

Influence of gap position and site preparation on gas exchange dynamics and leaf area of *Picea glauca* and *Populus tremuloides* seedlings in mixedwood stands

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Abstract

One challenge for managers of boreal and sub-boreal mixedwood stands is to successfully establish and maintain the competitive status of white spruce (*Picea glauca* (Moench) Voss in relation to aspen (*Populus tremuloides* Michx.) and other competitors following harvesting. Underplanting spruce within harvest gaps has been suggested as one potential strategy, but questions remain regarding the kind of harvest gap environment most conducive to the growth of spruce in relation to aspen. We used linear mixed-effects models to test the effect of harvest gap position and Meri-crusher versus brush-saw vegetation treatment on leaf area per wet weight, leaf photosynthesis, stomatal conductance, and transpiration in low- and full-light conditions, and on photosynthetic plasticity to changing light conditions. Overall aspen maintained higher leaf area per unit wet weight than spruce across the gap, but spruce leaf area was more sensitive to changes in gap position. Aspen also maintained higher photosynthesis and transpiration rates than spruce under both light conditions and in both vegetation treatments, but the magnitude of difference in gas exchange rates between the two species depended significantly on vegetation treatment and gap position for photosynthesis, and on gap position for transpiration. Plasticity of photosynthetic response to changes in light were not significantly different for both species, and did not vary significantly for either species between gap positions or site preparation treatments.

Introduction

Throughout the North American boreal and sub-boreal forests a natural disturbance regime of relatively frequent catastrophic fires (Armstrong 1999) facilitates the occurrence of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) in both single- and stratified mixed-species stands. On mixedwood sites of this region (Rowe 1972), aspen is an early-successional pioneer (Connell and Slatyer 1977), dominating during stand initiation and stem exclusion phases of stand development (Oliver and Larson 1996). Following fire events, aspen typically regenerates quickly through vigorous root suckering to form a dense, closed canopy within about five years (Frey et al. 2003, Li et al 2009). Initial colonization by aspen is then followed by a period of intense competition and self-thinning before maturity at around 60-80 years, at which point the aspen component of the stand begins to decline. White spruce can either colonize from veteran seed-bearing trees that either have survived the disturbance (Cumming et al. 2009, Solarik et al. 2010) or that are at the edges of the disturbed area. In either case, white spruce enters the regenerating cohort via two principal successional pathways. Spruce can either establish via initial floristics, colonizing immediately following disturbance alongside aspen, or it can establish later in stand development with the formation of canopy gaps (Lieffers et al. 1996, Greene et al. 1999, Bergeron 2000, Purdy et al. 2002, Hill et al. 2005). In either case, on mixedwood sites growth of the more shade-tolerant spruce typically lags behind that of intolerant hardwoods, with the spruce component occupying the lower strata beneath aspen for several decades until being released through localized disturbance or the breakup of the overstory (Dix and Swan 1971, Peterson and Peterson 1992).

Because of the economic value of white spruce, however, managers of these forests often seek promote spruce volumes on a shorter time scale than the natural dynamics of mixedwood stands would ordinarily facilitate. Doing so has frequently meant converting these stands to intensively managed spruce plantations that rely on site preparation and chemical methods to control the establishment and competitive status of the white spruce crop trees in relation to hardwood competitors. While such intensive management practices are undeniably an integral component of the suite of forest land uses at the landscape level (Seymour and Hunter 1999), they are neither appropriate for all sites nor for achieving all management objectives. Compared to intensive, single-species plantations, more extensively managed mixed spruce-aspen forests can also offer considerable benefits, including protection of habitat crucial to maintaining biodiversity, (Robichard and Villard 1999, Mills and Macdonald 2004, Chavez and Macdonald 2012), increased ecosystem resilience to changes in patterns of disturbance (Holling 1973), and potential increases in stand-level productivity (Kabzems et al 2011).

Sustainable management of the boreal forest as a whole therefore calls upon managers to produce fully-stocked spruce-aspen mixtures that are also at least marginally commercially productive within typical investment time-frames and

financial constraints (Lieffers and Beck 1994, MacDonald 1995, Burton et al. 2006). Various extensive silvicultural strategies have been suggested to successfully manage these mixedwood stands, including shelterwood systems, strip clearcuts, and two-stage selection variable retention harvesting systems (Lieffers et al. 1996). Regardless of what approach is taken, however, success in mixedwood stands depends on the ability of forest managers to reliably secure adequate spruce regeneration and ensure its competitive status with respect to aspen, particularly during the juvenile growth stage (Bokalo et al. 2007, Pitt et al. 2010). Enrichment underplanting of white spruce beneath aspen or within canopy gaps has been suggested as one way to compensate for the documented difficulties of securing and managing natural spruce regeneration (Li et al. 2009, Martin-DeMoor et al. 2010). Even following successful establishment, however, the relatively slow growth rate of white spruce is often severely limited by competition from other woody plants and herbaceous vegetation, especially in the high-resource environments that typify post-fire sites and other open environments.

