some thinning in the forest matrix to achieve similar basal area across harvest treatments. In 2003, understory shrubs were cut with brush saws to facilitate planting. Thereafter (2004–2008), understory shrubs and *Populus* spp. suckers were cut annually in spring on half of each overstory treatment. Other species of tree regeneration were not removed during brushing. Since most shrubs are able to resprout, our brush cutting treatments had the effect of reducing shrub densities. Hereafter, we refer to understory treatments using the terminology "shrub reduction" and "shrub ambient" treatments.

2.3. Study species and sampling design

In spring 2003, we planted seedlings of three native pine species (*P. banksiana*, *P. strobus* and *P. resinosa*) at 2.7 m spacing across the entire treatment unit for the three harvest treatments, and within plots centered on sample points (see below) in the unharvested controls, since we anticipated high mortality in the uncut forest and saw no reason to waste resources by planting the entire control units. This resulted in a planting density of approximately 1200 seedlings ha^{-1} divided equally among the three species. Given the frequency of gap versus matrix conditions in the gap treatments, roughly 37% of measured seedlings were in gaps and the rest were in matrix or edge conditions. Seedlings were 2 year old bare root nursery stock grown from local seed sources. Because planting rows of trees with alternating species composition was logistically difficult, we alternated species identity by planting row. These species differ in light requirements for regeneration, allowing examination of the impact of shade tolerance on species responses. *P. strobus* is moderately shade tolerant, whereas *P. resinosa* and *P. banksiana* are intolerant. Of the latter, *P. banksiana* is

widely considered the least tolerant of shade. All three are capable of regenerating in conditions that occur after a heavy canopy disturbance (Fowells, 1965), including conditions that are found in stands managed using residual overstory retention. All seedlings were protected from browse each fall throughout the study using PlantSkydd® deer repellent (Tree World Plant Care Products, Inc., St. Joseph, MO).

We installed 20 sample points in each overstory treatment in each block. These sample points were stratified by understory treatment (4 overstory × 2 understory × 4 replicate blocks × 10 = 320 points). Sample points were installed prior to harvest. At each sample point various measurements were made as described below.

2.4. Resource measurements

To evaluate the effects of experimental treatments on resource availability, we measured light and nutrient availability at each of our sample points. We measured light availability during the 2004, 2005, 2007 and 2008 growing season (June–August) using a LAI-2000 Plant Canopy Analyzer (Li-Cor, Inc., Lincoln, NE, USA) or a sunfleck ceptometer (Decagon Devices, Inc. Pullman, WA, USA). Sensors were used in paired mode, with one sensor located in an open clearing serving as the above canopy sensor and another sensor taking readings at individual plots. This approach allowed calculation of % transmittance of light. Instantaneous measures of % diffuse transmittance are effective estimates of seasonal light environment (Machado and Reich, 1999; Parent and Messier, 1996), and are especially relevant to juvenile growth and survival (Kobe and Hogarth, 2007; Tobin and Reich, 2009). Measurements were made once per year on uniformly overcast days or at dawn and dusk at 1 m above the forest floor. This height was generally higher than the seedling crowns and within the shrub canopy. Four measurements taken in each cardinal direction were averaged at each point during every sampling year.

Nutrient availability was assessed using ion exchange resins (Giblin et al., 1994). Resins exchange NO_3^-, PO_4^-, and NH_4^+, providing an index of inorganic nutrient availability. We enclosed ~3 g of mixed-bed resin in a small bag made of nylon stocking and placed two bags ~2 m on either side of our sample points in the mineral soil layer (~5 cm depth). Resin bags were installed in the field in May 2007 and removed in late September/early October 2007. In the lab, resin bags were rinsed in deionized water and air-dried. The resin beads were removed from their bags, weighed and extracted with 2 M NaCl in 0.1 M HCl. Extractant was analyzed on a Lachat QuikChem 800 Automated Ion Analyzer (Hach Co., Loveland, CO) at the analytical lab of the USDA Forest Service, Northern Research Station, Grand Rapids, MN. Our resin bag nutrient assay is reflective of both supply and demand: greater nutrients may reflect reduced demand or enhanced supply. Since we do not know the exact mechanism, we consider our assay a measure of potential nutrient availability to the roots of a seedling.

