Physiological performance of three pine species provides evidence for gap partitioning

Matthew D. Powers a,*, Kurt S. Pregitzer b, Brian J. Palik c

a School of Forest Resources and Environmental Science, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, United States
b Department of Natural Resources and Environmental Science, University of Nevada, 1000 Valley Road, Reno, NV 89512, United States
c USDA Forest Service Northern Research Station, 1831 Hwy 169 East, Grand Rapids, MN 06514, United States

1. Introduction

Canopy gaps provide a source of environmental heterogeneity in forests that benefits the regeneration of many tree species. Researchers in tropical forests first suggested that the gradients in resource availability running from the center of a canopy gap into the surrounding closed-canopy forest provide an assortment of regeneration niches, which fosters diverse species assemblages by partitioning the optimal performance of species with different life history traits along different portions of the gradient (Ricklefs, 1977; Denslow, 1980). The gap partitioning hypothesis has also been applied to temperate forests (Poulson and Platt, 1989; Wright et al., 1998; Sipe and Bazzaz, 1994, 1995; Gray and Spies, 1996, 1997; Kneeshaw and Bergeron, 1999; Holladay et al., 2006; Raymond et al., 2006), although much of this research has focused on gap size rather than gap position (e.g. Runkle, 1982; Runkle and Yetter, 1987; Poulson and Platt, 1989; Whitmore, 1989; McClure and Lee, 1993; Gray and Spies, 1996; Coates, 2002; Seiwa, 2007).

Differences in the direction and scale of the availability of individual resources within canopy gaps should provide the potential for habitat partitioning among species with varied tolerances for shade and water stress. Light availability varies asymmetrically in gaps located in higher latitudes such that irradiance increases in a northern direction across gaps and the northern portions of gaps receive the most sun (Canham, 1988; Poulson and Platt, 1989; Whitmore, 1989; McClure and Lee, 1993; Gray and Spies, 1996; Coates, 2002; Seiwa, 2007). Air temperature, surface soil temperature (Gray and Spies, 1997; Gray et al., 2002; Wright et al., 1998; Raymond et al., 2006), and evaporative demand in canopy gaps...
follow the same spatial pattern as light availability. Soil moisture availability, however, is generally greater around the geographical center of canopy gaps and decreases towards gap edges (Wright et al., 1998; Ritter et al., 2005; Raymond et al., 2006), presumably due to differences in rooting density (Silver and Vogt, 1993; Denslow et al., 1998). Thus, light availability reaches its local maxima in gap positions with the greatest potential for moisture stress, while water stress should be lowest in gap positions with intermediate to low light availability. This dichotomy suggests species that are drought tolerant and shade intolerant should perform best in northern gap positions, while species with greater shade tolerance or susceptibility to moisture stress should compete better in central or southern gap positions.

Most studies of gap partitioning have focused on comparing demographic parameters (recruitment, survival, growth, etc.) between species or functional groups. This approach provides valuable information about gap dynamics, but provides little direct evidence for the causes of variability (or lack thereof) in performance. Variations in leaf morphology and carbon assimilation rates have been related to partitioning of the light gradient in canopy gaps (Sipe and Bazzaz, 1994, 1995; Grassi and Bagnaresi, 2001), but the cumulative effects of light and moisture gradients on gap partitioning are less clear. The light-saturated carbon assimilation rate ($A_{\text{max}}$) is generally higher in leaves exposed to direct sunlight (Hochinger, 1989; Elser, 1990; Reich, 1993) so we might expect seedlings in northern gap positions to grow fastest, but moisture stress may lead to reductions in stomatal conductance ($g_s$) that reduce transpiration ($E$), which limits carbon assimilation rates (Comstock and Ehleringer, 1984; Walters and Reich, 1989; Maier and Teskey, 1992). Thus, species with high water use efficiency (WUE, the ratio of net carbon assimilation to transpiration) should have a competitive advantage in the high light, low moisture environments found along the northern edges of large gaps.

