Leaf area dynamics of a boreal black spruce fire chronosequence

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Summary Specific leaf area (SLA) and leaf area index (LAI) were estimated using site-specific allometric equations for a boreal black spruce (Picea mariana (Mill.) BSP) fire chronosequence in northern Manitoba, Canada. Stands ranged from 3 to 131 years in age and had soils that were categorized as well or poorly drained. The goals of the study were to: (i) measure SLA for the dominant tree and understory species of boreal black spruce-dominated stands, and examine the effect of various biophysical conditions on SLA; and (ii) examine leaf area dynamics of both understory and overstory species for well- and poorly drained stands in the chronosequence. Overall, average SLA values for black spruce (n = 215), jack pine (Pinus banksiana Lamb., n = 72) and trembling aspen (Populus tremuloides Michx., n = 27) were 5.82 ± 1.91, 5.76 ± 1.91 and 17.42 ± 2.21 m² kg⁻¹, respectively. Foliage age, stand age, vertical position in the canopy and soil drainage had significant effects on SLA. Black spruce dominated overstory LAI in the older stands. Well-drained stands had significantly higher overstory LAI (P < 0.001), but lower understory LAI (P = 0.022), than poorly drained stands. Overstory LAI was negligible in the recent (3–12 years old) burn sites and highest in the 70-year-old burn site (6.8 and 3.0 in the well- and poorly drained stands, respectively), declining significantly (by 30–50%) from this peak in the oldest stands. Understory leaf area represented a significant portion (>40%) of total leaf area in all stands except the oldest.

Keywords: age sequence, boreal forest, leaf area index, Picea mariana, Pinus banksiana, Populus tremuloides, specific leaf area, understory.

Introduction

Leaf area index (LAI)—the amount of leaf area per unit ground area—strongly influences energy, water and carbon dioxide exchange between terrestrial ecosystems and the atmosphere (Campbell and Norman 1998, Law et al. 2001a). In forest ecosystems, LAI is tightly coupled with photosynthesis, litterfall, microclimate and productivity (Gower et al. 1999), and is an important parameter in terrestrial biogeochemical models and remote sensing (Bonan 1993, Chen et al. 1997). Leaf area index is strongly influenced by species, climate, soil fertility, water availability, tree density (Gholz 1982, Gower et al. 1995, Wang et al. 2001), evapotranspiration and photosynthesis (Kozlowski and Pallardy 1997). Thus, quantifying LAI dynamics is necessary to understand the structure and function of forest ecosystems at various spatial scales.

In most even-aged stands, LAI reaches a maximum relatively early in the life of the stand, subsequently declining by 25–50% (Landsberg and Gower 1997, Ryan et al. 1997). Many data have been published for temperate forests, but to our knowledge LAI dynamics have never been quantified for a boreal black spruce (Picea mariana (Mill.) BSP) chronosequence, although LAI dynamics of boreal Norway spruce (Picea abies (L.) Karst.) have been studied (Stenberg et al. 1999, Küßner and Mosandl 2000). Several approaches have been proposed to estimate LAI; the two most common are optical and allometric methods. Allometry models are vulnerable to cumulative errors in sampling, selection of model form and model application (C. Wang et al., unpublished data), but are the most accurate (Gower et al. 1999) in conifer stands, where optical instruments underestimate leaf area because of foliage clumping (Smith et al. 1991, Stenberg et al. 1995, Chen et al. 1997, Küßner and Mosandl 2000). Variations in light absorptivity of needles and the contribution of woody material to total plant area index (PAI) can also cause large errors in optical LAI estimates (Smolander and Stenberg 1996, Serrano et al. 1997). The correction of optical data to compensate for foliage clumping has, however, become increasingly refined (Whitehead et al. 1990, Chen et al. 1997, Stenberg et al. 1999, Law et al. 2001a).