Known differences in the regeneration ecologies of spruce and aspen suggest that a gap-based approach to silvicultural treatments (Coates and Burton 1997) combined with vegetation management or soil preparation techniques (Johnstone 2005, Fleming and Smith 2011) may ultimately prove successful in overcoming some of the difficulties of promoting the establishment and growth of underplanted spruce. It has been well documented globally that a gradient in microclimatic conditions and resource availability typically exists across natural and harvest-induced forest canopy gaps. In the northern hemisphere the northern edge of gaps experience direct sunlight while the southern edge and understory experience primarily diffuse radiation (Canham et al. 1990, Lieffers et al. 1999), with resulting temperature and humidity differences within and between gaps of various size and shape (Carlson and Groot 1997, Marenholtz et al. 2010). Light, moisture and temperature gradients interacting with differences in species autecology have been shown to result in some degree of species partitioning or differential performance across the gap environment in numerous forest types (Whitmore 1989, Sipe and Bazzaz 1994, Sipe and Bazzaz 1995, Messier et al. 1999, Coates 2000, Coates 2002). Within boreal mixedwood stands, therefore, certain positions within harvest gaps should prove more conducive to the successful establishment and growth of white spruce than others. Other studies have shown impacts of shelter on young spruce growth (Groot 1999), and in the same experimental area as the current study, Milakovsky et al. (2011) documented differences in light, soil temperature between positions within a harvest gap, and that white spruce seedling growth and survivorship is affected by harvest gap position and soil preparation treatment.

The physiological drivers of such observed differences in spruce growth and survivorship in varying soil and air microenvironments across harvest gaps have not been fully explored, however, nor have spruce physiological responses to these different microenvironments been compared with those of competitors such as trembling aspen. The objective of this study was to contribute to

current understandings of potential physiological mechanisms driving growth and competitive dynamics of juvenile white spruce and trembling aspen across the harvest gap environment at different light levels and under different site preparation techniques. Given its successional role, relative shade tolerance, and low root to shoot ratios, evidence suggests that white spruce seedlings may trade off net assimilation in order to avoid water stress by more tightly controlling stomatal aperture than aspen in the high temperature, low moisture environments typical of exposed conditions (Grossnickle and Blake 1987, Marsden et al. 1996, Groot 1997, Grossnickle 2005). Such physiological responses should result in lower maximum photosynthesis rate than aspen across the gap environment, though potentially higher photosynthesis rates within the understory, and the relative shade tolerance of spruce in comparison to aspen also suggests that spruce should show greater acclimation to microenvironmental conditions than aspen (Awada and Redmann 2000, Landhausser and Lieffers 2001, Roberts and Zwiazek 2001).

In order to explore the physiological drivers of spruce and aspen competitive dynamics across the harvest gap environment under different light and soil conditions, we measured gas exchange rates at two light levels for white spruce and trembling aspen seedlings located within harvest gaps in transects prepared with either a brush saw or Meri-crusher treatment. We took measurements of photosynthesis (A_{net}), stomatal conductance (g_{sw}) and transpiration (E) rates at photosynthetic photon flux densities of $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ for individuals of both species in each of five gap positions - southern understory (SU), southern edge (SE), center (C), northern edge (NE), and northern understory (NU). From photosynthesis and transpiration rates we calculated an index value measuring plasticity of photosynthetic response to differences in the two light conditions (PPI). For white spruce we also measured leaf area per unit wet weight across gap positions. We formulated and tested the following hypotheses: 1) spruce maximum gas exchange rates are lower than aspen within canopy gaps and higher than aspen in the understory; 2) maximum spruce gas exchange rates and leaf area would show greater overall sensitivity to (greater differences across) gap position than those of aspen; 3) spruce maximum gas exchange rates are highest in the southern edge and center of the gap; 4) increases in soil evaporation from intensive site preparation negatively impacts spruce gas exchange rates. To test these hypotheses, we used linear mixed-effects models to evaluate the effect of harvest gap position and Meri-crusher versus brush-saw vegetation treatment on leaf area per wet weight, photosynthetic plasticity index, and leaf photosynthesis, stomatal conductance, and transpiration at low-light and full-light conditions.

