Variation in microclimate and early growth of planted pines under dispersed and aggregated overstory retention in mature managed red pine in Minnesota

JeriLynn E. Peck, Eric K. Zenner, and Brian Palik

Abstract: Retention harvests are proposed as mechanisms for introducing two-aged structure into even-aged red pine (*Pinus resinosa* Ait.) stands, yet little is known about seedling responses to overstory abundance and resource availability under potential harvesting treatments. We related spatially explicit measurements of overstory abundance, proportional diffuse radiation, and soil temperature and moisture to first-year mortality and 2-year growth of underplanted jack pine (*Pinus banksiana* Lamb.), eastern white pine (*Pinus strobus* L.), and red pine seedlings under four harvest treatments: no-harvest control, single-tree (dispersed) thinning, small (0.1 ha) gap group harvesting, and large (0.3 ha) gap group harvesting. Growth of all species was greater in all cut treatments than in the control, but the only difference among cut treatments was greater jack pine height growth in large-gap harvests than in small-gap harvests. Proportional diffuse radiation and soil moisture varied considerably by location within the gaps and were highest in gap centers. Seedling growth responses increased from the forest edge into gap centers where overstory influence was least. All three cut treatments could be expected to result in the development of a two-aged stand structure in mature red pine stands such as these. When an aggregate retention harvest is implemented, higher initial mortality and growth could be anticipated for seedlings near the center of the gap.

Résumé : Les coupes à rétention variable sont proposées comme mécanismes d'introduction d'une structure bi-étagée dans les peuplements équiennes de pin rouge (*Pinus resinosa* Ait.) bien qu'on connaisse mal la réaction des semis à l'abondance du couvert dominant et à la disponibilité des ressources à la suite de traitements de récolte potentiels. Nous avons relié des mesures spatialement explicites d'abondance du couvert dominant, de rayonnement diffus relatif et de température et d'humidité du sol à la mortalité survenue la première année et à la croissance des deux premières années de plants de pin gris (*Pinus banksiana* Lamb.), de pin blanc (*Pinus strobus* L.) et de pin rouge dans quatre traitements de récolte : un témoin non traité, une éclaircie par pied d'arbre (dispersée), une coupe par trouées de petite taille (0,1 ha) et une coupe par trouées de grande taille (0,3 ha). La croissance de toutes les espèces était meilleure dans tous les traitements de récolte que dans le témoin, mais la seule différence entre les traitements de récolte était une plus grande croissance en hauteur du pin gris dans la coupe par trouées de grande taille par rapport à la coupe par trouées de petite taille. Le rayonnement diffus relatif et l'humidité du sol variaient considérablement à l'intérieur des trouées et étaient plus élevés au centre des trouées. La croissance des plants a augmenté de la bordure vers le centre des trouées où l'influence du couvert dominant était minimale. Les trois traitements de récolte pourraient conduire au développement d'une structure forestière bi-étagée dans des peuplements matures de pin rouge tels que ceux qui ont été étudiés. Lorsqu'une coupe à rétention variable par trouées est effectuée, une plus forte mortalité initiale et une meilleure croissance peuvent être anticipées dans le cas des semis situés près du centre des trouées.

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Introduction

Forest management objectives now typically include the restoration of natural ecosystem structures and functions, the maintenance of viewscapes and recreational areas, fuels management, and the continued production of sawtimber, fiber, and other forest commodities. Forest science, however, struggles to keep up with societal demands (Kimmins 2002), sometimes resulting in the implementation of management tools before the full range of their ramifications are understood. This is the context of the past decade in which aggregate retention (usually implemented through cutting gaps and thus leaving 'aggregates' of trees around the gap edge; Franklin et al. 1997) has become an accepted management

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tool in a variety of North American ecosystems (Palik et al. 2003*a*; Pritchard and Comeau 2004; York et al. 2004). Retention systems that leave some overstory during the regeneration harvest presumably promote structures (e.g., two- or multicohort stand structure) that more resemble those resulting from natural disturbances (Franklin et al. 2007; Seymour and Hunter 1999). In addition, leaving variably sized aggregations of trees can have aesthetic advantages over clearcuts (cf. Bliss 2000) and may provide the flexibility needed to protect biodiversity hotspots (Neitlich and McCune 1997). Incorporating or developing structural features associated with natural disturbances can be part of extensive management in which extended rotations allow for the development of greater ecological complexity as well as commodity production, or part of reserve management, in which restoration may be the goal (Gilmore and Palik 2006).

Retaining aggregations of overstory trees is now being proposed for both reserve and extensive management of the pine forests of the Great Lakes region (Palik and Zasada 2003). This region has over a million acres of red pine (*Pinus resinosa* Ait.) forest (Gilmore and Palik 2006), most of which is managed and structurally relatively simple compared with naturally developed pine forests (Palik and Zasada 2003). Jack pine (*Pinus banksiana* Lamb.), eastern white pine (*Pinus strobus* L.), and red pine are all fire-adapted species that once covered millions of acres in this region (Heinselman 1973). It is thought that frequent ground fires once facilitated the development of multiaged mixed pine forests by creating suitable germination conditions via exposure of mineral soil and reduction of competing vegetation (Wendel and Smith 1990; Frelich and Reich 1995; Fraver and Palik 2011). Importantly, the susceptibility of small-diameter pine (<20 cm) to surface fire (Beverly and Martell 2003) also meant a relatively open canopy and higher levels of light than are now often seen. Subsequently, the silvics of these species traditionally indicated clearcut or shelterwood regeneration methods (Rudolf 1990; Rudolph and Laidly 1990; Wendel and Smith 1990). More recently, the creation of small gaps (resulting in aggregate retention) has been proposed (Dickmann 1998; Groot et al. 2001). However, the trade-off for increased overstory retention has been shown to be reduced growth in the understory (Palik et al. 1997, 2003*a*; Seymour and Hunter 1999). The successful implementation of aggregate retention therefore depends upon a clear understanding of the relations between the residual overstory and desired regeneration in the understory (Van Pelt and Franklin 1999).