2.5. Shrub density measurements

We assessed response of the shrub layer in a 1.26 m radius circular plot centered on each sampling point. Three times between 2004 and 2009, all woody stems >1 m tall but less than 2.5 cm diameter at 1.4 m were counted and identified to species. Most of these woody stems were ramets of the shrub species, *C. cornuta* (beaked hazel).

2.6. Seedling growth measurements

We censused seedling diameter and height in summer 2003, immediately after planting, on five marked individuals of each

species occurring within a 16.1 m radius of each of the 10 sample points dispersed across each overstory–understory treatment combination. We subsequently measured seedling size and survival on these individuals in spring 2004 and fall 2004, 2005, 2007 and 2009. Seedling diameter was measured at a marked point on the stem ∼5 cm from the soil surface. Seedling height was measured from the marked point on the stem to the tip of the leader. In spring 2004, we added additional seedlings to the census to increase sample size due to first year mortality (e.g., if 2 of the original five jack pine at a point had died we added 2 additional seedlings to maintain a sufficient sample size for analysis of growth). To estimate initial size of each added seedling, we developed regression equations based on the relationship of seedling size in 2004 to size in 2003 for each overstory–understory treatment in each block. Average R^2 across 48 regressions was 0.25 for an average N of 120 seedlings. All regressions were significant with 39 of 48 at $P < 0.0001$. At each census we noted degree of damage by various agents, including browsing, insects, and diseases. Seedlings with severe damage were removed from the analyses.

2.7. Statistical analysis

We analyzed final seedling diameter and height by species using a split–split plot mixed-model ANCOVA for block (r), overstory treatment (i), understory treatment (j), sample point (k), and individual (l). Block and sample point were random effects. Sample point was included since we measured multiple individuals at each point. Initial diameter or height was used as a covariate to account for differences among individuals in initial size. Size metrics were $\log_{10}$ transformed in order to meet to assumptions of parametric statistical analysis. The form of the model was:

$$\log_{10}Y_{r(ijklm)} = \mu + \theta\log_{10}yr_{(ijkl)} + \alpha_i + \eta_{r(i)} + \beta_j + (\alpha\beta)_{ij} + \xi_{r(ijk)} + \gamma_l$$
$$+ (\alpha\gamma)_{il} + (\beta\gamma)_{jl} + (\alpha\beta\gamma)_{ijl}\varepsilon_{r(ijk)}$$

$$\eta_{r(i)} \sim N(0, \sigma^2_{\text{split-plot}})$$

$$\xi_{r(ijk)} \sim N(0, \sigma^2_{\text{split-split-plot}})$$

$$\varepsilon_{r(ijkl)} \sim N(0, \sigma^2_{\text{error}})$$

We used contrasts to test hypotheses about the effect of overstory and understory treatments. We used the same model to test for differences in resource availability except there was no covariate and point was not included since we only had one measure of light, N or P at each point. We used a proportional hazards model (Fox, 1993; Walters and Reich, 2000) to test for effects of overstory treatment, understory treatment and their interactions on seedling survival (days survived after planting). Seedlings that survived until the final censuses were right-censored. Since the proportional hazards model does not characterize differences among experimental treatments, we also used the product-limit (Kaplan–Meier) approach to analyze pairwise comparisons of overstory and understory treatments (Walters and Reich, 2000). For Kaplan–Meier pairwise comparisons, we tested for significant differences with log-rank and Wilcoxon tests. All statistics were conducted in JMP 9.0 (SAS Institute, Cary, NC, USA).

3. Results

3.1. Survival

In the full proportional hazards model, overstory treatment, understory treatment, and species were all significant as main

effects and there were significant interactions as well (Table 1). For both jack and red pine, overstory treatment significantly affected survival but the direction of response differed between species (interaction $P < 0.0001$) and was dependent on understory treatment (interaction $P < 0.0001$ [Table 1 and Fig. 1]). In contrast, there were no significant effects of experimental treatments on white pine, which had high survival (>90%) in all treatments. Given significant interactions and the fact that the proportional hazards model does not characterize differences among the treatments, in the remainder of this section, we present results of species-specific proportional hazards models (main effects = overstory and understory treatments) and Kaplan–Meier pair-wise comparisons of overstory and understory treatments for each species.