Leaf area may be calculated from leaf mass using specific leaf area (SLA), the ratio of fresh foliage surface area to unit dry foliage mass. Many ecosystem process models require SLA as an input to estimate LAI from carbon allocated to foliage mass (McMurtrie et al. 1994, Landsberg and Gower 1997, Kimball et al. 2000), as SLA reflects photosynthetic capacity and foliar nutrition (Kozlowski and Pallardy 1997). Specific leaf area typically varies with tree species and soil conditions, decreases with foliage age and higher canopy position, and is correlated with potential growth rate (Lambers and Poorter 1992, Gower et al. 1995) and leaf longevity (Reich et al. 1992, 1997, Gower et al. 1993). Some of these effects have been studied in plantation seedlings for the dominant trees of
central boreal Canada (Brand 1991), but much less thoroughly in situ, particularly over the lifetime of a boreal stand. In northern Manitoba, this lifetime typically involves early dominance by shade-intolerant species such as jack pine (Pinus banksiana Lamb.) and trembling aspen (Populus tremuloides Michx.) before they are shaded out by the closure of the black spruce canopy.

Overstory LAI has a strong influence on understory light availability and thus regeneration and succession dynamics (Lambers et al. 1998). Most studies in conifer and boreal forests have focused on overstory LAI, but a few have measured both overstory and understory leaf area (Constabel and Lieffers 1996, Moola and Mallik 1998, Aubin et al. 2000). One study showed that understory LAI could account for 20% or more of LAI in a coniferous forest (Law et al. 2001b). In the boreal forest, where wildfire is a frequent disturbance and regeneration is relatively slow, understory leaf area may be the dominant leaf cover for a significant portion of the stand life, and highly significant in carbon cycling (De Grandpré et al. 1993). Forest researchers, process-based models and remote sensing studies all need accurate data on understory SLA and LAI (Law and Waring 1994).

The objectives of this study were to (i) measure SLA for the dominant tree and understory species of boreal black spruce-dominated stands in northern Manitoba, Canada, and examine the effect of various biophysical conditions on SLA; and (ii) examine leaf area dynamics for well- and poorly drained stands in a boreal black spruce fire chronosequence.

Materials and methods

Study areas

The study was conducted west of Thompson, Manitoba, near the BOREAS Northern Study Area (55° 53’ N, 98° 20’ W), on seven, different-aged black spruce forests. The stands included in this chronosequence encompassed the natural age range of forest stands in the region. All stands were within 40 km² except the most recently burned stands (1998 and 1995 burns), which were located in Leaf Rapids, Manitoba, about 100 km northwest of the older stands. Annual mean temperature was 0.8 °C. Mean temperatures in January and July were −19.7 and 16.5 °C, respectively. Mean annual precipitation was 438.5 mm.

All stands originated from stand-killing wildfires, and at the time of sampling ranged in age from 3 to 131 years. One “wet” (poorly drained) and one “dry” (well drained) stand were located in each separate burn area, and stand names in this paper consist of “D” or “W” (dry or wet, respectively) followed by year of burn, e.g., D1995 or W1930. Stands were classified as wet or dry depending on edaphic condition and species composition. Wet stands had saturated or poorly aerated soil and supported plants adapted specifically to such soil conditions (National Wetlands Working Group 1988). In the boreal forests of northern Manitoba, common wet-site species include a sphagnum (Sphagnum spp.) ground cover, a bog birch (Betula glandulosa var hallii Michx.) understory and a tamarack (Larix laricina (Du Roi) Koch.) or black spruce overstory. Drier stands commonly have a feathermoss (Pleurozium or Hylocomium spp.) ground cover with a Labrador tea (Ledum groenlandicum Oeder) and Vaccinium spp. understory. The 14 stands differed in age, tree stocking density, diameter class distribution, canopy height and basal area (Figure 1).