These relations can be explored directly, investigating the competitive influence of the overstory on the understory, or indirectly by investigating the influence of subsequent changes in environmental conditions on the understory. Several studies have suggested that aggregating retention can promote seedling growth by reducing the area subject to overstory–understory competition (e.g., Palik et al. 1997). Leaving only very small gaps, however, may be ineffective, as they are sometimes indistinguishable from intact forest (Coates 2000; Muscolo et al. 2007). Conversely, although seedling growth is often best in the center of the largest gaps (Palik et al. 1997; Coates 2000; Gagnon et al. 2003), there is a diminishing point of return as gap size increases (Coates 2000; York et al. 2004). Studies in other ecosystems have begun to characterize resource variation with gap size, observing that light availability tends to increase as gap size increases (Battaglia et al. 2002; Pritchard and Comeau 2004; Muscolo et al. 2007), temperature extremes are greatest in larger gaps (Pritchard and Comeau 2004; Muscolo et al. 2007), and nutrient concentrations can increase (nitrogen; Palik et al. 1997) or decrease (phosphorus; Muscolo et al. 2007) with increasing gap size. Relatively few studies, however, have linked seedling growth to spatially explicit overstory abundance or resource availability (Gagnon et al. 2003; Powers et al. 2008).

The purpose of the current study was to explore early (first two growing seasons) seedling responses to differences in overstory abundance and microclimate resource availability resulting from various overstory residual abundances in mature red pine in an established experiment designed to add structural and compositional complexity to managed red pine (Palik and Zasada 2003). This experiment implemented four harvest treatments: a no-harvest control, single-tree (dispersed) thinning, and two scales of aggregate retention, small-gap (0.1 ha) group harvesting and large-gap (0.3 ha) group harvesting (Palik et al. 2003*b*). Our approach was to relate spatially explicit measurements of overstory abundance, proportional diffuse radiation, and soil temperature and moisture conditions to the mortality and growth of underplanted jack, eastern white, and red pine seedlings. Our objectives were to determine how microsite resource availability and seedling mortality and growth varied as a function of (*i*) these four harvest treatments and (*ii*) the location of seedlings within the treatment plots and particularly the group harvesting gaps.

Materials and methods

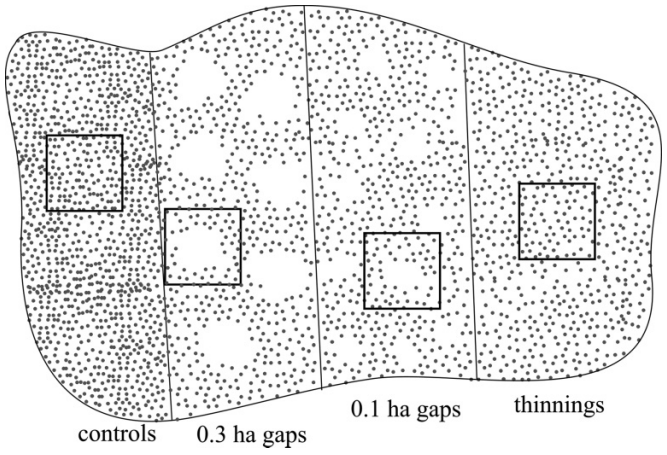
Study sites and treatment design

Four treatments were applied in a complete block design replicated in three blocks on deep loamy sand soils at an elevation of 400–450 m (averaging ~85 mm/month of precipitation during the growing season) on the Chippewa National Forest in northcentral Minnesota (47°24′45″–47°32′53″N, 94°04′15″–94°08′45″W) (Palik et al. 2003*b*). All stands originated 75–100 years ago (Zenner and Peck 2009) following a seed cut, had been lightly thinned between 1959 and 1978 (Palik et al. 2003*b*), and consisted of red pine with an admixture of eastern white pine and very low densities of other species (e.g., balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss)), and trembling aspen (*Populus tremuloides* Michx.)).

Each block consisted of four 16–20 ha stands, each receiving one of four randomly assigned overstory treatments (Fig. 1): uncut control ("controls"), dispersed thinning ("thinnings"), small circular gap harvest ("small-gap harvests", 0.25 acre = 0.10 ha), and large circular gap harvest ("large-gap harvests", 0.75 acre = 0.30 ha). The residual forest around the gap harvests was lightly thinned and the target residual basal area for all cutting treatments was roughly 18 m^2/ha, with red pine the favored crop species (Table 1). Harvests were conducted during winter 2002–2003 (Palik et al. 2003*b*).

The variable understory shrub layer (primarily beaked hazel (*Corylus cornuta* Marsh.) with pretreatment densities of

Fig. 1. One 1.21 ha square plot was placed within each of the four stands of blocks 1 and 2 in a relatively homogenous area. The four treatment types (from left to right) were unharvested control, large-gap harvests (0.3 ha), small-gap harvests (0.1 ha), and dispersed thinning. Within the gap harvests, plots were centered on a gap.



up to ~20 000 stems/ha) was standardized in spring 2003 by brushing (i.e., cutting) all woody species >0.3 m in height and <6.4 cm diameter at breast height (DBH), with the exception of conifers, maples (*Acer*), and oaks (*Quercus*) (Palik et al. 2005). Brushing was repeated in 2004 in half of the stands (block 1 thinning and small gap harvests, block 2 thinning and small gap harvests, and block 3 small and large gap harvests).

Overstory structure

In summer 2002, after marking but prior to harvest, a 1.21 ha sampling plot (110 m × 110 m) was established within each stand in blocks 1 and 2 in areas with >80% red pine basal area; gap plots were centered on an actual gap (Fig. 1). The position of each live or dead tree >5 cm DBH was then stem-mapped and slope-corrected distances and azimuths were converted to Cartesian coordinates. Species and DBH were recorded for all mapped trees. In the gap plots, tree heights were also recorded for overstory trees on the edges of the gap (averaging 19.5–25.3 m, standard deviation 1.4–3.1 m). In the summer of 2003, the cut plots in blocks 1 and 2 were revisited to verify which trees remained following harvest. Block 3 could not be sampled until after harvest in the summer of 2003 when fixed-radius circular plots were established in each plot. In the controls, thinnings, and small-gap harvests of block 3, plots were 36 m radius (0.4 ha), while plots in the large-gap harvests were 45 m radius (0.64 ha) to encompass the entire gap. Either all trees (control and thinning) or the residual gap-edge trees (small- and large-gap harvests) were stem-mapped and measured as described above. Post-harvest basal area was recorded in block 3 plots following the harvest treatment at five points around plot center using a 2 m BAF wedge prism.

To estimate local overstory competition, we used both total overstory basal area within 10 m diameter subplots centered on each seedling and an adaptation of an index of local competition (Stoll et al. 1994) known as the overstory abundance index (Battaglia et al. 2002), which is calculated as the sum for all trees within the subplot of their basal area weighted by

Table 1. Overstory characteristics following treatment for the two replicates of each treatment; letters indicate significant ($P < 0.1$) differences among the four treatments following harvest.

