

## LARGE ONTOGENETIC DECLINES IN INTRA-CROWN LEAF AREA INDEX IN TWO TEMPERATE DECIDUOUS TREE SPECIES

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**Abstract.** The widespread occurrence of age-related changes in leaf morphology and allocation suggests that the leaf area index of individual trees (intra-crown LAI) may decline late in ontogeny. We used direct, within-canopy measurements to quantify the LAI of canopy trees with exposed crowns of two temperate deciduous species. Intra-crown LAI declined from ~7 to 4 in *Acer saccharum*, and from ~9.5 to 6.5 in *Betula alleghaniensis*, as tree size increased (from 15 to 72 cm diameter at breast height [dbh]). For *A. saccharum*, age (which varied from 30 to 160 years) was a significantly better predictor of LAI decline than dbh. We also modeled the effect of ontogenetic declines in LAI on understory light availability and found that light transmission increases significantly as canopy trees grow and mature. Our results thus suggest that gradual declines in LAI with tree age may play an important and overlooked role in contributing to the heterogeneity of sub-canopy light regimes in mature forests.

**Key words:** *Acer saccharum*; *Betula alleghaniensis*; canopy dynamics; crown structure; gap dynamics; leaf area index; light transmission; tree ontogeny.

### INTRODUCTION

Leaf area index (LAI), the one-sided area of foliage per unit ground ( $\text{m}^2/\text{m}^2$ ), is a key structural feature of forests that is fundamentally important for the exchange of carbon, water, and nutrients, as well as the transmission of light (Campbell and Norman 1989, Fassnacht and Gower 1997, Gower et al. 1999). It is widely recognized that LAI generally declines late in the development of even-aged stands, following an increasing phase that typically culminates with canopy closure (Ryan et al. 1997, King 1999). For example, Ryan et al. (1997) reviewed 13 studies that compared the LAI of stands spanning a broad range of ages, and found that LAI decreased with age in 12 of the 13 studies, by an average of ~40%. Such stand-level declines in LAI are usually attributed to population processes that decrease canopy cover, such as tree mortality and crown abrasion (Long and Smith 1992, Ryan et al. 1997, Meng et al. 2006), but an alternative explanation is that they are driven by ontogenetic changes in the LAI of individual canopy trees. Several studies have shown that the LAI of individual trees does change rapidly in early development (King 1999), and declines have been noted in short-lived early-successional species (Shukla and Ramakrishnan 1984, Osada 2005). However, to our knowledge, no study has examined ontogenetic changes in the LAI of canopy-dominant trees, or attempted to dis-

gregate stand-level LAI declines into population- and individual-level components.

It is well documented that specific leaf area (SLA) decreases with tree size, and that this pattern continues well after trees reach the canopy (Thomas and Winner 2002, Kenzo et al. 2006, Ryan et al. 2006). Decreasing SLA should lead to a decline in the LAI of canopy trees, unless compensated for by increased biomass allocation to leaves, most likely via production of a greater number of leaves and branches. However, the production of leaves and branches may also decline because the allocation of carbon and nitrogen to reproduction generally increases throughout ontogeny at the expense of growth (Gross 1972, Thomas 1996, Kelly and Sork 2002, Leal and Thomas 2003), as does allocation to chemical and structural defenses (Loehle 1988, Jackson et al. 1999, Boege and Marquis 2005). Indeed, the onset of reproduction has been shown to coincide with observed declines in area of individual leaves in some species (Thomas and Ickes 1995).

Trees also experience a continuous loss of branches throughout ontogeny due to damage, disease, and senescence (Liu et al. 2002, Lehtonen et al. 2004). Thus, if canopy trees fail to replace the branches that die, LAI will decline as these losses accumulate, even if the total leaf area is maintained by the growth of apical meristems around the circumference of the crown (Begin and Filion 1999). Many tree species replace lost branches through release and growth of epicormic shoots (Remphrey and Davidson 1992, Ishii and Ford 2001, Ishii et al. 2002), but it is not certain whether most species can use this strategy to maintain LAI indefinitely.

Given the strong influence that LAI has on the transmission of light through crowns, ontogenetic

Manuscript received 29 March 2007; revised 10 July 2007; accepted 19 July 2007. Corresponding Editor: F. C. Meinzer.

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declines in LAI could have a profound effect on sub-canopy light regimes. In particular, such declines may be an important source of heterogeneity in light availability in mature stands. However, previous studies have primarily focused on one source of heterogeneity in light availability, namely canopy gaps, so the effect of ontogenetic declines in LAI remains unexamined.