Vegetation varied with stand age and soil drainage, but the stands were dominated by six tree species: trembling aspen, paper birch (Betula papyrifera Marsh.), black spruce, jack pine and willow (Salix spp.). At the youngest stands (1998, 1995 and 1989 burns), trees were present only as seedlings and small saplings. Bog birch, paper birch and willow were often present. Fireweed (Epilobium angustifolium L.), blueberry (Vaccinium myrtillus Michx.), red raspberry (Rubus idaeus L., var. strigosus (Michx.) Maxim.) and horsetail (Equisetum spp.) were common understory species. Medium-aged stands (1981 and 1964 burn sites) generally had large numbers of black spruce saplings, but were often dominated by jack pine or aspen in drier sites and tamarack in wetter sites. Hazel (Corylus cornuta Marsh), willow, Labrador tea, serviceberry (Amelanchier alnifolia (Nutt.) Nutt.) and bog birch were present in the understory. The ground cover species were bearberry (Arctostaphylos uva-ursi (L.) Spreng.), reindeer lichen (Cladina spp.) and feathermoss, except on wet sites, where ground cover was usually limited to sphagnum and Labrador tea. The oldest stands (originating from burns in 1930 and 1870) were dominated by a black spruce overstory. Understory was sparse and included Labrador tea, wild rose (Rosa spp.) and green alder (Alnus crispa (Ait.) Pursh). Ground cover species were feathermoss in dry stands or sphagnum in the wet stands. This general understory succession is similar to patterns seen in other studies of boreal black spruce (Black and Bliss 1978, Viereck et al. 1993).

Study sites were matched as well as possible to have the same soil types. Soils of these stands were composed of sedimentary materials deposited by glacial Lake Agassiz. The dry sites were usually on upland, moderately drained montmorillonite clay soils classified as Gray Luvisols (Boralfs), characterized by the formation of a clay-enriched B horizon (Veldhuis 1995). Some stands (D1995 and W1995 in this study) derived from morainal deposits of sand and gravel, and are generally weakly developed Dystric Brunisols (Cryochrepts) (H. Veldhuis, Agriculture Canada, Winnipeg, MB, unpublished data). The wet stands were usually located on poorly drained clay soils, underlain by discontinuous permafrost at 100–150 cm, and generally classified as Luvic Gleysols (Aqualfs), Terric Fibrisols (shallow Fibrists). One poorly drained stand with very deep peat (W1981) had Fibrisols, Mesisols and organic Cryosols. Most of the boreal trees described here, black spruce particularly, have fairly shallow rooting systems (Strong and La Roi 1983) and are rarely subject to serious water stress (B. Ewers, University of Wyoming, Laramie, WY, unpublished data).
Foliage mass measurement

Nine 5 × 10-m plots were established in each different-aged burn area: four in the well-drained stand and five in the poorly drained stand. Plots were located at least 200 m inside a burn to minimize edge effects. The plots in the well-drained stands were randomly located, and the plots in the poorly drained stands were oriented end-to-end (because of the design considerations of a concurrent study). An inventory of all trees, saplings and seedlings at each study site was performed using standard mensuration techniques (Gower et al. 1997). Site-specific allometric equations were developed relating stem diameter to foliage biomass for all overstory tree species (Bond-Lamberty et al. 2002). The allometry was based on samples of 8–12 trees per species per stand and used standard log–log forms ($\log F = a + b \log D$, where $F$ is foliage and $D$ is tree diameter at breast height or soil surface, 1.37 m). Understory biomass was measured in July 2001 in five 0.25-m² clip plots in each replicate plot. Ground cover bryophytes (e.g., Sphagnum and feathermoss) were not sampled. Sampled understory vegetation was separated into woody and foliage components by species, and foliage samples were taken for determination of SLA by species and leaf age.

Foliage samples were taken from all tree species at each stand in late July 2001, after full leaf development but before senescence in deciduous species. At each stand, three typical dominant or codominant trees were randomly selected for SLA analysis. A foliage sample was collected from the top, middle and bottom of each tree canopy using clippers or a shotgun in the case of tall trees. Samples were placed in airtight bags and transported in 3 °C coolers to Madison, WI for analysis.