While there is strong evidence for resource gradients in gaps, many studies have failed to find differences in species composition or performance associated with gap position (Busing and White, 1997; Dalling et al., 1998; Wilder et al., 1999; Wright et al., 1998; Dalling et al., 2004). Resource gradients may be too narrow to produce significant differences in tree regeneration performance in small gaps, or if dense understory shrub layers dampen the effects of gap formation (Denslow, 1987; Gray and Spies, 1997; Dalling et al., 1998). Microsite conditions may also supersede the effects of larger scale resource gradients on growth and survival through their influence on initial establishment (Denslow, 1987; Pousson and Platt, 1989; Gray and Spies, 1997; Wright et al., 1998; Coates, 2002). Finally, tree growth in gaps with abundant advance regeneration may be more reflective of relative sapling size and vigor preceding gap formation than environmental gradients after canopy removal (Marquis, 1982; Brokaw and Busing, 2000).

Gap partitioning may also provide a mechanism for enhancing species diversity and structural complexity in forests that have been simplified by anthropogenic influences. Pine forests in North America’s Great Lakes region, for instance, covered large areas prior to European settlement, including many stands of red pine (P. resinosa Ait.) mixed to varying degrees with jack pine (P. banksiana Lamb.) and eastern white pine (P. strobus L. [Heinselman, 1973; Whitney, 1986, 1987; Palik and Pregitzer, 1992; Friedman et al., 2001]). Disturbance regimes dominated by mixtures of frequent, low to moderate intensity surface fires and less frequent, stand replacing fires produced both single and multi-cohort age structures in Lake States mixed pine forests (Spurr, 1954; Heinselman, 1973; Whitney, 1986; Butson et al., 1987; Bergeron and Brisson, 1990). This complex disturbance regime, and the presence of remnant multi-cohort stands composed of a mosaic of small patches or groves of individual cohorts (Spurr, 1954; Heinselman, 1973) suggest gap-causing fires could have played an important role in the dynamics of some pre-settlement mixed pine forests.

Red pine is a shade intolerant species that depends on mixed-severity fire regimes which create a mineral seedbed and reduce overstory competition while leaving some mature residual trees as a seed source for regeneration (Van Wagner, 1970; Whitney, 1987). White pine is moderately tolerant of shade, and more capable of regenerating on organic soil beneath an established canopy than red pine, but also relies on residual trees to regenerate after disturbance. Both red pine and white pine develop thick bark as they mature that can resist low to moderate intensity surface fires, allowing multi-cohort stand development when small flame-ups create canopy gaps. Jack pine, on the other hand, is very intolerant of shade and susceptible to fire as both a juvenile and adult, but grows rapidly and develops persistent, serotinous cones early in life. These features generally promote the development of even-aged, jack pine dominated stands on sites characterized by frequent, stand replacing fires, but jack pine is also capable of forming multi-cohort mixtures with red pine on xeric sites with patchy fuels or natural fire breaks and frequent fires (Whitney, 1986; Bergeron and Brisson, 1990). Jack pine and red pine are considered fairly drought tolerant, while eastern white pine seedlings are more susceptible to moisture stress (Burns et al., 1998). These varying tolerances for shade and drought suggest the potential for niche partitioning in Lake States mixed pine forests that experience patchy disturbances, which may enhance or maintain overstory diversity in these forest types.

In this study, we examined the physiological performance of three pine species that vary in shade and drought tolerances across large (0.3 ha) silvicultural gaps. By focusing on planted seedlings in large gaps we hoped to minimize the effects of microsite conditions on seedling establishment and maximize potential resource partitioning across the gap. An understory release treatment was also included to investigate the effects of understory competition on both resource gradients and seedling physiological performance at different gap positions. We predicted increasing light availability along a south–north transect through the gaps, and increasing moisture availability from gap edges to gap centers. We also expected patterns of $A_{\text{max}}$ to parallel those of light availability, while $E$ and $g_s$ were predicted to be lowest in northern gap edges and highest around gap centers. Shade intolerant pines with high WUE were expected to perform best in northern gap and northern edge positions, while more shade tolerant pines with greater susceptibility to moisture stress were expected to perform better in southern gap positions and southern edges. Understory release treatments were expected to increase resource availability at all gap positions, and strengthen partitioning of the gap resource gradient.