	Controls			Thinnings			Small-gap harvests			Large-gap harvests		
	1	2		1	2		1	2		1	2	
Mean DBH (cm)	24	26	a	28	29	bc	28	31	c	25	26	ab
DBH standard deviation (cm)	14	10	a	10	11	a	11	13	b	9	12	a
Basal area (m/ha)	44	36	a	17	17	b	19	23	b	15	20	b
Density (trees/ha)	617	479	a	212	191	b	217	216	b	222	261	b
Trees >40 cm DBH trees/ha)	67	33	a	14	12	a	10	60	a	3	23	b
Snags (trees/ha)	52	23	a	6	2	b	7	2	b	4	15	b

their distance to the center of the subplot (setting the minimum distance to 1 m to prevent overemphasis of very close trees).

Planted seedlings

In spring 2003, equal numbers of 2-year-old nursery-raised bare-root red, eastern white, and jack pine seedlings were underplanted at a roughly 2.7 m spacing in portions of each plot (Palik et al. 2003*b*). Due to *Diplodia pinea* (Desm.) Kickx infection of the red pine seedlings, and subsequent mortality rates two to three times that of the jack and eastern white pine, mortality data are reported only for jack and eastern white pine.

Seedlings were initially sampled in the first summer after planting (2003) to assess baseline condition. In thinnings and controls, a 30 m radius circular subplot was centered within each planted patch. Within each of eight equally sized wedges within each subplot, three or four seedlings of each species were randomly selected, tagged, and measured (i.e., 30 per species per subplot). In gap plots, subplots were centered on the gap and extended into the residual forest, either 30 m in radius (small-gap harvests) or 50 m in radius (large-gap harvests), resulting in either 30 or 90 seedlings of each species being sampled, respectively. Due to planting errors, only 10 seedlings of each species were available for sampling in the block 2 control and only 60 per species in the block 2 large gap.

Each tagged seedling was stem-mapped and the distance and azimuth of location converted to Cartesian coordinates. Data collected for each included species, collar diameter using calipers, height, and rooting medium (soil, duff, or slash). Tagged seedlings were reevaluated for mortality in the first fall (2003) and in the second summer (2004). A random subsample of 20 seedlings of each species in each plot was remeasured in the third summer (2005) for collar diameter and height and an estimate was made of the percent cover of competing vegetation within a 1 m diameter circle centered on each seedling at that time. Seedlings with obvious signs of deer browse were excluded from the analyses of height growth (23% of the 2005 subsample).

Collar diameter and height growth thus reflect 2 years worth of growth as the difference between the first (2003) and third (2005) summers. To focus on the treatment signal, mortality was divided into first-summer mortality (between the first summer and first fall) and first-year mortality (between the first fall and second summer).

Microsite conditions

In the first summer, proportional diffuse radiation, soil moisture, and soil temperature were recorded once at each tagged seedling. Proportional diffuse radiation at seedling height (DIFN from the C2000 program, which estimates diffuse radiation penetrating the canopy) was calculated as the ratio of visible sky in open (nonforested) and subcanopy (i.e., at seedling locations) positions from simultaneous paired readings from calibrated LI-COR LAI-2000 plant canopy analyzers taken at dawn or dusk. Soil moisture (reported as a percentage of the volumetric water content) was taken adjacent to each seedling at a depth of 20 cm using a Field Scout TDR soil moisture probe between the hours of 11 a.m. and 2 p.m. Soil temperature was recorded at the same depth and time as moisture using a Cooper-Atkins VersaTuff thermometer. Because soil moisture and temperature readings were not able to be taken on the same day for all plots even within a stand, values were standardized for comparison across plots by dividing the value for each seedling by the highest value observed for any seedling in that plot (i.e., proportion of maximum observed). Soil moisture and temperature were measured again during the second summer.

The proportional diffuse radiation and soil moisture and temperature data are shown using continuous distribution functions fit to a normal distribution (in PC-ORD v. 5.2). Values for these resources, as well as collar diameter and height growth, are also summarized for presentation by smoothing across the spatial extent of the gap harvests using a running average to enable a visual assessment of variation within the gap plots.

Data analyses

Harvest treatment effects were evaluated based on differences in mean plot-level values using ANOVA (proc GLM in SAS v. 9.1) for pre-planned contrasts. Due to the very small sample size, contrasts are considered significant up to $\alpha = 0.10$. Contrasts were among treatments for microsite conditions and seedling mortality and growth by species. Block, treatment, species, rooting medium, and whether or not a plot had been brushed were included in the models, as appropriate and dependent variables were log-transformed to improve normality as needed (after checking residuals). Regression analyses at the plot level were used to describe relationships of average seedling mortality (logistic regression, proc GENMOD) and growth (ANOVA, proc GLM) by species with microsite resources.

Location effects were evaluated based on regression analyses at the individual seedling level of patterns in microsite resources (ANOVA, proc MIXED) and seedling mortality (proc GENMOD) and growth (proc MIXED) by species with respect to the following spatial variables: minimum distance to the nearest tree, minimum distance to an edge tree, distance to the southernmost gap edge, total basal area, the overstory abundance index, a classification for seedling position on the north or south side of the plot as well as by quadrants, and a position classification of "out" (under the residual canopy), "edge" (within 5 m of the gap edge), "in" (>5 m from the gap edge), or "center" (within an inner 5 m (small gap) or 10 m (large gap) circle around the gap center but at least 10–11 m from the nearest residual tree, which was half the average edge tree height). The association between seedling growth and location within the gap plots was evaluated using the Mantel test in PC-ORD (McCune and Mefford 2006), which is a test of spatial autocorrelation when used with a matrix of $[X,Y]$ coordinates.

Variation in microsite conditions was summarized using principal components analysis ordination (PCA in PC-ORD). The understory competitive environment for each seedling within the gap plots was modeled by ordinating the three first-summer measurements of microsite conditions (proportional diffuse radiation, soil moisture, and soil temperature, after relativization). For both gap harvests, only the first two synthetic axes explained more variation than expected by chance (Monte Carlo procedure, $P < 0.05$). Due to similarity of pattern, only the ordination graph for the large gap har-

Fig. 2. Percent frequency distributions of first-summer microsite conditions in each treatment. Different letters indicate significant ($P < 0.001$) treatment differences. (A) The average proportional diffuse radiation at seedling height was lower and less variable in the controls than in the cut treatments. (B) The average proportion of maximum observed soil temperature was lowest in the large-gap harvests, then small-gap harvests, and greatest in thinnings and controls. (C) The average proportion of maximum observed soil moisture did not differ among treatments. Treatment effects were observed, however, in the second summer (see text).