Specific leaf area measurement and calculation of leaf area index

Leaf samples were scanned at 800 dpi with a backlit flatbed scanner (Umax AstraNET e5470, Umax Technologies, Fremont, CA). All leaves were physically separated before scanning. The image files were converted from grayscale to black and white based on a threshold luminosity value of 170 (on a 0–255 scale), which yielded pixel counts virtually identical ($y = 2765 + 0.958x$, $P = 0.155$ for intercept, $P < 0.001$ for slope, $r^2 = 0.995$) to those based on counting image pixels by eye (B. Bond-Lamberty, unpublished data). Projected leaf area (PLA) was computed by dividing the number of black pixels in the image by the scan resolution in pixels per unit area.

Leaf area index is defined here as hemisurface leaf area (HSLA), or one-half total leaf area per unit ground area. Pro-
Projected leaf area for flat-leaved species (aspen, birch and willow) was assumed to be equal to HSLA. Scanned needle areas for conifers (black spruce and jack pine) were converted to HSLA using published relationships (Chen et al. 1997), modified by Bond-Lamberty et al. (unpublished data). Samples were dried to a constant mass in a forced-air oven at 70 °C and weighed. Specific leaf area was computed as HSLA (m²) divided by leaf mass (kg). Understory leaf samples were processed identically to tree leaf samples, and SLA computed for the dominant understory species by assuming all understory foliage was flat (i.e., PLA was equal to HSLA). Leaf area index was computed by multiplying foliage biomass, calculated from the site-specific allometric equations and plot inventory data, by specific leaf area for each species.

Statistical analysis
A mixed effects model was used to examine the effects of potential factors on SLA. Soil drainage, foliage position in the canopy, foliage age, year of burn and all possible interactions were defined as fixed effects, with soil drainage nested inside of burn year. Insignificant terms (α = 0.05) were eliminated using a backward elimination procedure. Tree number within a stand was treated as a random effect, and used to test for autocorrelation of the SLA measurements with Wald Z-tests of the covariance parameter estimates. If found, autocorrelation was modeled with an AR(1) (first-order autoregressive) model. A contrast test (α = 0.05) was used to determine if SLA differed significantly among different-aged stands. A paired t-test was conducted to examine the effect of soil drainage on LAI.

Results

Significant effects on specific leaf area
Deciduous species occurred at three of the 14 stands (D1964, D1989 and W1989). Specific leaf area differed significantly with canopy position for aspen (P < 0.001) and willow (P = 0.020), but not for birch (P = 0.067) (Table 1). Average SLA values at the canopy top and bottom were, respectively, 15.38 and 18.85 for aspen, 16.30 and 20.20 for birch and 11.43 and 14.77 m² kg⁻¹ for willow. Average SLA was greater for aspen and birch than for willow (Table 2). Soil drainage did not significantly affect SLA for any deciduous species. Year of burn (stand age) was not significant for aspen, the one deciduous species that occurred in multiple stands.

Black spruce was present in all stands. Stand age (P < 0.001), canopy position, foliage age and soil drainage all significantly affected black spruce SLA (Table 1). Contrast tests showed that SLA did not differ significantly (α = 0.05) between the 1870, 1930, and 1964 stands. Therefore, the stands were grouped as follows: (I) the 1870, 1930 and 1964 burn year stands; (II) the 1989 burn year stands; and (III) the 1995 burn year stands. For Group I, soil drainage, canopy position, foliage age and the interaction of canopy position and foliage age were all highly significant (P < 0.01). Average SLA decreased in older needles, on wetter sites, and higher in the canopy (Table 2). The canopy position effect, while significant, resulted in only small (~0.2 m² kg⁻¹) numerical changes in SLA depending on canopy position. Specific leaf area decreased significantly with stand age for younger black spruce (Groups II and III), but SLA did not differ significantly between wet and dry stands. In addition, the 1995 samples (Group III) exhibited covariance within individual trees (P < 0.001). Canopy position was significant in the 1995 stands but not the 1989 stands, with SLA varying from the mean about 0.5 m² kg⁻¹ with canopy position.

Jack pine SLA differed significantly (P = 0.033) between the 1995 and 1964 burn years, and these data were analyzed separately. Needle age was the only significant effect (P = 0.015) for jack pine samples from the 1995 burn site. Needle age was significant for jack pine from the 1964 burn site, and the data also exhibited covariance within individual trees (P = 0.007). Canopy position was not a significant effect for jack pine SLA (P = 0.552). Specific leaf area decreased in older needles and the older stand (Table 2).