There was a highly significant overstory × understory treatment interaction for red pine survival ($\chi^2 = 26.04$, $df = 3$, $P = <0.0001$) and near significant interaction for jack pine ($\chi^2 = 6.75$, $df = 3$, $P = 0.0802$). The general trend was toward higher survival in retention treatments than uncut controls. However, differences among retention treatments varied with understory treatment (Fig. 1). For jack pine, when shrubs were at ambient levels, survival after six years was significantly lower in uncut control (58%) than the retention treatments (mean = 80%) and there were no differences among retention treatments in survival. In contrast, when shrubs were reduced by brush cutting there were no significant differences in survival among any of the overstory treatments (mean = 81%). Thus jack pine seedling survival was uniformly high except when faced with competition from both an uncut overstory and an intact shrub layer. For red pine, when shrubs were at ambient levels, highest survival was in the large gap aggregate retention treatment (80%) followed by dispersed (59%) and small gap (54%) with lowest survival in the uncut control (10%). Retention treatment order differed when shrubs were reduced with highest survival in the dispersed retention treatment (87%) followed by large and small gap aggregate retention (73% and 64%, respectively) with lowest survival again in the uncut control (12%). Thus red pine survival was highest when growing with reduced shrub competition and when overstory competition was reduced but uniform spatially.

3.2. Growth

For both diameter and height, there were significant main effects of species, overstory and understory as well as significant species × overstory and overstory × understory interactions (Tables 2 and 3). In general, all species grew taller and greater in diameter when shrubs were reduced and in the retention versus uncut overstory (Table 4). These effects were greater than additive: retention treatments (versus uncut) stimulated growth more when shrubs were reduced, and reducing shrubs enhanced growth more

Table 1
Proportional hazards model fit to survival data for seedlings of three species (*Pinus strobus*, *P. banksiana*, and *P. resinosa*) grown under four overstory and two understory manipulations in red pine forest in N. Minnesota, USA. Overstory treatments included uncut control, dispersed retention and small and large aggregated retention. Understory treatments included shrub reduction by brush cutting and ambient levels of shrubs. Seedlings were planted in May 2003 and last censused in September 2009 (right censored).

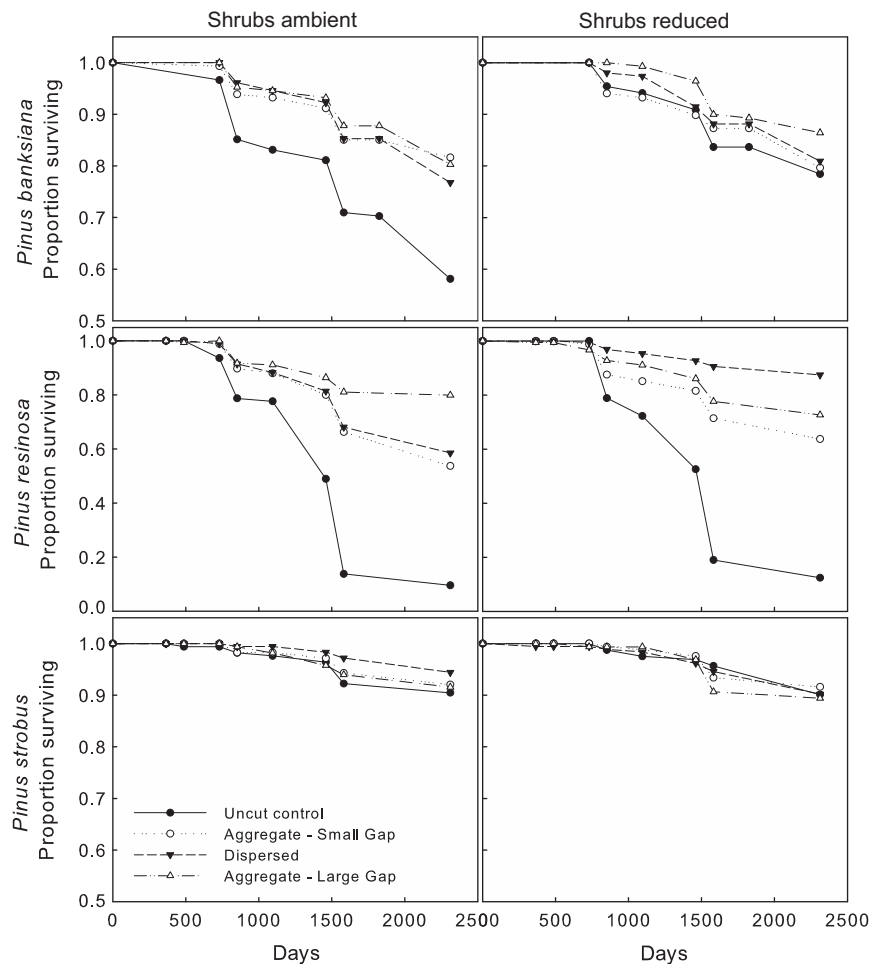| Source	df	Likelihood ratio Chi-square	P
Species	2	342.04	<0.0001
Overstory	3	64.48	<0.0001
Species * overstory	6	73.96	<0.0001
Understory	1	4.66	0.0309
Species * understory	2	10.01	0.0067
Overstory * understory	3	2.18	0.5353
Species * overstory * understory	6	25.79	0.0002