Methods

Field Methods

Additional information regarding site layout and experimental design can be found in Milakovsky et al. (2011). The area of study is in west-central Saskatchewan, Canada, near the community of Meadow Lake, on lands owned by the Cree First Nation and managed by Mistik Management Ltd. This region lies within the Boreal Plain Ecozone, a transition between prairie to the south and the Boreal Shield in the north of the province (MacLaughlan et al 2010). Soils in this region are classified as gray luvisols on sandy loam subsoil (Agriculture Canada 1992). The climate of the study area is continental, with mean annual precipitation of around 406 mm, and average temperatures ranging from a daily mean high of -13.7 C in January to 24.2 C in July (Environment Canada 1993). Forest vegetation includes mixed forests of predominantly white spruce and trembling aspen, blending with minor overstory components of balsam poplar, jack pine, and black spruce.

In 1997, four experimental linear gaps (ELGs) were created within each of two experimental blocks in which a TIMCO feller-buncher removed all trees greater than two meters in height. Gaps measured 340 meters (E-W axis) by 80 meters (N-S axis) and were arranged north-south within the stand, with a 100 meter buffer of uncut forest between each gap. Within each ELG, nine transects were laid out to which unique combinations of three herbivory exclusion and three vegetation management treatments were applied. The vegetation management treatments included a Meri-Crusher treatment that destroyed all residual vegetation and harvesting slash, a release treatment in which residual vegetation was cut using a brush saw, and a control treatment in which no management was applied. The herbivory exclusion treatments were not experimental factors in this study, but are detailed in Milakovsky et al. (2011).

Five transects were chosen from three of the ELGs, (three release treatments and two sprout treatments, without herbivory exclusion) in which to conduct gas exchange measurements. Within each transect five 4m wide (N-S) gap positions were delimited: southern understory (SU: 20 meters from the southern edge of the ELG into the forest), southern edge (SE: the first four meters of opening at the southern side of the ELG), center (C: centered 40 meters from the N and S edges of the ELG), northern edge (NE: the first four meters of opening at the northern side of the ELG), and northern understory (NU: 20 meters from the northern edge of the ELG into the forest).

Within each gap position, we established a single centered 4 x 8 meter plot, further subdivided into eight 2 x 2 meter subplots. Four out of eight 2 x 2 meter subplots at each gap position were randomly selected for spruce plantings, within which nine 4-month-old containerized white spruce seedlings were planted at 1 x 1 meter spacing during the first two weeks of June, 1996. Therefore for each gap position within an ELG a total of 36 seedlings (9 seedlings x 4

subplots) were planted. Planted spruce seedlings were of native provenance from the Mistik Management Nursery stock, averaging 15 cm in height at the time of planting. Aspen seedlings within these subplots were all naturally occurring. Gap positions and plots were laid out prior to harvesting of the openings, and harvesting machinery was confined to trails between gap positions so as to prevent soil compaction and damage to residual vegetation.

Measurements were collected over three consecutive summers, from 1998-2000, with aspen measurements taken from July 2-7, 1998 and from July 25-30, 1999. Spruce measurements taken from July 25-30, 1999 and from June 21-28, 2000. Gas exchange measurements were taken using the Li-Cor (Lincoln, NE) LI-6400 Portable Photosynthesis System. Within each gap position in a given transect, net assimilation rate of CO₂ (A_{net}), stomatal conductance to H₂O (g_{sw}), and transpiration rate (E) were measured twice for six randomly selected individuals at a high light level of 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) and at a low light level of 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. During the 1998 field season, leaf area and wet weight of samples were recorded immediately following the collection of gas exchange measurements. Leaf area samples were collected within the same experimental block from six individuals in each of the five gap positions in two transects.

Data analysis

All data processing and analyses were conducted in RStudio version 0.97.336 (RStudio 2013) calling R64 version 3.0.1 (R Development Core Team 2013). Data visualization was accomplished using the ggplot2 (Wickham 2009), pander (Daroczi 2013), and knitr (Xie 2013) libraries. All mixed-effects models were fit using the lmer() function within the lme4 package (Bates et al. 2013).

Because of imbalances in collection of leaf area data, measurements from the southern and northern understory positions were pooled prior to analysis. Differences in the ratio of leaf area to wet weight (LAW) for spruce and aspen in each of four gap positions were then tested within a mixed model framework with a random effect at the transect level.

In analyzing gas exchange rates, the data were first standardized for leaf area and cleaned of errors by removing negative values and other implausible outliers. Photosynthetic plasticity index (PPI) was defined as $\frac{A_{1200} - A_{50}}{A_{1200}}$. For A_{net} , g_{sw} , and E, mixed-effects models were fit testing the effect of light level, species, gap position, site preparation and all interaction terms on each response variable, with random effects included for block, transect, plot, and individual to reflect the hierarchical experimental design structure. A PPI model with the same random effects structure was similarly fit testing the effects of species, gap position, site preparation, and all interaction effects. For all models, we examined plots of residuals versus fitted values, normal quantile-quantile plots, histograms of residuals, and observed versus predicted values in order to examine fit and verify assumptions. Following initial model fitting to untransformed data, A , g_{sw} , and

E were squareroot transformed, PPI was logit transformed, and models were re-fit in order to meet assumptions of homoscedasticity and normality of residual error.