Specific leaf area varied by a factor of three among the major understory species (Table 3). Labrador tea and bearberry had SLA values similar to conifers (6–10 m² kg⁻¹), whereas most deciduous species had SLA values typical of deciduous trees (15–20 m² kg⁻¹). Green alder had the highest SLA (21.42 m² kg⁻¹), although the samples size was very small (n = 2). New and older foliage SLA did not differ significantly for bearberry (P = 0.849) or Labrador tea (P = 0.088), the two evergreen species measured, although in both cases SLA declined in the older leaves. The thick, leathery leaves of Labrador tea had the smallest SLA (7.82 and 6.60 m² kg⁻¹ for current and older foliage, respectively). The SLA values of lily and rose were highly variable (37–47% of mean SLA), possibly due to high leaf morphology plasticity. Understory SLA was positively correlated with overstory LAI in well-drained stands (r = 0.66, P = 0.002), but not in poorly drained stands (r = 0.07, P = 0.686).

Leaf area dynamics
Total LAI ranged between 1.1 and 7.5 in the dry stands, and 1.1 and 3.7 in the wet stands (Figure 2). Black spruce comprised the greatest percent of overstory LAI in most stands, although jack pine and aspen were dominant at the medium-aged (1964 and 1981 burn) stands (Figure 3). Overstory LAI was negligible in the recently burned (1998, 1995 and 1989) stands, highest in the 70-year-old stands, and declined significantly in the oldest (1870) stands. For a given stand age, total LAI was significantly greater (P < 0.001) for the dry stands than the wet ones, except at the very youngest stands (1998 and 1995 burn sites). Understory LAI exhibited a roughly bell-shaped curve across the chronosequence (Figure 2), and was greater in wet than in dry stands (P = 0.022). Total understory LAI was dominated in most stands by Labrador tea and Vaccinium spp., with green alder, Rosa spp. and bearberry significant presences in a few stands.
Discussion

Black spruce is the dominant tree species of the North American boreal forest (Gower et al. 2001), and its slow growth makes the chronosequence approach useful for studying ecosystem structure and function over the life of a stand. Chronosequence results must however be interpreted with caution. Distinguishing the effects of time and changes in treatment can be difficult (Powers and Van Cleve 1991, Foster and Tilman 2000, Yanai et al. 2000) and limit the inferences drawn from the study. In this discussion we assume that these study sites do represent a true black spruce chronosequence.

Direct measurement of LAI in forest stands is destructive and time consuming. But because direct measurements are not subject to uncertainties due to foliage clumping, tissue absorptivity and instrument calibration, they provide essential verification of other types of estimates (Gower et al. 1999). Leaf area index values in this study were comparable to, or slightly higher than, those in previous studies of temperate and boreal aspen, jack pine and black spruce (Woods et al. 1991, Chen et al. 1997). The leaf area decline in the oldest stands investigated here has been seen in many other forest chronosequence studies (Ryan et al. 1997). To facilitate comparison with older studies, the hemisurface leaf area values reported in this study can be re-expressed as projected leaf area (Table 4). We also anticipate comparing the LAI values reported here to both op-

Table 1. Summary of significant main and random effects (α = 0.05) on SLA, by species. Number of samples (n), degrees of freedom (DF, numerator/denominator), F- and P-values are given. An asterisk denotes the interaction of two main effects.