Fig. 1. Survival curves for seedlings of three species grown in four overstory and two understory manipulations in red pine forest in N. Minnesota, USA. Overstory treatments included uncut control, dispersed retention and small gap and large gap aggregated retention. Understory treatments included shrub reduction by brush cutting and ambient levels of shrubs.

Table 2
Analysis of covariance model results for average final diameter ($\log_{10}$-transformed) of seedlings of three pine species (*Pinus banksiana*, *P. strobus*, *P. resinosa*, grown under four overstory and two understory manipulations in red pine forest in N. Minnesota, USA. Overstory treatments included uncut control, dispersed retention and small and large aggregated retention. Understory treatments included shrub reduction by brush cutting and ambient levels of shrubs. Seedlings were planted in May 2003 and last censused in September 2009.

Source	df_{num}	df_{den}	F	P
Species	2	2790	109.1	<0.0001
Overstory	3	14.08	79.44	<0.0001
Understory	1	46.48	36.84	<0.0001
Species * overstory	6	2787	9.954	<0.0001
Species * understory	2	2786	2.713	0.0665
Overstory * understory	3	2784	11.09	<0.0001
Species * overstory * understory	6	2784	1.207	0.2994
$\log_{10}$ initial seedling diameter	1	2805	393.9	<0.0001

Table 3
Analysis of covariance model results for average final height ($\log_{10}$-transformed) of seedlings of three pine species (*Pinus banksiana*, *P. strobus*, *P. resinosa*, grown under four overstory and two understory manipulations in red pine forest in N. Minnesota, USA. Overstory treatments included uncut control, dispersed retention and small and large aggregated retention. Understory treatments included shrub reduction by brush cutting and ambient levels of shrubs. Seedlings were planted in May 2003 and last censused in September 2009.

Source	df_{num}	df_{den}	F	P
Species	2	2790	577.4	<0.0001
Overstory	3	12.88	65.54	<0.0001
Understory	1	43.38	10.83	0.0020
Species * overstory	6	2785	10.82	<0.0001
Species * understory	2	2783	2.09	0.1239
Overstory * understory	3	2745	3.771	0.0102
Species * overstory * understory	6	2781	0.8842	0.5055
$\log_{10}$ initial seedling diameter	1	2800	136.2	<0.0001

in retention treatments than in uncut stands. Species differed in the order of growth across retention treatments and that order in some cases depended on whether shrubs were reduced or ambient. For red pine, there were no differences in height or diameter among retention treatments. In contrast, white pine grew taller in dispersed retention than either aggregate retention treatments. Jack and white pine showed interacting effects of overstory and understory on diameter (jack and white) and height (jack). For jack

pine, there was no difference among retention treatments in height when shrubs were at ambient levels. In contrast, when shrubs were reduced, jack pine had greatest height growth in dispersed followed by large gap and small gap treatments. For diameter, both jack and white pine showed no difference in growth among retention treatments when shrubs were at ambient levels. However when shrubs were cut, both species had greatest diameter growth in dispersed treatments followed by large and small gap treatments.