In this study, we used direct, in-canopy measurements to quantify the LAI of individual trees (intra-crown LAI) belonging to two species (*Acer saccharum* Marsh. and *Betula alleghaniensis* L.) and spanning a wide range of sizes (15–72 cm diameter at breast height) and ages (30–160 years). The study was designed to address the following questions: (1) Does LAI decrease as the size of canopy trees increases? (2) Does LAI decrease with age, independently of increases in size? (3) Does the magnitude of LAI decline differ between species? (4) In addition, we used a model of light transmission and reflection to ask, how does the observed variation in LAI affect the transmission of light through tree crowns?

## METHODS

### *Selection of sites and trees*

This study was conducted in Haliburton Forest and Wildlife Reserve, near Haliburton, Ontario, Canada (45°15' N, 78°34' W). Situated in the Great Lakes–St. Lawrence forest region, the upland hardwood forests in Haliburton are dominated by *Acer saccharum*, *Fagus grandifolia* Ehrh., *Tsuga canadensis* L., and *Betula alleghaniensis*. The forest has been managed under selection silviculture for the past 40 years, and was selectively harvested for *B. alleghaniensis* and *Pinus strobus* L. prior to that time. Thus, most of the upland stands are uneven-aged, with stand basal areas ranging from 15 to 30 m<sup>2</sup>/ha, and average canopy heights ranging from 20 to 25 m.

Two sampling sites were selected with a good representation of large, old trees on relatively even topography to enable canopy access. One of these had been disturbed by a severe windstorm in 1995, allowing us to sample smaller canopy trees that nevertheless had full crown exposure. Neither site had been harvested in the previous 30 years. To select suitable trees for sampling, we worked outward from the center of each site, locating *A. saccharum* and *B. alleghaniensis* trees that were within 50 m of access trails. As sampling proceeded, the sample size was increased by adding a roughly equal number of small (<35 cm), medium (35–55 cm), and large (>55 cm) diameter trees, ensuring spatial interspersed and an equal representation of size classes. The total sample size was 33 *A. saccharum* and 16 *B. alleghaniensis* trees.

### *Estimation of leaf area index*

We used the line intercept sampling method following Thomas and Winner (2000) to measure intra-crown LAI for individuals of both species. In this method, LAI is

measured by dropping a weighted line through the canopy and counting the number of contacts with leaves along the vertical line transect. If all leaves contacted are in a horizontal position, the LAI is equal to the number of foliage contacts. However, because leaves are rarely horizontal, the number of foliage contacts must be divided by an extinction coefficient that accounts for the angular distribution of leaves (Campbell and Norman 1989, Thomas and Winner 2000):

$$\text{LAI} = \frac{N}{K} \quad (1)$$

where  $N$  is the number of contacts and  $K$  is an extinction coefficient that is calculated from measured leaf angles (see *Methods: Leaf angle measurements*).

### *Line intercept sampling of foliage*

Line intercept sampling was conducted between 1 July and 31 August 2005. To access the canopy, we used a 24-m working height mobile canopy lift (Scanlift SL240, Kesla Oyj, 2 Metsolantie, Kesälahti, Finland), equipped with a line-drop mechanism consisting of a modified fishing downrigger (Cannon Uni-troll downrigger, Cannon Products, Mankato, Minnesota, USA), with a telescoping aluminum pole (9 m) that functioned as a boom. A high-visibility, thin line (<2 mm) with a 0.34-kg weight was used to minimize bias due to line thickness relative to the size of the foliar elements (Warren-Wilson 1963). The downrigger was equipped with a gauge permitting estimation of foliage contact height to ±0.30 m.

For each sampled tree the lift basket was maneuvered into position above the crown, the weighted line was dropped through the crown of the tree to the ground below, and the position of the line drop relative to the stem was recorded as a distance and a compass bearing. The line was then slowly raised back up through the canopy and the number and height of foliage contacts along the vertical transect ( $N$ ) recorded with the assistance of observers equipped with binoculars positioned beneath the tree crown and in the personnel basket. Contacts were only recorded once line sway had ceased, and when there was minimal foliage movement. To ensure that these conditions were met, sampling was only performed in the morning and on still days (see Plate 1).

Ten line drops were conducted in each tree crown. This number was chosen based on a preliminary sampling effort in which we found that the mean number of contacts ( $\bar{N}$ ) changed by <5% as the number increased from 10 to 30 line drops. The locations of the 10 line drops within each crown were chosen to maximize the dispersion of sampling points throughout the entire crown, including points within 1 m of the crown's edge. While logistical considerations prohibited a strict randomization of transect positions, analyses of the spatial dispersion of points indicated no bias relative to direction or proximity to the bole (data not shown).