<table>
<thead>
<tr>
<th>Species</th>
<th>Burn year</th>
<th>Effect</th>
<th>n</th>
<th>DF</th>
<th>F-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Populus tremuloides</em></td>
<td>1964, 1989</td>
<td>Canopy position</td>
<td>27</td>
<td>2/14</td>
<td>18.97</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td><em>Betula papyrifera</em></td>
<td>1989</td>
<td>Canopy position</td>
<td>18</td>
<td>2/9</td>
<td>3.70</td>
<td>0.067</td>
</tr>
<tr>
<td><em>Picea mariana</em></td>
<td>All</td>
<td>Year of burn</td>
<td>215</td>
<td>4/77</td>
<td>66.56</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Canopy position</td>
<td>2/56</td>
<td>6.87</td>
<td>18.70</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Foliage age</td>
<td>2/48</td>
<td>61.56</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Soil drainage</td>
<td>0/49</td>
<td>6.62</td>
<td>&lt; 0.012</td>
<td></td>
</tr>
<tr>
<td><em>Picea mariana</em></td>
<td>1870, 1930, 1964</td>
<td>Soil drainage</td>
<td>144</td>
<td>1/84</td>
<td>20.12</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Canopy position</td>
<td>2/34</td>
<td>7.84</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Foliage age</td>
<td>2/84</td>
<td>150.84</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Specific leaf area (SLA; m² kg⁻¹) values for overstory species, by foliage age (1, 2–5 and 5+ years). Species- and foliage age-specific means are presented, although SLA varied with canopy position for most species. Soil drainage was categorized as dry (D) or wet (W). Samples from different stands (different soil drainages or years) were combined if means did not differ significantly (α = 0.05). Values in parentheses represent one standard deviation.

<table>
<thead>
<tr>
<th>Species</th>
<th>Burn year</th>
<th>Soil</th>
<th>Foliage age (years)</th>
<th>1</th>
<th>2–5</th>
<th>5+</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>n</td>
<td>SLA</td>
<td>n</td>
<td>SLA</td>
</tr>
<tr>
<td><em>Populus tremuloides</em></td>
<td>1964, 1989</td>
<td>D</td>
<td>27</td>
<td>17.42 (2.21)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Betula papyrifera</em></td>
<td>1989</td>
<td>D</td>
<td>18</td>
<td>18.48 (2.91)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salix spp.</td>
<td>1989</td>
<td>D, W</td>
<td>18</td>
<td>12.86 (2.34)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Picea mariana</em></td>
<td>1870, 1930, 1964</td>
<td>D</td>
<td>26</td>
<td>6.03 (0.50)</td>
<td>27</td>
<td>4.98 (0.35)</td>
</tr>
<tr>
<td></td>
<td>1870, 1930, 1964</td>
<td>W</td>
<td>20</td>
<td>5.29 (0.82)</td>
<td>27</td>
<td>4.24 (0.48)</td>
</tr>
<tr>
<td></td>
<td>1989</td>
<td>D, W</td>
<td>17</td>
<td>7.02 (0.83)</td>
<td>17</td>
<td>6.19 (0.77)</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>D, W</td>
<td>16</td>
<td>9.78 (1.23)</td>
<td>16</td>
<td>8.93 (1.70)</td>
</tr>
<tr>
<td><em>Pinus banksiana</em></td>
<td>1964</td>
<td>D, W</td>
<td>18</td>
<td>5.64 (0.62)</td>
<td>18</td>
<td>4.21 (0.44)</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>D, W</td>
<td>17</td>
<td>7.60 (2.19)</td>
<td>18</td>
<td>5.83 (1.99)</td>
</tr>
</tbody>
</table>
tically and litterfall-derived estimates in a future study.

High LAI values do not necessarily imply canopy closure in boreal conifer-dominated forests. In this study, complete canopy closure existed only at the 1930 well-drained stand (B. Bond-Lamberty, personal observation), where overstory LAI was 6.8. The D1870 and W1930 stands had overstory LAI values of 5.3 and 3.0, respectively, even though canopy closure was not complete. These high values in open canopies are a function of the strong spatial clumping at the shoot, whorl and tree levels exhibited by conifer stands in general and black spruce in particular (Chen et al. 1997, Kurcharik et al. 1997, 1998a).

Understory LAI showed an inverse relationship with overstory LAI across the chronosequence (Figure 4). At the oldest stands (1870 and 1930 burns), high overstory LAI limited understory growth by restricting light availability beneath the canopy. Understory LAI reached a maximum in the middle-aged stands, 20–35 years after wildfire, where understory LAI often exceeded overstory LAI. Changes in the understory light regime during stand succession can be pronounced and have important implications for understory development and succession (Ross et al. 1986). Understory LAI recovered immediately after wildfire, with the youngest stands (1998–1995) having an understory LAI of 1–2. The spatial heterogeneity in LAI of these young stands is reflected in the high variability of measured leaf area, with a number of stands having a coefficient of variability of ~50% (see vertical error bars in Figure 4).