Table 4

Geometric means and 95% confidence intervals of height and diameter of 8-year old seedlings of three pine species (*Pinus banksiana*, *P. strobus*, *P. resinosa*), grown under four overstory and two understory manipulations in red pine forest in N. Minnesota, USA. Overstory treatments included uncut control, dispersed retention and small gap and large gap aggregated retention. Understory treatments included shrub reduction by brush cutting and ambient levels of shrubs. Seedlings were planted in May 2003 and measured in September 2009. Letters refer to significant differences in pairwise comparisons among overstory treatments. Stars (*) or ns (not significant) indicate significant pairwise differences between understory treatments. These are present only in case with significant overstory × understory interactions in species-specific models. Means presented are not adjusted by the ANCOVA.

Species	Understory treatment	Overstory treatment							
		2009 Diameter (mm)				2009 Height (cm)			
		Uncut control	Dispersed retention	Aggregated small gap retention	Aggregated large gap retention	Uncut control	Dispersed retention	Aggregated small gap retention	Aggregated large gap retention
P. banksiana	Ambient	6.01a (5.7–6.3)	14.6b (13.3–16.0)	14.6b (12.8–14.6)	16.8b (14.5–19.5)	64.2a (59.5–69.2)	142.7c (128.6–158.4)	138.7ab (124.7–154.3)	143.3bc (129.1–158.9)
	Reduced	6.54a (6.0–7.1) ns	23.6c (21.3–26.2) *	20.1ab (17.2–23.4)	22.9bc (19.1–27.4) *	68.4a (63.3–73.9) ns	204.8b (187.8–223.2) *	176.9b (161.1–194.3)	171.3b (154.1–190.5) *
P. resinosa	Ambient	5.10a (4.3–6.1)	10.1b (9.2–11.1)	9.2b (8.3–10.1)	10.4b (9.3–11.5)	33.9a (26.6–43.2)	63.2b (58.5–63.4)	56.7b (51.6–62.3)	59.8b (54.8–65.2)
	Reduced	5.13a (4.6–5.8)	13.1b (12.1–14.1)	11.2b (10.0–12.5)	13.7b (11.8–15.9)	32.8a (27.9–38.6)	75.0b (70.4–79.9)	65.2b (59.3–71.7)	70.0b (63.9–76.6)
P. strobus	Ambient	6.41a (6.1–6.7)	14.7b (13.5–16.1)	13.3b (12.3–14.4)	13.2b (12.0–14.5)	47.9a (45.9–50.0)	99.6c (93.4–106.1)	88.0b (82.1–94.3)	77.4b (71.3–83.9)
	Reduced	7.20a (6.8–7.6) *	21.3c (20.0–22.8) *	17.0b (15.0–19.3) *	19.6b (17.4–22.2) *	51.6a (49.1–54.3)	122.5c (116.5–128.7)	100.2b (92.8–108.3)	95.4b (88.0–103.4)

3.3. Shrub density

Mean shrub densities before treatment (2002) averaged around 13,000 ± 1426 (std) stems ha^{-1}. Between 2004 and 2009 (shrubs cut annually), shrub densities did not differ among retention treatments ($P = 0.19$) but were lower in shrub reduction (2500 stems ha^{-1}) compared to shrub ambient treatments (17,500 stems ha^{-1}; $P > 0.0001$).

3.4. Resource availability

Across all treatments, overstory treatment ($F_{3,13} = 57.8$, $P < 0.0001$), shrub treatment ($F_{1,367} = 39.1$, $P < 0.0001$) and their interaction ($F_{3,367} = 4.23$, $P = 0.0059$) were significant predictors of light availability in the full model (Table 5; full model $R^2 = 0.58$). In general, and as expected, uncut stands had lower mean light availability than all three retention treatments, regardless of understory treatment. Across retention treatments, shrub reduction plots had higher light availability than shrub ambient plots. As with growth, effects of retention treatments (versus uncut) and shrub reduction treatment were more than additive (light availability was enhanced by each more when the other was also present). Dispersed and aggregated retention did not differ from each other in average light availability regardless of understory treatment. Comparing only the aggregated retention treatments, the large gap aggregated retention had higher mean light availability than the small gap aggregated retention, but only when shrubs were reduced by brush cutting (see also Boyden et al., 2012).