2. Methods

2.1. Study sites and species

Our study was conducted on the Chippewa National Forest in north-central Minnesota, USA (47°35′N, 93°54′W). Four, naturally regenerated, 70–90-year-old red pine stands were harvested in the winter of 2002–2003 using a variable retention harvesting system that created 0.3 ha canopy gaps surrounded by a forest matrix that was thinned to produce residual basal areas around 13 m² ha⁻¹. The gaps were circular in shape with a diameter of approximately 62 m. The surrounding canopy averaged 23 m in height, and the forest matrix between gaps was thinned from an average of 37 m² ha⁻¹ to approximately 20 m² ha⁻¹. Half of each stand
received an understory release treatment in which all shrubs and aspen regeneration (*Populus tremuloides* Michx. and *Populus grandidentata* Michx.) were cut with brush saws in the spring following harvesting. The release treatment was repeated for three additional years after harvesting. All stands were located on deep, well-drained sands in the Hiwood-Zimmerman association of mixed, frigid Aquic Udipsamments and mixed, frigid Lamellic Udipsamments or the Grayclay-Menahga association of mixed, frigid Lamellic Udipsamments and mixed, frigid Typic Udipsamments. Bare root, 2–0 seedlings of jack pine, red pine, and eastern white pine were planted at 2.7 m × 2.7 m spacing throughout each stand in the spring following harvesting. Seedling diameters (± one standard error) averaged 7.6 (±0.29) mm for jack pine, 5.9 (±0.68) mm for red pine, and 6.6 (±0.31) mm for white pine at the time of planting.

Understory vegetation in the treatment stands was dominated by similar species in both the understory release and understory control treatments. *Maianthemum canadense* (Desf.), *Pteridium aquilinum* (L.) Kuhn, *Vaccinium angustifolium* Ait., and *Amelanchier* spp. were the most abundant species in both understory treatments, with total herb cover averaging 57.9% (S.E. = 9.1%) in understory release treatments and 56.2% (S.E. = 4.8%) in understory controls. The shrub layer was dominated by *Corylus cornuta* Marsh. and *Amelanchier* spp. in both understory treatments, but total shrub densities were much lower in the understory release treatment (2005 ± 1806 seedlings/ha) than in the understory control treatment (5714 ± 2550 seedlings/ha).

We selected two gaps for study in each of the four treatment stands. Study gaps were selected at random, with one in the understory release side of each stand and the second in the understory control side. A transect consisting of five points was marked along a north–south axis through the center of each study gap with study points placed at gap centers, 15 m from gap center (north gap and south gap), and 30 m from gap center (north edge and south edge). This spacing placed edge points immediately adjacent to the projected canopy of the forest matrix around each gap. Crown expansion following harvesting and the irregular nature of residual tree crowns along gap edges caused some edge points to be partially covered by canopy. We selected the closest jack pine, red pine, and white pine to each point for data collection. All measurements described below were made in 2007, during the fifth growing season after planting.

### 2.2. Resource availability data

Light availability was measured at each sample point as photosynthetically active radiation (PAR) transmittance 1 m above the ground surface using a linear PAR/LAI ceptometer (LP-80, Decagon Devices, Inc., Pullman, WA). PAR readings were taken between 12:00 and 15:00 h on clear days in the second week of June. We took 30 readings at each sample point while rotating the ceptometer in a circle centered on the point (Law et al., 1992). Open-canopy readings were taken in large (>1 ha) clearings immediately before and after PAR sampling in each gap, and the average of these values was used to compute PAR transmittance. Light measurements for each gap pair were completed on the same day.

Predawn xylem water potentials (Ψpd) were measured on the three beaked hazel (*C. cornuta* Marsh.) stems nearest to each sample point in early June, July, and August as an estimate of soil moisture availability in the rooting zone (Reich and Hinkley, 1989). Hazel was chosen for Ψpd measurements because it was a ubiquitous shrub that could be found within 1 m of every sample point. Primary shoots were excised from the main stem with a sharp knife, and immediately placed into a pressure chamber (PMS Instrument Company, Corvallis, OR). The average of the three Ψpd readings taken at each point was used in statistical analyses. Water potential measurements for each gap pair were completed on the same morning.