Significance ($\alpha = 0.05$) of fixed-effects for full models were tested using Type II Analysis of Deviance Wald F tests with the Kenward-Rogers adjustment to denominator degrees of freedom implemented using the car package (Fox and Weisberg 2011). Post-hoc pairwise comparisons of marginal means for all treatment levels of experimental fixed-effects were conducted using Tukey's Honestly Significant Differences tests as implemented by the lsmeans package (Lenth 2013).

Results

Leaf Area

Analysis of deviance results for LAW are displayed in Table 1. Predictably, we found that aspen had higher LAW ratios than spruce in all gap positions, and that both species maintained their highest LAW ratios when in the understory. Within the harvest gap, however, spruce and aspen showed distinctly divergent patterns. Once out of the understory, LAW ratios did not vary significantly for aspen across any of the internal gap positions, while for spruce it declined steadily moving from the southern edge of the gap to the northern edge (Figure 1).

Gas Exchange

Analysis of deviance results for fixed effects in full gas exchange models are shown in Tables 2-4, and estimates of standard deviations of random effects of experimental design factors are displayed in Table 5. Based on parameter estimates from the full models, there appeared to be a high degree of interaction between experimental factors in all three gas exchange models. Significant four-way interactions between light, species, gap position, and vegetation treatment were indicated by the photosynthesis ($p = 0.0054$) and stomatal conductance ($p = 0.0072$) models. Likewise, results from the transpiration model indicated a significant ($p < 0.0001$) three-way interaction between light level, species, and gap position. In addition to being difficult to meaningfully interpret, however, the *prima facie* statistical significance of such high order interactions may at least in part be an artifact of fitting complex models to relatively noisy data, particularly at low light levels, and therefore not entirely demonstrative of strong physiological signals. Even with this caution in mind, however, estimates of gas exchange rates based on post-hoc comparisons of marginal means for fixed effects show some clear differences in patterns of species gas exchange rates in response to experimental factors.

Photosynthesis and Photosynthetic Plasticity Post hoc comparisons of spruce and aspen photosynthesis rates by light level, gap position, and vegetation treatment are presented in Figure 2. At low light levels there were some differences across gap positions and vegetation treatments, but these differences did not demonstrate a clearly interpretable pattern. In low light levels both spruce and aspen appeared to be similarly limited, with rates in no gap position/vegetation treatment combination conclusively better than any other, and with neither species holding a clear advantage.

By contrast, at full light aspen photosynthesis rates were both relatively constant and consistently higher than spruce, with the magnitude and significance of these differences between the two species varying by site preparation treatment and gap position. In full light and in transects prepared with the brush saw treatment photosynthesis rates for aspen did not vary significantly by gap position, and were higher than spruce in all gap positions but the center. Spruce showed a more dynamic response, with photosynthesis rates significantly higher in the center than in surrounding gap positions, though with no detectable variation between the other gap positions.

In transects prepared with the Meri-crusher treatment a wholly different pattern occurred, however. Aspen photosynthesis rates were again higher than spruce under full light conditions in four of the five gap positions, but the location in which the two species did not vary significantly was instead the southern understory. Aspen photosynthesis rates were also variable rather than static from one gap position to another, while spruce was instead static. The pattern of aspen photosynthesis rates across gap positions in the Meri-Crusher treatment were both surprising and difficult to interpret given lower rates in the southern understory and center gap positions in comparison to relatively non-significantly different rates in all other gap positions. Because of the difficulties of interpretation of this pattern, it is tempting to regard the relatively low aspen photosynthesis rate in the Meri-Crusher treatment as a statistical artifact. Photosynthetic plasticity was not significantly different for spruce and aspen across all gap positions.

Stomatal Conductance Post hoc comparisons of spruce and aspen stomatal conductance by light level, gap position, and vegetation treatment are presented in Figure 3. Aspen stomatal conductance was higher than that of spruce in all gap positions, regardless of changes in vegetation treatment or light level. Neither species showed distinct differences in stomatal conductance under changing light conditions, but aspen also showed very little variation across either gap environment or between site treatments.

By contrast spruce showed distinctly different patterns in stomatal conductance rates between site preparation treatments, showing a more dynamic response to changes in gap position in the brush saw than the Meri-crusher transects. In brush sawn transects spruce stomatal conductance displayed an increasing pattern from the southern understory, peaking in the center of the gap and falling to very low levels in the northern understory. In transects prepared with

the Meri-Cruther treatment, however, spruce stomatal conductance was highest in the southern edge of the gap, and did not vary significantly between all other gap positions.