For both N and P availability, we found significant overstory × understory interactions (N: $F_{3,368} = 4.23$, $P = 0.006$; P: $F_{3,334} = 4.92$, $P = 0.002$), although the explanatory power of the full models was low (N: full model $R^2 = 0.20$; P: full model $R^2 = 0.16$).

Table 5

Geometric means and 95% confidence intervals of % diffuse transmittance, N (mg N g^{-1} resin) and P (mg P g^{-1} resin) in four overstory and two understory manipulations in red pine forest in N. Minnesota, USA. Overstory treatments included uncut control, dispersed retention and small gap and large gap aggregated retention. Understory treatments included shrub reduction by brush cutting and ambient levels of shrubs. Letters refer to significant differences in pairwise comparisons among overstory treatments within understory treatments. Stars (*) or ns (not significant) indicate significant pairwise differences between understory treatments within overstory treatments. Means presented are not adjusted by the ANCOVA.

Resource	Understory treatment	Overstory treatment			
		Uncut control	Dispersed	Aggregated Small gap	Aggregated Large gap
Light (% T)	Ambient	12.7[a] (10.9–14.4)	38.4[b] (35.1–41.8)	38.8[b] (35.2–42.4)	44.7[b] (39.9–49.6)
	Reduced	13.7[a] (12.3–15) ns	50.6[b] (47.8–53.5) *	46.1[b] (41.7–50.5) *	58.3[c] (53.9–62.7) *
Phosphorus (PO$_4^-$)	Ambient	0.137[a] (0.112–0.167)	0.195[a] (0.161–0.236)	0.156[a] (0.130–0.188)	0.149[a] (0.126–0.178)
	Reduced	0.097[a] (0.075–0.125) ns	0.190[ab] (0.152–0.238) ns	0.176[ab] (0.135–0.229) ns	0.235[b] (0.194–0.286) *
Nitrogen (NH$_4^+$ + NO$_3^-$)	Ambient	0.127[a] (0.106–0.140)	0.171[a] (0.133–0.220)	0.160[a] (0.132–0.194)	0.129[a] (0.109–0.152)
	Reduced	0.099[a] (0.081–0.120) ns	0.174[ab] (0.139–0.219) ns	0.180[ab] (0.143–0.227) ns	0.204[b] (0.166–0.251) *

Uncut stands had lower N and P than retention stands but only when shrubs were reduced. No other contrasts were significant.

4. Discussion

There is significant interest in silvicultural systems that emulate natural disturbance and increase structural complexity, spatial heterogeneity, and biological diversity in managed forests (Drever et al., 2006; Franklin et al., 2002). Variable retention harvesting has emerged as one strategy to achieve such goals (Gustafsson et al., 2012; Lindenmayer et al., 2012). However, the consequences of variable retention harvesting for new cohort growth and survival at the stand level are not well characterized in many forest ecosystems. Moreover, the relative importance of resource preemption by existing ground layer vegetation after variable retention harvests is unclear. We hypothesized that forests with equivalent average structures (e.g., basal area) would have higher stand-level seedling growth and survival in aggregated retention versus dispersed retention stands. However, variable retention harvest resulted in relatively small differences in growth and survival across three retention treatments (although all differed as expected from uncut controls). Similarly modest differences among retention treatments were found after the first two growing seasons (Peck et al., 2012).

What are the underlying mechanisms for lack of strong retention treatment differences? Our growth and survival differences among the full set of treatments were almost certainly a result of differences in resource availability among treatments. Related work shows that light availability is strongly correlated with individual growth for all species (Boyden, Montgomery, Palik and Reich, unpublished data) and that shrub competition can reduce growth and survival of all three pines species in this system through reductions in resource availability (Shirley, 1945; Strothmann, 1967; Montgomery et al., 2010). The stand-level growth results largely parallel patterns of stand-level resource availability (Tables 4 and 5). We expected that among retention treatments differences in the spatial pattern of competitors would lead to differences in stand-level resource availability and thus growth. This occurred only when shrubs were reduced by brush cutting (Table 5; Boyden et al., 2012). We did find higher variability and higher maximum values of resource availability in aggregated treatments (Boyden et al., 2012); however, stand-level averages of resource availability mask those differences among retention treatments.