### 2.3. Growth and physiology data

Seedling diameter and height were measured in early May, before leaf-out of deciduous species or shoot extension of the pines. Diameter was measured 2.5 cm above the mineral soil surface with digital calipers, and height was measured with a meter stick or tape. Net carbon assimilation, transpiration, and stomatal conductance were measured on 1-year-old needles on the same days as Ψpd in June, July, and August using a portable gas-exchange system equipped with a CO2 supply and a 6 cm² cuvette (LI-6400, Li-Cor Biosciences, Lincoln, NE, USA). Two fascicles (four needles) of jack pine and red pine foliage or one fascicle (five needles) of white pine foliage were excised from the middle third of the canopy and immediately placed in the LI-6400 cuvette under a red/blue light source providing a photosynthetic photon flux density of 1500 μmol m⁻² s⁻¹. This level of irradiance meets or exceeds the light saturation points reported for each study species, so carbon assimilation rates are reported as light saturated (Amax). WUE was calculated from gas exchange data as Amax/E. Gas exchange measurements were made on clear or mostly sunny days.

The diameter of each needle was measured at two points using a digital caliper immediately after gas exchange measurements were completed, and the average of these two measurements was used to compute the all-sided leaf area enclosed in the LI-6400 cuvette. Leaf area was calculated based on the assumption that needles represent segments of a cylinder (Johnson, 1984) using the caliper-radius method described by Svenson and Davies (1992). The all-sided surface area of each needle in a sample was summed to provide a measure of total leaf area in the cuvette, and gas exchange data were recalculated on an all-sided leaf area basis. Foliage from each tree was collected, dried and ground to a fine powder for determination of mass-based foliar nitrogen content (Nmass, Fisons NA Elemental Analyzer).

### 2.4. Statistical analysis

PAR transmittance and season mean Ψpd data were analyzed using a split-plot analysis of variance (ANOVA) with a randomized complete block design (RCBD). Understory treatment was used as the whole-plot factor, gap location as the split-plot factor, and stand as the blocking variable. Preliminary tests indicated analyses using raw PAR transmittance data did not satisfy ANOVA normality assumptions, so an arcsin square-root transformation was applied and the tests were rerun. Monthly Ψpd data were analyzed using repeated-measures, split-plot ANOVA. Whole-plot, split-plot, and blocking variables were the same as described for the season mean Ψpd test, but month of measurement was added as a repeated-measure. Means comparisons were made using orthogonal contrasts to test our initial hypotheses. These contrasts included south edge vs. all other locations, south gap vs. gap center, north gap and north edge, center vs. north gap and north edge, and north gap vs. north edge for PAR transmittance and edges vs. gap positions, north edge vs. south edge, center vs. north gap and south gap, and north gap vs. south gap for Ψpd.

Seedling diameter, height, Nmass, and season mean gas exchange data (computed as the average of values from the three measurement periods) were analyzed using a split-split-plot ANOVA with a RCBD. Understory treatment was used as the
whole-plot factor, with gap location as the split-plot factor, species as the split-split-plot factor, and stand as the blocking variable. Although we focused on season mean gas exchange data, monthly data was also analyzed using repeated-measures, split-split-plot ANOVA. Natural logarithm transformations were applied to diameter, height, E, and gs data to normalize the ANOVA error residuals and homogenize error variances. ANOVA model assumptions were evaluated using normal probability plots of residuals, plots of residuals against predicted values, and the Kolmogoroff–Smirnoff test. Significant main effects and interactions were investigated using Tukey’s HSD to make comparisons among means. Means from the three study species were also analyzed within each gap location using Tukey’s HSD. Because individual pairwise tests that control experiment-wise error rates are valid even when the ANOVA’s F test is not significant (Day and Quinn, 1989). All statistical tests were performed at the $\alpha = 0.05$ significance level using SAS version 9.0 (SAS Institute, Cary, NC).