The variations in SLA seen here with species, canopy position, soil drainage and foliage age have been documented in many species (Kozlowski and Pallardy 1997), but rarely in boreal trees. The black spruce SLA values reported here are similar to those found for Norway spruce in Austria (Hager and Sterba 1985). The correlation in black spruce and jack pine SLA between needles from the same sample tree is to be expected, given the strong influence of microsite soil and light conditions on boreal conifers (Brand 1991, Roy et al. 1999). Perhaps more surprising is that needle canopy position can significantly affect SLA, even in relatively open boreal conifer forests. This implies that care must be exercised when computing leaf area from an average leaf biomass, as few published allometric equations for boreal trees include canopy position parameters (Penner et al. 1997).

Although canopy position had a statistically significant effect on SLA for most species, its overall effect on the calculation of total stand leaf area was small. For most stands in this study, leaf area calculated using canopy position-specific SLA and biomass allometry differed by ±0–3% from leaf area calculated using a mid-canopy SLA mean. The one exception was D1989, where the difference between the two methods was ~6%. The foliage distributions of black spruce, jack pine and aspen tend to peak in the mid-canopy (Landsberg and Gower 1997). An earlier study showed that mid-canopy foliage biomass accounted for 40–50% of total foliage biomass for all three species, with the balance roughly equally divided between the top and bottom canopy sections (Gower, unpub-

<table>
<thead>
<tr>
<th>Species</th>
<th>Current-year foliage</th>
<th>Older foliage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>SLA</td>
</tr>
<tr>
<td>Alnus crispa</td>
<td>2</td>
<td>21.42 (0.96)</td>
</tr>
<tr>
<td>Arctostaphylos uva-ursi</td>
<td>14</td>
<td>9.28 (4.84)</td>
</tr>
<tr>
<td>Betula glandulosa Michx.</td>
<td>5</td>
<td>15.55 (2.27)</td>
</tr>
<tr>
<td>Cornus canadensis L.</td>
<td>7</td>
<td>13.56 (3.85)</td>
</tr>
<tr>
<td>Epilobium angustifolium</td>
<td>17</td>
<td>11.17 (2.28)</td>
</tr>
<tr>
<td>Ledum groenlandicum</td>
<td>11</td>
<td>7.82 (1.85)</td>
</tr>
<tr>
<td>Liliaceae spp.</td>
<td>7</td>
<td>16.53 (7.78)</td>
</tr>
<tr>
<td>Rosaceae spp.</td>
<td>11</td>
<td>15.84 (3.14)</td>
</tr>
</tbody>
</table>

Figure 2. Leaf area index and foliage biomass (Mg ha⁻¹) across the chronosequence and dry and wet stands.
lished data). Thus, although canopy position was significant, the small magnitude of its effect (~0.2 m^2 kg^{-1} in black spruce) and the mid-canopy peak in foliage biomass of these species mean that using mid-canopy average SLA is probably an acceptable compromise in most situations.

The LAI estimates presented here ignore \( \alpha \), the contributions of wood tissue to total PAI, and should not be used as a simple measure of forest floor light availability (Gower et al. 1999). By comparing allometric and optical LAI estimates, Chen et al. (1997) reported \( \alpha \) values between 3\% (young jack pine stand) and 28\% (old jack pine); the D1870 stand studied here had an \( \alpha \) value of 16\% in the previous study. By progressively removing branches while measuring LAI, Smolander and Stenberg (1996) found wood interception comprised 14\% of PAI in a boreal Scots pine stand. Estimates made for \( \alpha \) in a ponderosa pine (\textit{Pinus ponderosa} Dougl. ex Laws.) stand by Law et al. (2001b) ranged from 2 to 31\%, with an average of 15\%. An average woody area index of 15–30\% seems reasonable to assume for these stands, but the issue is complicated because leaf area may preferentially cover up (i.e., be correlated with) branch area (Gower et al. 1999). For this reason, Kucharik et al. (1998b) suggested that branches may be ignored for fully leaved canopy PAI for these conifer-dominated stands.