4.1. Shade tolerance and response to retention harvests

Shade tolerance plays an important role in determining post-harvest successional processes in managed forests. We hypothesized that species would differ in their responses to VRH treatments based on their shade tolerance. Specifically, we expected that the most tolerant species, *P. strobus*, would have highest growth and survival in dispersed retention (and be least sensitive to treatments) and the least tolerant species, *P. banksiana*, would have highest growth and survival in the large gap aggregated treatment (and strongest overall sensitivity to treatments). Our expectations were partially supported. White pine survival was much less sensitive across all treatments than red pine or jack pine (Fig. 1), but growth differences did not track survival trends. We found that white pine indeed achieved its highest growth in the dispersed treatment, but so did jack pine. We argue that white pine had the highest survival across all treatments due to its tolerance to competitors and the fact that shrubs can have a facilitative effect on white pine performance (Montgomery et al., 2010). Red pine did not differ in growth across the three retention treatments and also grew much less than the other two species. This was likely

due to response to competition and to risk of disease. Adult red pine trees harbor *Sirrococcus* and *Diplodia* fungal spores, both significant agents of seedling mortality in red pine (Ostry et al., 2012). Thus, regeneration of red pine under a canopy of red pine will require high stocking levels to account for higher mortality rates.

Our growth and survival results were somewhat surprising for jack pine, often considered a quintessential shade intolerant species. Historically, jack pine was often among the first species to colonize after stand replacing crown fires due to its propensity to produce serotinous cones and its shade intolerance. How do we reconcile the regeneration ecology of jack pine with its performance in this study? Our survival results suggest a revision of our expectations of shade tolerance for jack pine. If shade tolerance is defined as the ability to survive under 'low' light conditions, our results suggest that jack pine may be much more shade tolerant than once thought; able to survive under closed canopy conditions provided it can become established (we avoided this bottleneck by planting) and provided it does not face additional competition from shrubs (Fig. 1). Under current natural regeneration conditions, seedling establishment under canopies may be hindered by dominance of serotinous genotypes in the population (Gauthier et al., 1996), lack of appropriate seedbed requirements (e.g., bare mineral soil) and high levels of shrubs in forests protected from fire. In contrast to our survival data, our growth data suggest that jack pine response partially support our hypotheses related to species shade tolerance. First, when overstory competition was reduced (harvest treatments) jack pine showed the greatest growth of the three species, especially in terms of height (Fig. 1). Second, although high growth in dispersed retention treatments was unexpected, it may stem from light conditions that maximized photosynthetic photon flux density (PPFD) use efficiency for all species. One hypothesis to explain optimal photoysynthetic function of plant canopies invokes maximization of photosynthetic PPFD use efficiency (Posada et al., 2009). In general, maximal PPFD use efficiency occurs at intermediate light levels (Posada et al., 2009), which represent the most common resource condition in the dispersed retention.

4.2. Critical importance of shrubs

Tree regeneration and forest dynamics result from interactions between seedlings, the abiotic environment, and already established vegetation (e.g., adult trees, shrubs, herbs, etc.). Interactions between seedlings and adults have been well studied (e.g., gap phase regeneration [Brokaw, 1985]), whereas interactions between seedlings and understory vegetation are less well understood. In particular, there are few studies that compare the relative importance of the overstory versus the woody understory for regeneration processes in forests (e. g. Lorimer et al., 1994). Such comparisons are important for understanding the consequences of natural disturbance and retention harvesting for the growth and survival of a new cohort of trees. Our results suggest a critical role of shrub competition in structuring tree regeneration in red pine forests. Indeed, despite major difference in the spatial pattern of the residual overstory, growth and survival differences among retention treatments were seen only when shrub density was reduced through brush cutting (Fig. 1; Table 4), and differences of retention treatments versus unharvested controls were also larger under these conditions. Differences in growth were often larger across understory treatments than among retention treatments (Table 4). For example, averaging the three retention treatments, jack pine seedlings were 43 cm taller when shrubs were reduced compared to when shrubs were at ambient levels. In contrast, comparing final jack pine height among retention treatments; height varied by an average of only 3 cm when shrubs were at ambient

levels and 22 cm when they were reduced. These results contrast with early growth and survival results in this system that found relatively minor effects of shrubs (Peck et al., 2012).