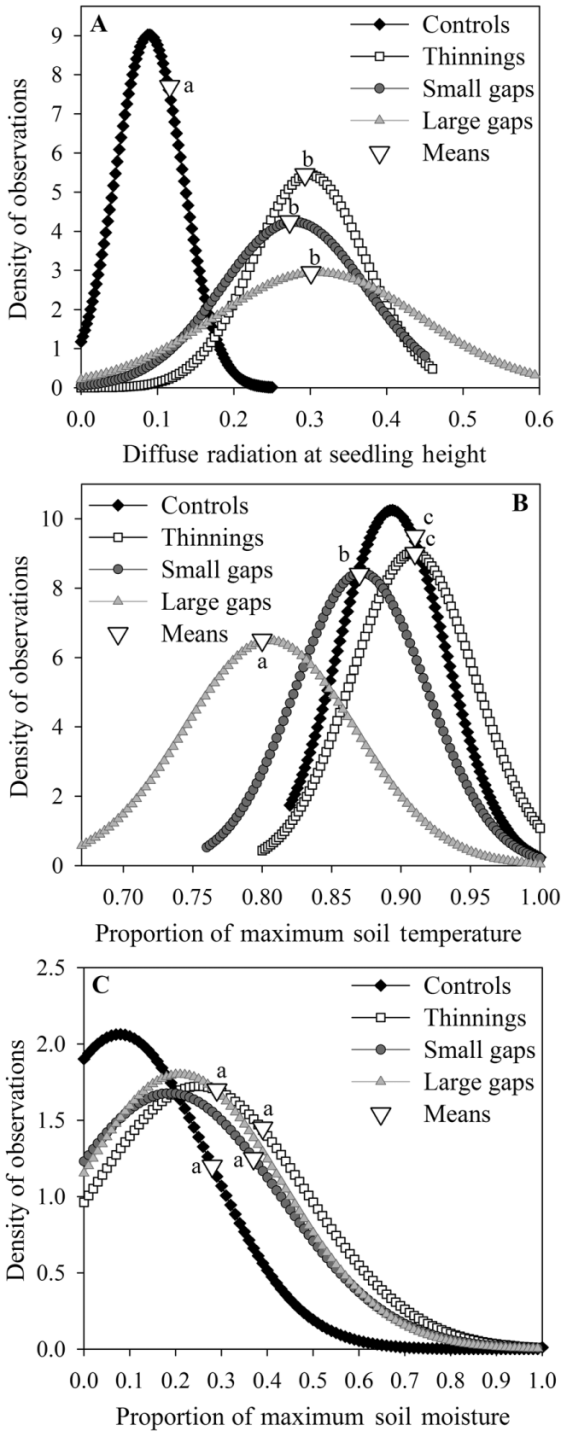
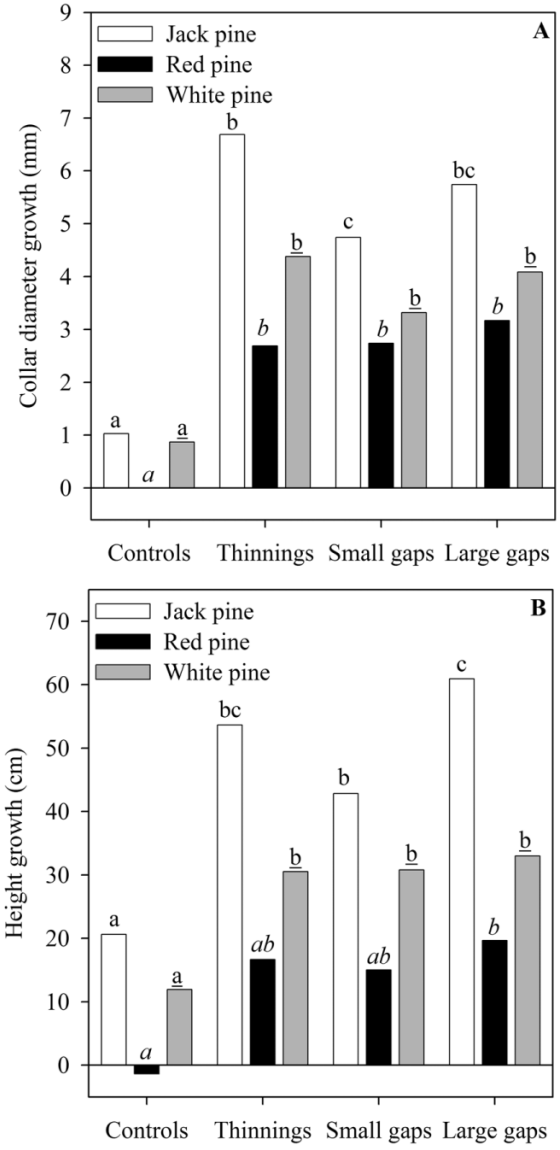


Fig. 3. Two-year (A) collar diameter and (A) height growth by treatment for jack pine (*Pinus banksiana*), red pine (*Pinus resinosa*), and eastern white pine (*Pinus strobus*). Different letters indicate a significant ($P < 0.1$) treatment effect following harvest (across treatments). The only differences among cut treatments were greater jack pine collar diameter growth in thinnings than in small-gap harvests and height growth in large-gap harvests than in small-gap harvests.



vests is shown. Ordination scores were correlated with growth parameters and class variables for location within the gap plot. Except where otherwise noted, reported statistics are for the ANOVAs.

Results

Harvest treatment effects

Proportional diffuse radiation and competing vegetation

The average amount of first-summer proportional diffuse radiation at seedling height was significantly higher in all cut treatments than in the uncut control (df = 35, $P < 0.001$) but did not differ among the cut treatments (Fig. 2A). The

variation in proportional diffuse radiation differed significantly between the uncut controls and the small- and large-gap harvests (df = 35, $P < 0.001$) and among all cut treatments (df = 35, $P < 0.04$), with a gradient of increasing variation from controls to thinnings to small-gap harvests to large-gap harvests. The percentage of third-summer competing vegetation around the subset of unbrowsed seedlings was significantly and substantially (50%) greater in all cut treatments than in the uncut control (df = 32, $P < 0.003$) but did not differ among cut treatments. The variation in competing vegetation was greater in the small- and large-gap harvests than in the thinnings (df = 32, $P < 0.02$).