Transpiration Post hoc comparisons of spruce and aspen transpiration by light level and gap position are presented in Figure 4. Because of the non-significance of differences in vegetation treatment and interactions with vegetation treatment in the transpiration model, these factors were excluded from post-hoc testing.

Transpiration was higher for aspen than spruce across all gap positions and both light levels, did not vary significantly by gap position within a given light level, and only varied between light levels at the northern edge of the harvest gap. Light level also made little difference in spruce transpiration rates. Similarly to other gas exchange measures, however, spruce showed a more dynamic response to changing gap position than aspen, with peak transpiration rates at the southern edge and center of the gap, and lowest transpiration rates in the two understory positions.

Discussion

Determining post-harvest conditions that are conducive to maintaining the competitive status of white spruce with respect to hardwood species such as aspen is crucial in formulating silvicultural strategies for successfully regenerating and managing growth in boreal mixedwood forests. Understanding the fundamental physiological characteristics that are the drivers of the competitive dynamics between these species is important in designing the timing and spatial patterns of harvests so as to generate the microenvironmental characteristics that will facilitate spruce survival and maximize growth. This study identifies significant differences between spruce and aspen in terms of leaf area and gas exchange rates in response to changing light conditions within different gap positions and subject to different site preparation treatments that reflect the distinct roles these species play in the development of mixedwood stands. Though at low light levels differences between the two species were either not present or overly difficult to interpret, at high light levels some clear patterns emerged that provide insight regarding the competitive dynamics of the two species.

At high light levels in the brush saw treatment, aspen showed very little difference in either leaf area or gas exchange rates across gap position and vegetation treatments. The ability of aspen to display high leaf area per unit weight largely without regard to harvest gap positions and associated differences in microclimate is characteristic of the ‘go for broke’ strategy of an early-successional, short-lived species that is extremely competitive in a high-light environments. Based on our data, aspen would appear to have the capacity to maintain open stomates regardless of temperature, moisture, and light differences between microsites. This ability may be related to its nature as a prolific sprouter, which lends

seedlings a more robust root system for access to water. In this case, given the ability to maintain such high gas exchange rates, maximizing leaf area per unit leaf wet weight should result in higher growth and competitive advantage in comparison to more shade-tolerant moisture sensitive species such as white spruce.

By contrast, the successional role of white spruce in natural stands depends on the ability to persist beneath an aspen overstory, often for several decades. The role of spruce within these stands is therefore one that is characterized by slower initial growth but greater longevity and dynamic response to changes in stand structure in which spruce is forced to adapt to changes in light, moisture and temperature characteristics through extended episodes of competition and release. Given this typical life history, the ability to adapt photosynthetic physiology to microsite characteristics and thereby maintain a more finely-tuned balance between water loss and carbon gain is of theoretical advantage in both persisting across a variety of sites and in responding to changes in stand structure over time. It does not appear, however, to be the ability to maintain higher short-term photosynthesis rates than aspen at low light levels that allows spruce to persist beneath the understory.

The optimal post-harvest microsite conditions in terms of maximizing the competitive status of spruce with respect to aspen as indicated by our data appears to be the center of gaps prepared with the lower-impact brush saw site preparation treatment. Maximum photosynthesis and stomatal conductance rates for spruce were highest in these locations, and maximum photosynthesis rates did not differ significantly in these plots from those of aspen. These conclusions regarding optimal gap position corroborate growth measurements made by Milakovsky et al. (2011), who found that following an acclimation period in which ameliorative cover benefitted spruce, by the third year following planting white spruce height increment was highest in the center of the experimental linear gaps. Growth data from Milakovsky et al. showed, however, that height growth was greater for spruce located on sites prepared with the Meri-crusher treatment in comparison to spruce, which may indicate the need for further study regarding the interactions between site preparation, microenvironment, and growth.