3. Results

3.1. Resource availability

PAR transmittance was affected only by position along the gap transect ($P < 0.001$), and not understory treatment or the interaction between understory treatment and position. PAR transmittance was greater in northern edges and within gaps than at southern edges, but did not vary between other positions (Fig. 1). Predawn water potential was also impacted by position along the gap transect ($P < 0.001$), but not by understory treatment or the interaction between understory treatment and position. Water potentials were higher within gaps than at gap edges, and greater at southern edges than northern edges, but $\Psi_{pd}$ did not vary within gaps. Water potentials declined during the growing season ($P < 0.001$, Fig. 2), and the change between measurement periods varied with transect locations ($P < 0.001$), but not understory treatment or the interaction between understory treatment and transect location. In June and July, $\Psi_{pd}$ was similar across all positions, but in August $\Psi_{pd}$ was greater within gaps than at gap edges, higher at southern edges than northern edges, and greater at gap centers than northern and southern gap positions.

3.2. Seedling physiology

Photosynthesis varied among species ($P < 0.001$) and there was a significant understory treatment × species interaction ($P = 0.0114$), but no other factors or interactions were significant. On average, jack pine had higher $A_{max}$ than red pine or white pine, but there were no differences between red pine and white pine (Fig. 3). This main effect relationship was also true within the understory release treatment, but jack pine only had significantly higher $A_{max}$ than red pine in the understory control treatment (Fig. 4). Jack pine had the highest $A_{max}$ at all positions within gaps, but was only greater than white pine at northern edges, and there were no significant differences between species in southern edges (Fig. 5). Red pine and white pine had similar $A_{max}$ in all positions along the gap transect. Light-saturated photosynthetic rates declined from the June to August sampling periods ($P < 0.001$, Fig. 6), but the change was not affected by understory treatment, position, species, or any interaction among the three.

Transpiration varied with both position along the gap transect ($P = 0.047$) and species ($P < 0.001$), but not understory treatment or the interaction terms. Gap centers had higher $E$ than northern edges, but there were no other differences associated with position. Jack pine had higher $E$ than red or white pine, but red pine and white pine were not significantly different (Fig. 3). When position was considered, Jack pine had higher $E$ than red pine in gap centers, and higher $E$ than white pine in gap centers and northern edges (Fig. 5). Red pine and white pine had similar $E$ in all positions. Mean season $E$ declined during the summer (Fig. 6), but
understory treatment, position, species, and their interactions did not affect the rate of decline.

Trends in mean season $g_s$ also varied with position along the gap transect ($P = 0.036$) and species ($P < 0.001$), but were not affected by understory treatment or any interactions. Stomatal conductance was higher at southern gap positions than northern edges, but did differ among other positions. Jack pine had greater $g_s$ than red pine or white pine, but there was no difference between red pine and white pine (Fig. 3). Comparing species within individual positions along the gap transect, jack pine had greater $g_s$ than red pine at gap centers and southern gap positions, while $g_s$ of jack pine was greater than white pine at gap centers and northern edges (Fig. 5). Stomatal conductance did not differ among species at northern gap positions or southern edges. Stomatal conductance declined through the growing season ($P < 0.001$, Fig. 6), but the change was not affected by understory treatment, position, species, or any of their interactions.

There were no significant differences among positions along the gap transect, understory treatments, or species associated with WUE and there were no differences in WUE associated with species within any gap position. Water-use efficiency did not change during the growing season (Fig. 6) and WUE was not affected by understory treatment, gap position, species, or any interaction among these factors across the three measurement periods.

Foliar nitrogen content was influenced species ($P < 0.001$), but not by position along the gap transect, understory treatment, or any interaction between these three variables. Jack pine seedlings had the highest Nmass, followed by white pine, then red pine.
Jack pine had higher Nmass than red pine at all positions within gaps, while jack pine and white pine were only significantly different within northern edges (Fig. 5). Red pine and white pine were not significantly different within any gap position.