Soil temperature

The average proportion of first-summer maximum observed soil temperature was greater in the controls and thinnings than in the small- or large-gap harvests (df = 35, $P < 0.05$) and in the small-gap harvests than in the large-gap harvests (df = 35, $P < 0.001$) (Fig. 2B). The variation in first-summer soil temperature varied significantly among all treatments (df = 35, $P < 0.01$), with a gradient of increasing variation from controls to small-gap harvests to thinnings to large-gap harvests. Second-summer soil temperature was greater in the controls than in the thinnings (df = 23, $P = 0.02$) or large-gap harvests ($P = 0.002$) but no differences were observed among cut treatments and the variation in soil temperature was greater in the large-gap harvests than in the controls (df = 23, $P = 0.06$).

Soil moisture

The average proportion of first-summer maximum observed soil moisture did not differ among treatments (Fig. 2C), although variation was considerably lower in the uncut controls than in any cut treatment (df = 35, $P < 0.001$) and greater in the large-gap harvests than in either the thinnings or small-gap harvests (df = 35, $P < 0.01$). Second-summer soil moisture was greater in the large-gap harvests than in the thinnings or small-gap harvests (df = 23, $P < 0.03$) and greater in the controls than in the small-gap harvests (df = 23, $P = 0.08$), with more variation in the large-gap harvests than in the thinnings (df = 23, $P = 0.06$).

Mortality

Over 75% of mortality occurred between the first summer and first fall, compared with 17% over the following winter and 9% the next spring, and was strongly associated with the rooting medium (logistic regression, df = 1483, $P < 0.04$, with higher mortality in slash > duff > soil). No treatment effect was observed for mortality during either the first summer or the first year for either jack or eastern white pine. First-summer mortality did not vary with overstory structural or microsite conditions. First-year mortality of jack and eastern white pine decreased with increasing proportional diffuse radiation (logistic regression, df = 29, $P = 0.03$) and increasing second-summer soil moisture (logistic regression, df = 17, $P = 0.05$) but increased with increasing second-summer soil temperature (logistic regression, df = 17, $P = 0.02$).

Collar diameter growth

Collar diameter growth was higher in all cut treatments than in the uncut controls for all three species (df = 33, $P < 0.1$) and was higher in the thinnings than in the small-gap harvests for jack pine (df = 33, $P = 0.07$) (Fig. 3A). The variation in collar diameter growth was not significantly different among treatments for any species. Growth of all species decreased with increasing basal area of overstory trees within 10 m (df = 21, $P = 0.03$) and increasing overstory abundance within this zone (df = 21, $P < 0.001$). Jack pine collar diameter growth decreased with increasing first-summer soil temperatures in thinnings (df = 33, $P < 0.002$) and with increasing second-summer soil temperatures in all treatments (df = 22, $P = 0.008$). Growth of all species increased with increasing first-summer soil moisture in thinnings (df = 33, $P < 0.001$) and with increasing second-summer soil moisture in all treatments (df = 22, $P = 0.06$). Collar diameter growth was not significantly associated with competing vegetation or proportional diffuse radiation.

Height growth

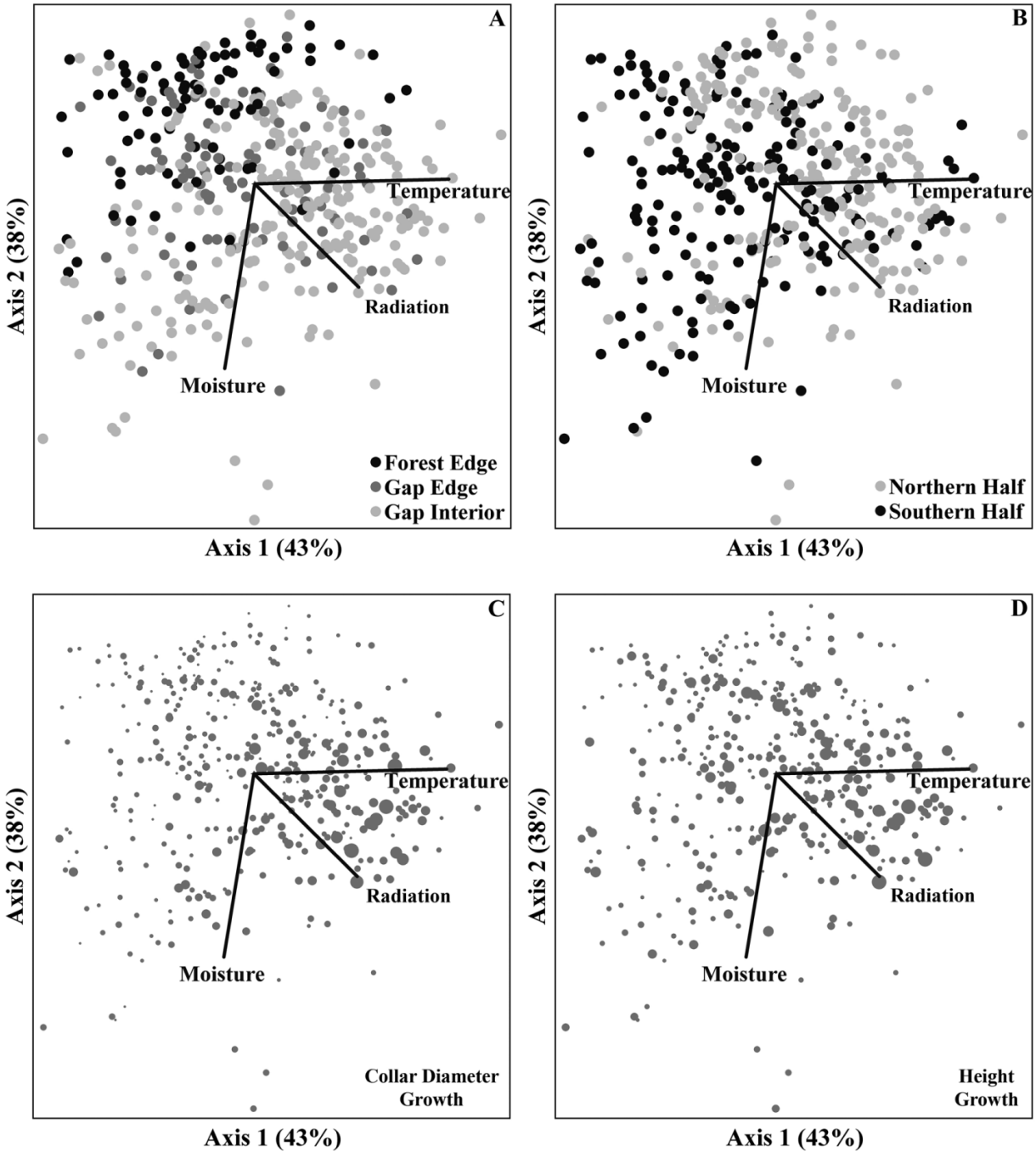
Height growth was higher in all cut treatments than in the uncut controls for jack and eastern white pine (df = 33, $P < 0.05$) but was only higher in the large-gap harvests than in the controls for red pine (df = 33, $P = 0.09$) (Fig. 3B). Jack pine height growth was higher in the large-gap harvests than in the small-gap harvests (df = 33, $P = 0.03$) but no cut treatment effect was seen for red or eastern white pine. Whereas the variation in growth was considerably greater in all cut treatments than in the uncut controls for all species (df = 32, $P < 0.03$), no difference was seen among cut treatments for any species. At low levels of basal area (0–16 m^2/ha) and overstory abundance, growth of all three species increased with increasing basal area and overstory abundance (df = 22, $P < 0.02$). At high levels of basal area (20–61m^2/ha) and overstory abundance, however, growth of jack and eastern white pine increased but that of red pine decreased with increasing basal area and overstory abundance. Growth increased with increasing competing vegetation in thinnings for both jack and red pine and in controls for jack pine (df = 32, $P \leq 0.06$). The relationship of proportional diffuse radiation and height growth varied among treatments and species (df = 33, three-way interaction, $P = 0.01$). Growth of jack pine decreased with increasing proportional diffuse radiation in thinnings and small-gap harvests but increased with increasing proportional diffuse radiation in large-gap harvests. Growth of red pine increased with increasing proportional diffuse radiation in large-gap harvests only. Growth of eastern white pine decreased with increasing proportional diffuse radiation in controls and increased with increasing proportional diffuse radiation in small-gap harvests, thinnings, and large-gap harvests (in that order). Growth decreased with increasing soil temperature in small-gap harvests for all species and for jack pine in all treatments (df = 33, $P < 0.04$). Growth of all species increased with increasing first-summer soil moisture in large-gap harvests (df = 35, $P = 0.01$) and with increasing second-summer soil moisture in all treatments (df = 22, $P = 0.06$).