References

Appendix 1: Tables

	F	Df	Df.res	Pr(>F)
S	658	1	95.2	1.6e-44
G	26.2	3	95.1	1.98e-12
SG*	3.51	3	95.1	0.0182

Table 1: Analysis of Deviance results on differences in leaf area per unit wet weight for species and gap position. The standard deviation of the modeled random effect for transect was 6.0441 and the standard deviation of the residual error at the individual level was 21.6106

	F	Df	Df.res	Pr(>F)
L	4677	1	590	1.11e-282
S	724	1	187	2.69e-66
G	0.203	4	10.3	0.931
V	0.0157	1	1.49	0.915
<i>LS*</i>	490	1	597	1.05e-79
<i>LG*</i>	33.9	4	591	1.82e-25
<i>SG*</i>	21	4	198	2.02e-14
<i>LV*</i>	29.7	1	592	7.32e-08
<i>SV*</i>	15.9	1	145	0.000105
<i>GV*</i>	0.564	4	10.1	0.694
LSG	2.98	4	598	0.0188
LSV	23.2	1	605	1.86e-06
LGV	8.99	4	594	4.71e-07
SGV	2.96	4	82	0.0244
<i>LSGV*</i>	3.71	4	607	0.00541

Table 2: Results from Analysis of Deviance on the effects of light level (L), species (S), gap position (G), vegetation treatment (V), and all interactions on photosynthesis rate

	F	Df	Df.res	Pr(>F)
L	11	1	565	0.000952
S	339	1	180	2.79e-43

G	1.37	4	9.33	0.316
V	0.00203	1	1.56	0.969
LS*	6.37	1	568	0.0119
LG*	6.67	4	565	3.01e-05
SG*	3.43	4	175	0.01
LV*	1.7	1	566	0.193
SV*	0.831	1	90.4	0.364
GV*	2.35	4	9.1	0.132
LSG	0.652	4	569	0.626
LSV	0.135	1	572	0.713
LGV	3.55	4	567	0.00709
SGV	1.02	4	79.3	0.4
LSGV*	3.55	4	572	0.00719

Table 3: Results from Analysis of Deviance on the effects of light level (L), species (S), gap position (G), vegetation treatment (V), and all interactions on stomatal conductance rates

	F	Df	Df.res	Pr(>F)
L	71.5	1	565	2.42e-16
S	385	1	189	1.84e-47
G	0.522	4	9.93	0.722
V	0.000224	1	1.81	0.99
LS*	6.14	1	568	0.0135
LG*	11.8	4	566	3.42e-09
SG*	3.54	4	193	0.00812
LV*	0.351	1	566	0.554
SV*	0.105	1	168	0.747
GV*	0.314	4	9.74	0.862
LSG	3.49	4	569	0.00785
LSV	0.847	1	572	0.358

LGV	0.677	4	567	0.608
SGV	1.07	4	77.4	0.378
LSGV*	1.11	4	573	0.353

Table 4: Results from Analysis of Deviance on the effects of light level (L), species (S), gap position (G), vegetation treatment (V), and all interactions on transpiration rates

	Block	Transect	Plot	Tree	Residual
Photosynthesis	0.4133	0	0.3505	0.192	0.3621
Conductance	0.007763	0.02554	0.05196	0.07564	0.05163
Transpiration	3.018e-05	0.1312	0.2022	0.1995	0.1419

Table 5: Standard deviations of experimental random effects for each of the three gas exchange models