### 3.3. Seedling size

Seedling height was affected by position along the gap transect \( (P = 0.021) \) and species \( (P < 0.001) \), but not understory treatment or any interaction among the three. Seedlings in gap centers were taller than those in southern edges, but there were no other significant differences between positions (Fig. 3). Jack pine seedlings were taller than the other species, and white pine were taller than red pine. Jack pine seedlings were taller than red pine within each individual position, and taller than white pine within north, center, and southern edge positions (Fig. 5). White pine were...
taller than red pine when compared within northern edges and gap centers, but similar within all other positions.

The main effects of treatments on seedling diameter were similar to those observed for seedling height, but within-position trends were different. Diameter was affected by position along the gap transect ($P = 0.046$) and species ($P < 0.001$), but not understory treatment or any interactions. The diameter of seedlings in gap centers was greater than those in southern edges, but no other pair of positions was significantly different (Fig. 3). On average, jack pine seedlings were larger in diameter than the other species, and white pine were larger than red pine. Jack pine seedlings were larger in diameter than red pine at all positions except southern edges, but only larger than white pine within north and south gap positions (Fig. 5). Red pine and white pine had similar diameters at most positions along the gap transect, but white pine were larger than red pine in gap centers.

4. Discussion

The data generally support our hypotheses regarding light and water availability. As expected, light availability was lowest at southern edge locations, but we did not find evidence of any increases from southern gap positions to more northern positions. Many of the studies reporting peak light availability in the northern portion of canopy gaps focused on individual tree to small group (<0.1 ha) gaps surrounded by undisturbed, closed-canopy forest (e.g. Canham, 1988; Poulsen and Platt, 1989; Wright et al., 1998; Raymond et al., 2006). Large gap sizes and diffuse radiation entering from the thinned forest matrix surrounding our gaps may have combined to provide higher PAR availability at more southerly gap locations than would occur in smaller canopy openings. Water availability followed our predictions more closely, showing the expected peak at central gap locations, and higher moisture availability at southern edges than northern edges due presumably to the increased evaporative demand associated with high light levels in northern edges.

Leaf-level physiological indices indicate the resource gradients we observed could contribute to niche partitioning. Jack pine's carbon assimilation rates were considerably higher than red pine and white pine at gap interior locations, suggesting jack pine may outperform the other species in the central portions of large canopy gaps. Jack pine was not as competitive at edge locations, and our results suggest both red and white pine could be competitive at the dry northern edges of gaps or the dry and shady southern edges. Jack pine's intolerance for shade likely contributed to its reduced competitiveness at gap edges. We must note, however, that this conclusion is based on qualitative comparisons of results from individual post hoc tests within each gap location rather than results from a single test ranking species across all locations simultaneously. Thus, our results should be interpreted cautiously with the recognition that we found only mild evidence of physiological partitioning across our gap transects.

These data only represent leaf-level measures of assimilation, and previous studies of gap or resource partitioning have found differences in leaf morphology and shoot architecture complicate the recognition that we found only mild evidence of future growth potential. Red pines were also the smallest seedlings in diameter at the time of planting, but initial size may not always be related to performance across canopy gaps (Sipe and Bazzaz, 1995).

Water relations may partly explain the carbon assimilation patterns observed across the gap transect. Jack pine had greater stomatal conductance and transpiration than red pine and white pine at gap centers where soil moisture availability was high, but there were fewer distinctions between species at north gap, south gap, and edge locations, where moisture availability was lower. This suggests jack pine was able to regulate stomatal control across the gap transect more tightly than the other species, allowing for profligate water use in environments where moisture was less limiting. Greater conductance would allow the high assimilation rates observed for jack pine in central gap locations, assuming photosynthesis was at least partly carbon limited and a capacity for increased assimilation rates at relatively high conductance. Jack pine seedlings did have higher $N_{mass}$ than the other species when averaged across gap locations, and nitrogen content is closely tied to photosynthetic potential (Field and Mooney, 1986; Reich et al., 1991, 1992; Ellsworth and Reich, 1993). High photosynthetic capacity in jack pine may promote high conductance at locations where light availability is high and water is less limiting. Red pine, on the other hand, maintains relatively high levels of stomatal conductance across a wider range of internal moisture stress (Pereira and Kozlowski, 1977; Schulte and Marshall, 1983), which may explain why this species was able to support assimilation rates similar to jack pine in the dry, sunny, northern edge positions despite the difference in foliar nitrogen concentrations between the two species. The finding that white pine, which can be susceptible to moisture stress as a seedling, also displayed competitive assimilation rates and growth in dry edge locations might be surprising, but white pine is also the most shade tolerant of the species studied so it would be expected to fare better in comparisons within shady southern edge environments.