Seedling location effects

Seedling-level microsite conditions and growth within the gap harvests

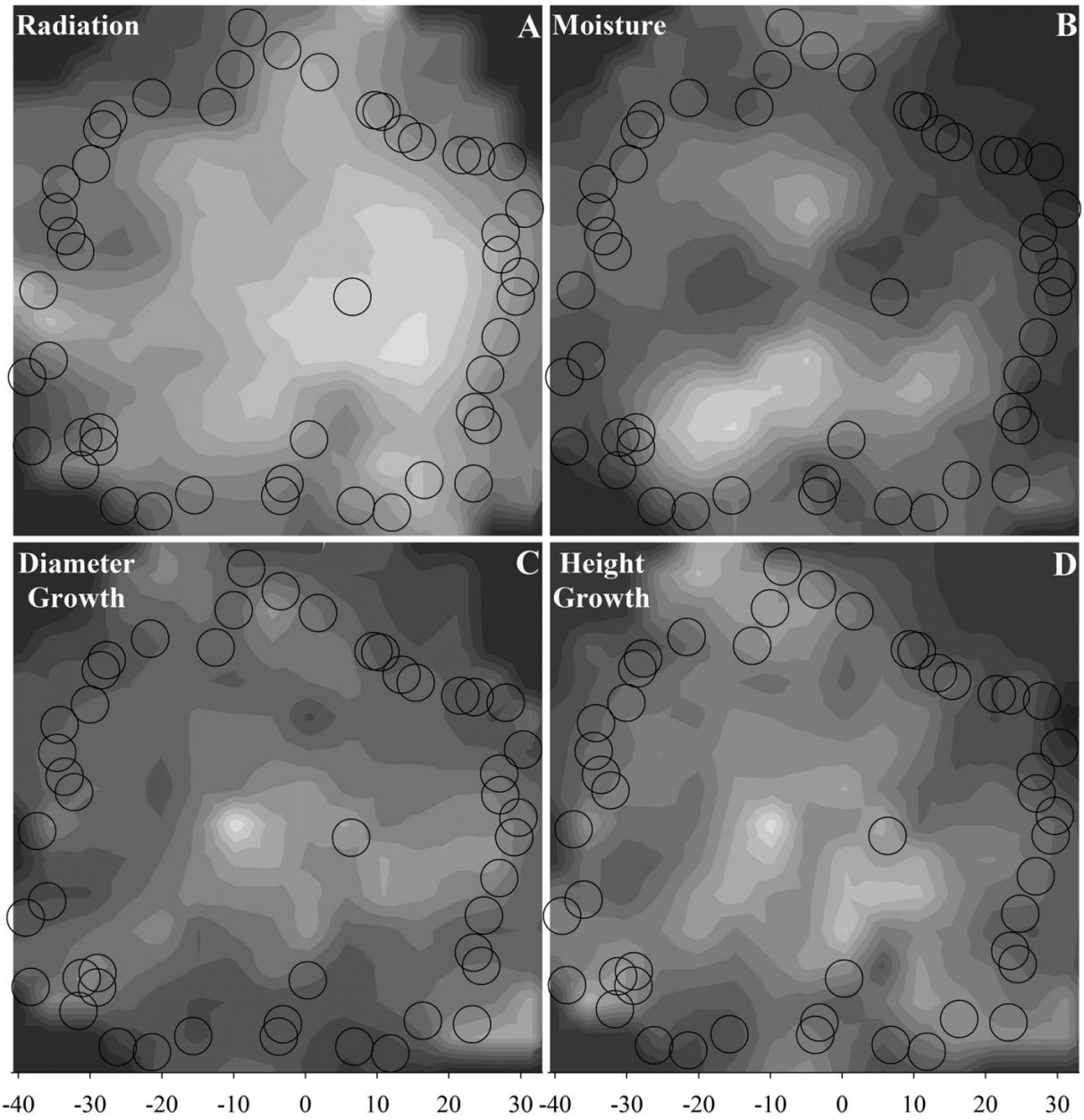
Patterns of microsite condition and seedling response with respect to position within the gaps were similar for both

Fig. 4. Principal components analysis ordination of the microsite conditions (proportional diffuse radiation at seedling height and proportion of maximum observed soil moisture and temperature) at each seedling in the three large-gap harvest plots. Points represent seedlings at which all measurements were taken; vectors indicate strong Pearson correlations between the indicated microsite variable and the ordination axes: the longer the vector, the stronger the association. (A) Proportional diffuse radiation and the extremes of both soil moisture and temperature increase from the forest edge into the interior of the gap. (B) Whereas soil temperature tended to be somewhat higher at seedlings in the northern half of the plot, soil moisture was a bit higher for seedlings in the southern half of the plot. (C) Collar diameter growth was slightly greater for seedlings experiencing higher proportional diffuse radiation and temperatures ($r = 0.36$ with axis 1) (D) but this trend was not observed for height growth ($r = 0.15$).