Appendix 2: Figures

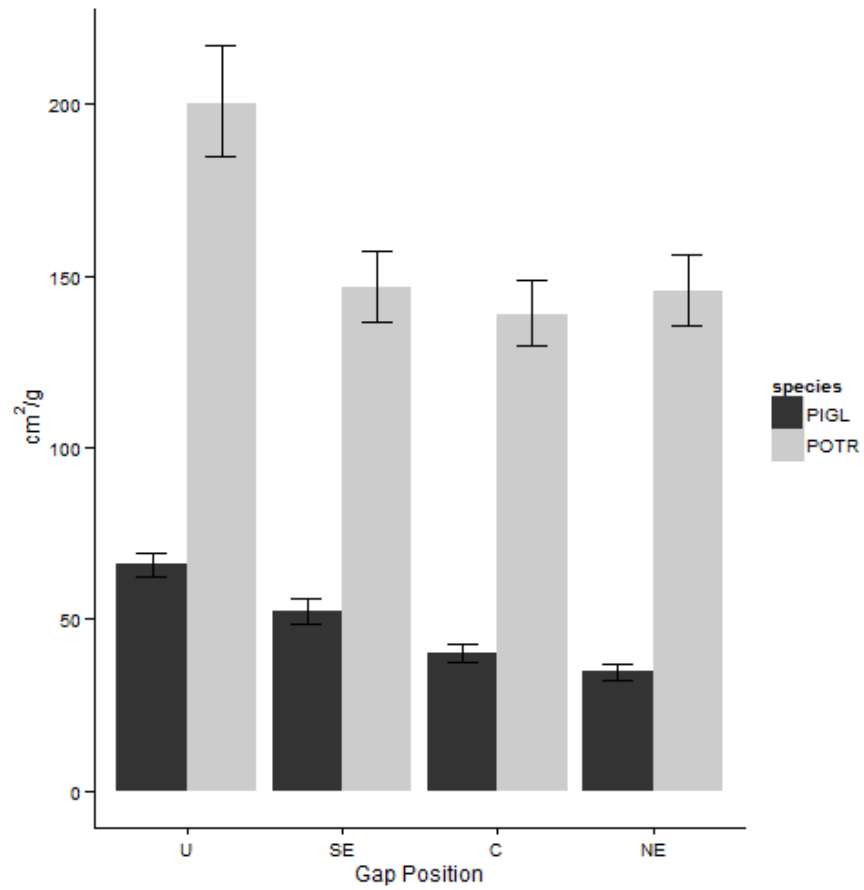


Figure 1: Leaf area per unit wet weight of white spruce and trembling aspen by gap position and vegetation treatment. Bar levels indicate marginal means and standard errors

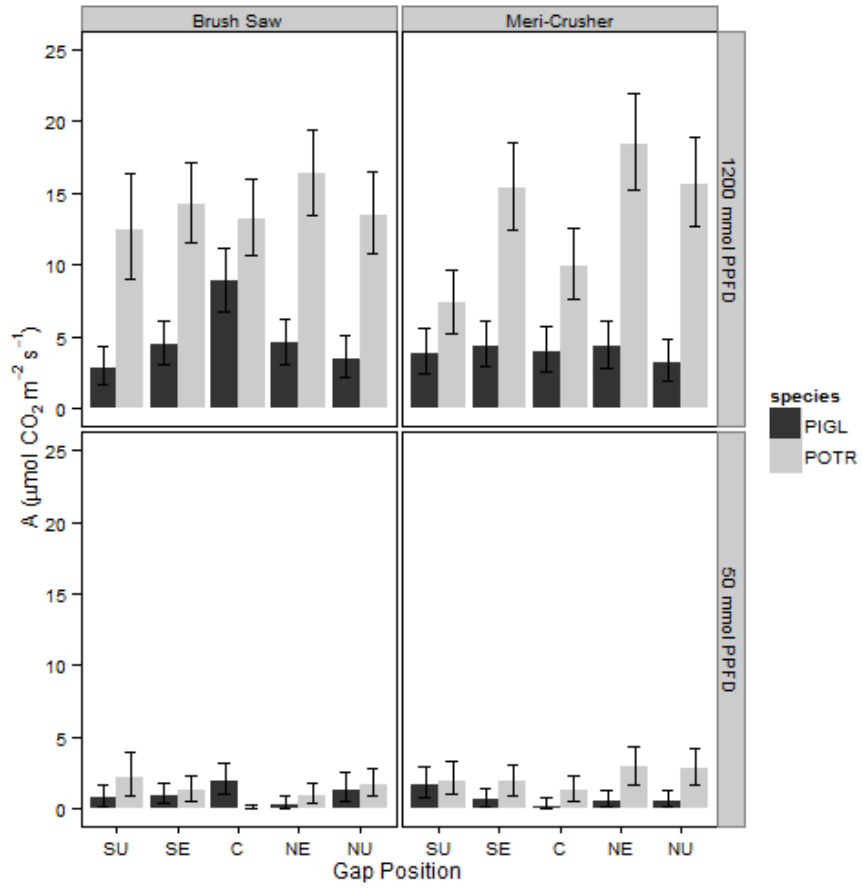


Figure 2: Photosynthesis rate of white spruce (PIGL) and trembling aspen (POTR) by light level (1200 or 50 mmol PPFD) and vegetation treatment (Brush Saw or Meri-Crusher) across the experimental linear gap. Gap positions: SU - southern understory; SE - southern edge; C - center; NE - northern edge; NU - northern understory. Bar levels indicate marginal means and standard errors