The impact of shrubs on growth and survival was likely due to resource competition (Strothmann, 1967; Montgomery et al., 2010) and dependent on overstory abundance. In all the retention treatments, we found higher light, N and P than in uncut controls, but for the latter two resources only when shrubs were removed. Similarly, understory treatments did not significantly impact any of the three resources in uncut overstories, but shrub reduction through brush cutting increased all of them significantly in at least one of the retention treatments. We interpret these results as indicating that overstory removal reduced demand for soil N and P thus raising the level in soil. This effect of trees on resources was only observed when shrubs were reduced suggesting that shrubs took advantage of greater resources in overstory removal plots and took up commensurately more of the soil nutrients (see also Boyden et al., 2012). Taken together, these results provide compelling evidence that shrubs preempt resources released by partial overstory removal in VRH stands and thus represent a significant barrier to post harvest regeneration with these approaches. Global trends indicate an increase in the prevalence of dense understories in many forest ecosystems (Royo and Carson, 2006). These are hypothesized to result from anthropogenic increases in canopy disturbance coupled with altered herbivory or fire regimes (Royo and Carson, 2006). Our results support the idea that dense understory layers, whether composed of shrubs, ferns or bamboos, have the potential to reduce tree regeneration in VRH stands, alter species composition and impact patterns of forest succession and floristic diversity.

4.3. Applying VRH approaches in red pine forests

Red pine dominated ecosystems occupy large areas in the western Great Lakes region, covering nearly 800,000 ha in the US Lakes States alone (Red Pine Web-based Forest Management Guide; http://www.nrs.fs.fed.us/fmg/nfmg/rp/index.html; accessed 11 May 2013). Moreover, red pine, is a particularly important commercial species, used widely for cabin logs, utility poles, saw timber, and pulpwood. Historically, forest management has structurally simplified red pine forests using even-aged regeneration techniques, often in monospecific plantations, on a 60–90 year rotation (Palik and Zasada, 2003). However, managing for ecological objectives, particularly enhanced structural complexity, has emerged as an approach to achieve multiple goals and to increase resilience of this ecosystem in the face of global climate change.

Increasingly, VRH approaches are promoted as a way to manage for structural complexity in red pine forests (Palik and Zasada, 2003) and beyond (Gustafsson et al., 2012; Lindenmayer et al., 2012), because they are designed to emulate the structural outcomes of natural regeneration disturbances and thus sustain the organisms and processes dependent on this structure. At the same time, managers of commercial forests need to be cognizant of the effects of their actions on growth of target timber species. Our experiment was designed to examine the effects of retention harvesting on regeneration growth of important timber species in red pine forests and to explore the potential to mitigate growth reduction caused by resource competition with the overstory through manipulation of the spatial distribution of competitive neighborhoods. Moreover by manipulating shrubs, we were also able to assess their impact on the efficacy of VRH. Our results demonstrate that all three common pine species found in red pine ecosystems can be regenerated using VRH approaches and planting. However, contrary to our expectation, and evidence from other ecosystems (Palik et al., 2003), growth and survival were relatively high and similar for all retention treatments. The practical

application (of the relatively small differences in growth and survival among retention treatments but large responses with shrubs) is that managers have some flexibility in implementing VRH approaches depending on overall goals and capacity to reduce shrub competition at key tree regeneration stages. Finally, within a single large harvest unit, a manager may vary retention patterns from dispersed to aggregated (with large openings) with similar expectations for survival and growth of target tree species, but with potentially very different responses for other ecosystem components, allowing diverse objectives to be met (Franklin et al., 1997). For instance, larger aggregates may perpetuate later successional ground layer plant species within the harvest unit (Nelson and Halpern, 2005), whereas low levels of dispersed retention are more likely to foster earlier successional species. In summary, our results imply that managers have considerable flexibility to employ various types of retention patterns coupled with planting in red pine ecosystems at least at the levels of retention studied here.

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