small- and large-gap harvests. Proportional diffuse radiation (df = 984), soil temperature and moisture (df = 998 and 595, respectively) in both years, and competing vegetation (df = 245) all increased with increasing distance from the nearest residual tree and the nearest gap-edge tree (all $P < 0.001$) and were greater in gap centers than at gap edges or under the residual canopy ($P < 0.001$). In the second summer, gap centers were also moister than elsewhere in the gap interior ($P < 0.1$). Although proportional diffuse radiation, soil moisture in both years, and competing vegetation decreased with increasing distance from the southernmost edge of the gap ($P < 0.05$), only competing vegetation and

Fig. 5. Microsite resources smoothed (using running averages) over the actual spatial extent (in metres) of one of the large-gap plots (block 3). Circles indicate residual trees following harvest. Light-shaded areas had high average values, whereas dark areas had lower averages. (A) Proportional diffuse radiation at seedling height tended to be somewhat higher in the eastern side of the gap and (B) soil moisture was somewhat higher in the southern portions of the gap. Variation within gaps in (C) collar diameter and (D) height growth rates, which increased toward the center of the gap, did not follow the spatial distribution patterns of either the radiation or moisture resource.



first-summer soil moisture were greater in the southern half of the gap than in the northern half ($P < 0.01$). Soil temperature increased with increasing distance from the southernmost edge of the gap ($P < 0.001$) and was thus higher in the northern than in the southern half of the gap ($P < 0.001$). The variation in microsite conditions by location within the gap plot is evident in the ordination of microsite conditions, which indicated higher proportional diffuse radiation and soil moisture out from the residual forest edge toward gap centers (Fig. 4A) and higher soil moisture in more southerly locations (Fig. 4B). This pattern is also visually evident in the smoothed response surface plots in which higher values (lighter shades) are concentrated in the gap center (proportional diffuse radiation, Fig. 5A) or southern half of the gap (soil moisture, Fig. 5B).

In small-gap harvests, the location of seedlings was associated with first-year mortality (Mantel test, $P = 0.05$) as well as the height growth of jack pine (Mantel test, $P < 0.08$). In large-gap harvests, location was associated with collar diameter (Mantel test, $P \leq 0.02$) and height growth (Mantel test, $P \leq 0.01$) and first-summer mortality (Mantel test, $P = 0.01$). First-summer mortality was higher for seedlings in the center of the gap than on the gap edge or just inside the residual forest (df = 994, $P = 0.03$). First-summer mortality

among seedlings within the gaps (i.e., excluding those in the residual forest) increased with increasing distance from the edge of the gap (df = 994, $P = 0.002$). First-year mortality, however, was higher for seedlings at the edge of the gap (df = 691, $P = 0.06$), but the distance to the edge made no difference.

Microsite conditions and growth with respect to location in all treatment plots

Regardless of treatment or year, proportional diffuse radiation increased with increasing distance from the nearest overstory tree (df = 1482, $P < 0.001$). Proportional diffuse radiation did not change with distance to the southernmost edge of the plot. Soil temperature increased in all treatments with increasing distance from the nearest residual tree and the southernmost edge of the plot in both years (df = 1498 and 909, respectively, $P < 0.001$). Soil temperature also increased with increasing distance from the nearest edge tree, was higher in the northern half of the gap than in the southern half ($P < 0.001$), and was higher in gap interiors than in gap edges or under the residual canopy ($P < 0.08$) in both years (df = 1498 and 909, respectively). First-summer soil moisture was higher in the southern half of plots in all treatments (df = 1498, $P = 0.001$) but was no longer so by the second summer. Soil moisture increased in all treatments with increasing distance from the nearest overstory tree ($P < 0.001$) and decreased with increasing distance from the southernmost edge of the plot ($P = 0.001$) in both years (df = 1498 and 909, respectively).

First-summer mortality decreased with increasing distance from the nearest overstory tree for both species in all treatments (logistic regression, df = 1488, $P = 0.01$). Collar diameter and height growth increased with increasing distance from the nearest residual tree for all species in all treatments (df = 232 and 185, respectively, $P < 0.06$) but did not vary with respect to the north–south gradient. Collar diameter and height growth increased with increasing distance from the nearest gap edge (df = 232 and 185, $P < 0.001$) for all species in order of decreasing effect size from jack to eastern white to red pine. Collar diameter and height growth were higher in gaps than under a residual canopy (df = 232 and 185, $P < 0.1$) for all species in the same order of jack, eastern white, and red pine but did not differ by location within the gap plots. No relationship was seen between growth and distance from the southernmost edge of the plot for any species. Averaged to the plot level, collar diameter growth, but not height growth, increased along a gradient from the forest edge through the gap edge into the gap interior for all species in both small- and large-gap harvests (df = 51, $P < 0.05$). Although these patterns with respect to location are again evident in the ordination of microsite conditions (Figs. 4C and 4D) and the smoothed response surface plots (Figs. 5C and 5D), there was only a weak association between the patterns observed for microsite conditions and those observed for seedling responses.

Discussion

Our results indicate that any of the three retention harvests used in this study could result in the establishment of two-aged stand structures in these mature red pine stands: early (first two growing seasons) mortality and growth responses of all three planted pine species were generally favorable. Consistently, strong growth responses of all three species were also recently found by Powers et al. (2008). The few differences that were observed among the three pine species reflected some known differences in their silvics and previously observed obstacles to successful regeneration. For instance, red pine grew very poorly in the uncut controls, which averaged <15% of proportional diffuse radiation (Fig. 2A), but performed better in the cut treatments in which at least some seedlings experienced light levels nearer those previously indicated as required for red pine (35% of full sunlight; Rudolf 1990). Similarly, the more shade-tolerant eastern white pine, which is thought to require ~20% of full sunlight (Wendel and Smith 1990), performed best in the cut treatments but also grew in the uncut controls. In contrast, however, the similarity of jack pine growth response among the cut treatments was somewhat surprising. Because it has been considered a shade-intolerant, early-successional, post-fire disturbance species, requiring <60% crown cover (Rudolph and Laidly 1990), it has previously been thought that regeneration would only be successful in clearcuts or very large gaps. Although jack pine growth was highest in the large-gap harvests, growth was considerable in the small-gap harvests and thinnings and even continued under the full canopy of the uncut controls, and mortality did not differ among treatments. This result is encouraging for the restoration of this species, which has declined in abundance on the landscape (Friedman and Reich 2005), because of the potential for successful regeneration in retention harvest scenarios.