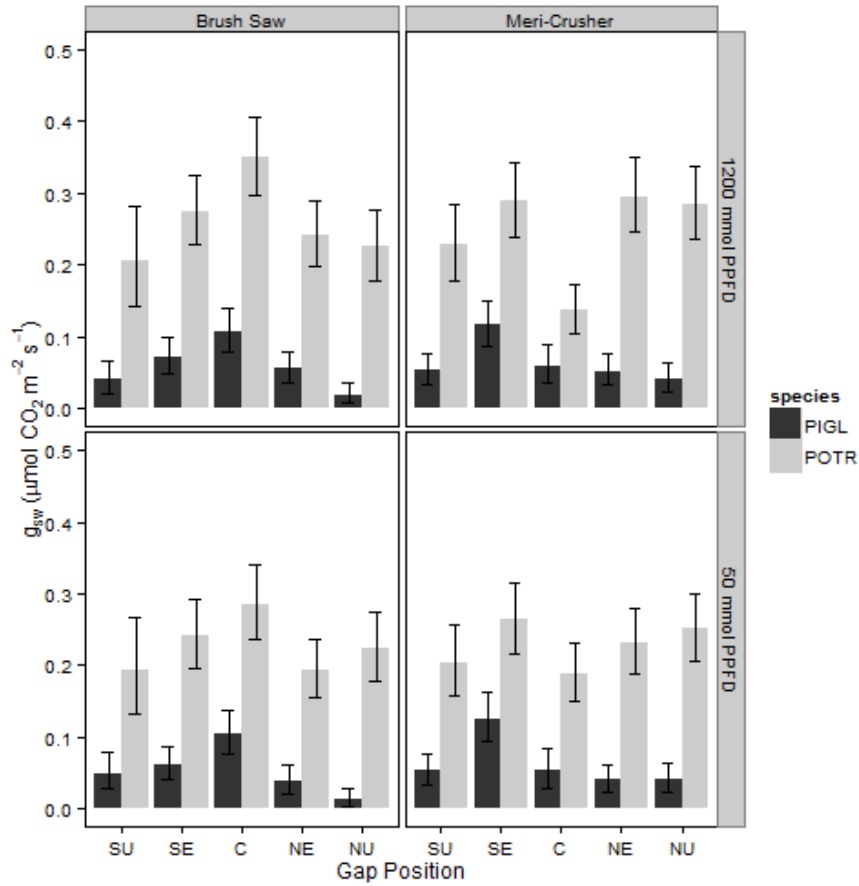


Figure 3: Stomatal conductance rate of white spruce (PIGL) and trembling aspen (POTR) by light level (1200 or 50 mmol PPFD) and vegetation treatment (Brush Saw or Meri-Crusher) across the experimental linear gap. Gap positions: SU - southern understory; SE - southern edge; C - center; NE - northern edge; NU - northern understory. Bar levels indicate marginal means and standard errors

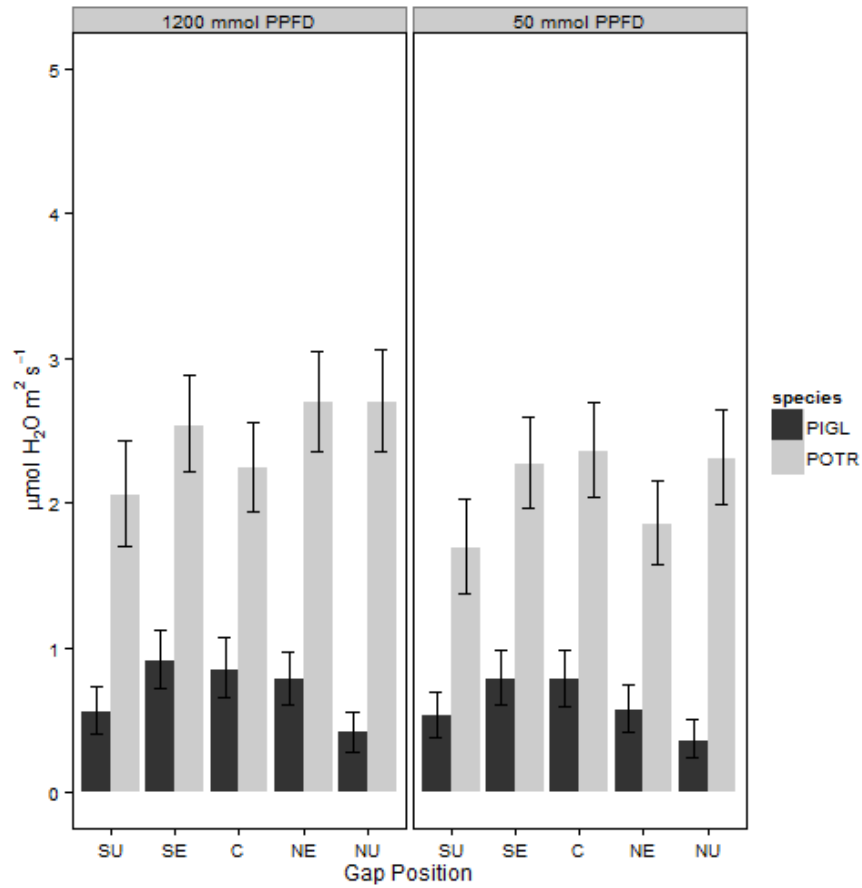


Figure 4: Transpiration rate of white spruce (PIGL) and trembling aspen (POTR) by light level (1200 or 50 mmol PPFD) and vegetation treatment (Brush Saw or Meri-Crusher) across the experimental linear gap. Gap positions: SU - southern understory; SE - southern edge; C - center; NE - northern edge; NU - northern understory. Bar levels indicate marginal means and standard errors