The data do not support our hypotheses regarding WUE and the effects of understory release treatments. We found no evidence of a trend in WUE across the gap transect, or partitioning based on individual species differences in WUE. Understory release treatments had no significant impacts on resource availability, and only jack pine showed any differences in physiological performance between understory treatments. A variety of studies suggest understory release treatments that follow overstory removal increase resource availability (Harrington and Edwards, 1999; Beckage et al., 2000; Wetzel and Burgess, 2001; Boucher et al., 2007), so our findings are somewhat surprising. Our split-split-plot analysis provided less power for detecting the whole-plot understory treatment effects than gap location or species effects, so further studies that avoid the randomization restrictions and associated error structure of split-plot designs might be better suited for exploring understory treatment effects in gaps.

In general, our findings are consistent with our understanding of the species that were considered. Jack pine, a fast growing, shade intolerant species that limits moisture stress through strong stomatal regulation was dominant in the open, high resource environment of the gap interior. Red pine and white pine, which are somewhat more tolerant of shade, and show less dramatic stomatal response to moisture stress were able to compete better at edge locations where dry conditions or shade limited jack pine's photosynthesis and growth. It is difficult to estimate what
proportion of the gap area would favor any given species since we only characterized environmental conditions, physiology, and growth in five discreet locations. However, even if the edge conditions that seem to benefit red pine and white pine extend only 5–7.5 m into the gap (one third to one half the distance between our study points), that would represent approximately 30–40% of the total gap area.

While these results are likely representative of shade intolerant to mid-tolerant conifers growing on xeric sites, they may not be applicable to other forests on more mesic soils. Sugar maple (Acer saccharum Marsh.) seedlings, for instance, show greater drought stress characterized by low Ψpd in open environments where high vapor pressure deficits limit gs and carbon assimilation (Ellsworth and Reich, 1992). Surface drying in northern and center gap locations has also been linked to poor seedling performance in northwestern North American conifer forests (Wright et al., 1998).

Although red pine dominated forests in the Lake States have traditionally been managed using even-aged techniques, there has been recent interest in promoting mixed species, multi-cohort stand development in these forests (Palik and Zasada, 2003; Gilmore and Palik, 2005). Our results suggest silvicultural systems that incorporate large gaps may be a viable method for achieving these goals, at least in the absence of pine shoot-blight diseases which can restrict multi-cohort management opportunities (Gilmore and Palik, 2005). Gap-based approaches for increasing diversity have been suggested for a variety of other forest types across North America (Coates and Burton, 1997; Gray and Spies, 1996; Wright et al., 1998; Raymond et al., 2006), although direct evidence of gap partitioning has been limited in some of these studies. Our results suggest gap-based systems may promote overstory diversity and multi-cohort structural development, even in forests characterized by shade intolerant tree species, by taking advantage of gradients in both light availability and moisture stress.

5. Conclusions

Our findings add to a large body of literature reporting gradients in resource availability across canopy gaps. Our study species also showed some evidence of niche partitioning across these gradients, and differences in performance based on carbon assimilation rates seemed to be regulated by both light availability and moisture stress. This represents an important extension to traditional interpretations of the gap partitioning hypothesis, which rely primarily on gradients in light availability to explain patterns of species dominance and diversity across the gap-intact canopy continuum. Our findings also suggest silvicultural systems that incorporate patch cuttings could promote species diversity in the pine forests of North America’s Great Lakes region by exploiting the potential for niche partitioning across large openings.

Acknowledgements

We thank Thomas Drummer, Linda Nagel, and Christopher Webster for their advice and comments throughout the development of this project. Julia Robinson assisted with sample preparation. Funding for this research was provided by the USDA Forest Service and the Ecosystem Science Center at Michigan Technological University.

References