The significant dry-stand correlation of understory SLA and overstory LAI was largely due to the dominance of green al-

**Table 4.** Comparison of hemisurface (HSLA) and projected leaf area index (PLA; m^2 m^{-2}) for chronosequence, overstory trees only. Values in parentheses are ± 1 standard deviation.

<table>
<thead>
<tr>
<th>Burn year</th>
<th>Well-drained stands</th>
<th>Poorly drained stands</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HSLA    PLA</td>
<td>HSLA    PLA</td>
</tr>
<tr>
<td>1870</td>
<td>5.3 (0.9) 3.5 (0.6)</td>
<td>1.1 (0.4) 0.7 (0.3)</td>
</tr>
<tr>
<td>1930</td>
<td>6.8 (0.7) 4.6 (0.4)</td>
<td>3.0 (0.8) 2.0 (0.6)</td>
</tr>
<tr>
<td>1964</td>
<td>1.8 (0.7) 1.5 (0.6)</td>
<td>0.3 (0.1) 0.3 (0.1)</td>
</tr>
<tr>
<td>1981</td>
<td>0.9 (0.2) 0.8 (0.2)</td>
<td>0.1 (0.1) 0.1 (0.1)</td>
</tr>
<tr>
<td>1989</td>
<td>0.0 (—) 0.0 (—)</td>
<td>0.0 (—) 0.0 (—)</td>
</tr>
<tr>
<td>1995</td>
<td>0.1 (0.2) 0.1 (0.2)</td>
<td>0.0 (—) 0.0 (—)</td>
</tr>
</tbody>
</table>

The significant dry-stand correlation of understory SLA and overstory LAI was largely due to the dominance of green al-

**Figure 4.** Understory versus overstory leaf area index (LAI; m^2 m^{-2}) for the chronosequence stands. Error bars show standard deviations.

**Figure 5.** Mean mass-weighted understory specific leaf area (SLA; m^2 kg^{-1}) versus overstory leaf area index (LAI). Understory SLA was significantly correlated with overstory LAI for the well-drained study sites (\( r = 0.66 \)), but not for the poorly drained sites (\( r = 0.07 \)).
der, with a high SLA in the light-poor understory of the 70-year-old stand (Figure 5). We speculate that the lack of correlation for the wet-stand chronosequence was because overstory LAI was never high enough in any stand to severely limit understory light availability, and thus change understory leaf morphology, or exclude shade-intolerant understory species. This could also have been due to differences in leaf response between deciduous and evergreen species, because the wet-stand understory species (Labrador tea and bearberry) tended to be evergreen, whereas dry-stand species (alder, fireweed, bunchberry (*Cornus canadensis* L.) and *Vaccinium*) were more frequently deciduous. The study design did not allow these effects to be tested easily. Light availability at the forest floor is not well correlated with overstory LAI or SLA under clumped boreal canopies (Smith et al. 1991, Brown and Parker 1994), although theoretical models relating the two have been proposed (Cannell and Grace 1993, Brunner 1998). This poor correlation is due to the heterogeneity of the understory vegetation and overstory canopy structure (Liefers and Stadt 1994, Constabel and Liefers 1996, Chen et al. 1997, Aubin et al. 2000).

In conclusion, leaf area changes with stand age and site conditions are complex, but central to understanding and modeling tree, canopy and landscape processes. Better estimates of SLA and LAI for boreal forests species and chronosequences will improve understanding of the structure and function of this critical biome.

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**References**


Veldhuis, H. 1995. Soils of the tower sites and super site, Northern Study Area (BOREAS), Thompson, Manitoba, Canada. Agriculture and Agri-Food Canada, Centre for Land and Biological Resources Research, Manitoba Land Resource Unit, 61 p.