In contrast, simply underplanting under existing mature pine overstories without reducing overstory abundance (i.e., our control treatment) would be less likely to result in mixed two-aged stands, particularly those including red pine regeneration. This result is in keeping with previous observations that overstory competition for light and moisture is lower in gap harvests and that this corresponds to commensurate increases in seedling growth responses (Palik et al. 1997, 2003*a*). However, whereas previous work using the same harvest treatments has concluded that aggregated retention, and particularly large-gap harvests, may optimize seedling growth in southern longleaf pine (*Pinus palustris* Mill.) ecosystems (Palik et al. 2003*a*), our results indicated only a slight advantage in the short term, and only for jack pine height growth, in large-gap harvests compared with the other cut treatments in northern red pine ecosystems. A primary difference between these findings may be the higher shade tolerance of eastern white and red pine compared with longleaf pine. Sufficient light for survival and growth may have been achieved in all cut treatments due to the thinning of the residual matrix, as was hypothesized when this treatment design was first proposed (Palik et al. 1997). Long-term responses may differ and will continue to be monitored.

Another factor affecting statistically significant treatment differences may have been the variability in resource availability within each cut treatment. Seedlings had higher first-year survival with higher levels of proportional diffuse radiation and moisture and lower levels of overstory abundance, regardless of treatment, yet the variation in proportional diffuse radiation and moisture also increased with the increasing scale of the gap harvests. Although some seedlings in the gap harvests experienced relatively high resource availability and

growth, because variation in these conditions was higher, overall responses averaged to roughly the same level as in the other cut treatments. Thus, considerable spatial variation in the actual competitive influence of the overstory on the understory resulted from these different treatments, supporting the observation that most nonspatial measures of overstory structural characteristics are unable to capture the true competitive environment of the understory (Palik et al. 2003*a*). These early results provide little evidence of suppression of growth from competing understory vegetation, even in nonbrushed areas. The positive association of jack and red pine height growth with third-summer competing vegetation in the thinning treatments may reflect spatial variation in microsites favorable to all vegetation.

Special consideration to seedling location may be warranted when implementing aggregated retention harvests such as large gaps due to the variation in both resources and seedling growth responses. The spatial distribution of light is important for community-level processes such as regeneration (Battaglia et al. 2002) and proportional diffuse radiation in this study increased with increasing distance from residual trees in all treatments. Average light availability did not increase with increasing gap size as in other studies (Battaglia et al. 2002; Pritchard and Comeau 2004; Muscolo et al. 2007), possibly reflecting a plateau in light with gap size at the extents considered here; growth responses, for instance, have been found to plateau after gaps exceed 0.1 ha (Coates 2000) or 0.3 ha (York et al. 2004) in size. Variation in proportional diffuse radiation, however, increased with increasing scale of gap harvests (cf. Battaglia et al. 2002). In keeping with previous gap studies, proportional diffuse radiation was heterogeneous within the gaps (Gagnon et al. 2003) and increased from the gap edge toward the gap center (Palik et al. 1997; Gagnon et al. 2003; Powers et al. 2008). However, in contrast with some of these studies (Gagnon et al. 2003; Powers et al. 2008), proportional diffuse radiation did not differ between the northern and southern halves of the plot. Whereas soil moisture may sometimes be higher in very small gaps due to higher levels of humus and organic matter (Muscolo et al. 2007), soil moisture levels in our gap harvests did not vary with the scale of the gap harvest, as was also found by Palik et al. (1997). Variation in soil moisture within gaps was clearly evident in our study with higher moisture levels in gap interiors and the southern portions of gaps. This pattern was also found by Powers et al. (2008) on similar sites, whereas the lack of within-gap variation in a longleaf pine ecosystem by Gagnon et al. (2003) has been attributed to extreme drought during their sampling period.

Gap partitioning theory (postulating that species divide up the resources available along the gradients in and out of gaps) has had mixed success in predicting overstory composition in temperate ecosystems, but somewhat better results explaining understory patterns (Fahey and Puettmann 2007). For instance, our results corroborate previous findings that seedlings in the center of gaps have higher initial mortality but ultimately higher growth rates than those in other gap locations (Gray and Spies 1996; Gagnon et al. 2003). However, our results also appear to indicate that although resource availability is partitioned within gaps, seedling growth responses do not necessarily follow the same pattern. Whereas seedling growth increased with increasing proportional diffuse radiation and was highest in gap centers where radiation was highest (as found by Coates 2000; Gagnon et al. 2003; York et al. 2004; Powers et al. 2008), the positive association between growth and soil moisture did not translate into higher growth in the southern portions of the plot where soil moisture was highest. The discrepancy in spatial pattern between resource availability and growth responses may reflect gradients in important factors not measured in this study, such as nitrogen levels (Palik et al. 1997) and underground competition (Brockway and Outcalt 1998). Further, over time, changes in gap-edge tree crowns may alter the competitive relationship between the overstory and understory (York et al. 2004). Thus, although at this early stage there is no evidence that these retention patterns created understory microclimate conditions so extreme as to be outside the range of tolerance for any of these three pine species, the question remains as to whether or not shade tolerances may be exceeded in the future as crowns fill in, perhaps necessitating subsequent entries to maintain and enlarge existing gaps (Hawley 1921; Seymour 2005).

Conclusions

Managers often have several options for how to initiate two-aged stands depending on current species composition, desired species composition and structure, and natural and artificial disturbance regimes. Undisturbed red and mixed pine stands in this region tend to succeed to northern hardwoods but even this transition can take centuries (Kittredge 1934). Managers interested in stimulating a swifter transition to two- or multiaged stands, particularly with the retention of a pine covertype, may therefore look to retention harvests to facilitate these changes. Our results indicate that if the primary objective is to produce a wide range of understory environmental conditions, perhaps to stimulate vegetative diversity, gap harvests at the 0.3 ha scale could be most appropriate. If, however, the objective is to reliably develop a two-aged stand structure, as indicated at this stage by low seedling mortality and high seedling growth rates, any of the retention patterns — including dispersed thinning — would suffice under mature red pine on sites such as these. When an aggregate retention harvest is selected, higher initial mortality should be anticipated for seedlings near the center of gaps, but longer term mortality may be higher at gap edges. Our results indicate that growth of all three pine species may decrease from gap interiors toward gap edges and be lowest under residual canopies, but only partially as a function of decreasing light and moisture. Such a pattern could be important for determining the ultimate species composition in gaps depending on the differential in growth rates among the desired pine and competitive broadleaved species.

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