### Leaf angle measurements

We expected leaf angles to vary vertically within crowns, so we visually divided each crown into three equal strata (upper, middle, and lower), and harvested one branch from each stratum of each sampled tree to measure leaf angles. Prior to cutting the branch, we measured the angle of the branch itself, permitting reorientation on the ground for leaf angle measurements. We chose 100 representative leaves from each branch and used a clinometer to measure the angle to the nearest 1° (Suunto MC-1, Suunto, Espoo, Finland). We did not collect branches from three *A. saccharum* trees, and for these individuals we substituted average values for leaf angles collected from other sampled *A. saccharum* trees.

### Extinction coefficients

Leaf angle measurements were used to estimate an empirical extinction coefficient ( $K$ ) for each portion of each crown.  $K$  is defined as the ratio of the total projected area of leaves (in their original orientation) on a horizontal plane to the total projected area of the leaves after being rotated to a horizontal position (Warren-Wilson 1965, Anderson 1966, Campbell and Norman 1989):

$$K_i = \frac{\sum_{j=1}^n \cos\theta}{n} \quad (2)$$

where  $\theta$  is the inclination angle of a leaf relative to horizontal, and  $n$  is the number of leaves in the  $i$ th stratum of the crown (upper, middle, and lower), and  $K_i$  is the corresponding extinction coefficient.

For each stratum, we then calculated the mean number of contacts per drop ( $N_i$ ), and divided by the appropriate value of  $K_i$ , to estimate the mean LAI for that portion of the crown:

$$\text{LAI}_i = \frac{N_i}{K_i} \quad (3)$$

Finally, the LAI of the whole tree crown was calculated as

$$\text{LAI} = \sum_{i=1}^3 \text{LAI}_i \quad (4)$$

### Crown measurements

LAI can decrease two different ways: crown depth can decrease or the density of leaves within the crown can decrease. Thus, we took additional measurements to distinguish between these two possibilities. We used a laser range finder (Impulse Laser, Laser Technology, Centennial, Colorado, USA) to measure both the distance from the bole to the edge of the crown (the drip line) in the four cardinal directions and crown depth. Crown area was estimated by calculating the area

of an ellipse, using the north–south and east–west crown extents as the two axes. These axes and the crown depth were then used to calculate the volume of an ellipsoid as an estimate of crown volume. Total leaf area per tree ( $\text{m}^2$ ) was estimated by multiplying LAI ( $\text{m}^2/\text{m}^2$ ) by crown area ( $\text{m}^2$ ); and leaf area density ( $\text{m}^2/\text{m}^3$ ) was estimated by dividing total leaf area ( $\text{m}^2$ ) by crown volume ( $\text{m}^3$ ).

### Tree age and size

The diameter (dbh) of each tree was measured at 1.3 m above the ground. We attempted to determine tree age by coring each tree to its pith and counting the number of annual rings. However, because larger trees were often hollow, or had severe heart rot, we could only obtain complete cores for a subset of the *A. saccharum* trees. Sampled cores were scanned (Epson Expression 1680, Epson Canada, Toronto, Ontario, Canada), and the number of rings counted at high magnification using a tree-ring analysis program (Windendro version 2005a, Regent Instruments, Quebec, Canada).

### Local basal area

We sampled trees with fully exposed crowns to minimize the variation in LAI due to local competition, but there was still considerable variation in the number and size of neighboring trees. Thus, we used a wedge prism (BAF 2) to measure the basal area in the vicinity of the sampled trees (Philip 1994). Local basal area ranged from 10 to 32  $\text{m}^2/\text{ha}$ , but preliminary analyses revealed that it did not explain any of the variation in LAI; therefore, it was not included in any of the subsequent analyses.

### Estimation of light transmission

We used the SAIL model (Verhoef 1984) to estimate the percentage of light transmitted through tree crowns over the range of LAI values observed (4–9). The SAIL model (WinSAIL, USDA-ARS, Hydrology and Remote Sensing Laboratory, Beltsville, Maryland, USA; Verhoef 1984) predicts daily percentage of photosynthetically active radiation (PAR, 400–700 nm) transmitted through a uniform canopy based on parameters that describe canopy structure and the optical properties of leaves. Model parameters include LAI, latitude, the proportion of direct and diffuse radiation, the proportion of leaves in each of nine leaf angle classes, and the percentage of PAR transmitted and reflected in each of 31 wavebands (see Appendix A for detailed description).

### Statistical analysis

We used SAS version 8.2 (SAS Institute, Cary, North Carolina, USA) to conduct a series of model I analyses, including ANOVA, ANCOVA, and regression. We opted against conducting model II analyses because, in most cases, the error in the independent variables (e.g., dbh) was deemed to be much smaller than the error in the dependent variables (e.g., LAI). ANCOVA was used

TABLE 1. Summary of the regression analyses relating crown metrics to the dbh of canopy trees of *Acer saccharum* and *Betula alleghaniensis*.

Variable	<i>Acer saccharum</i>				<i>Betula alleghaniensis</i>			
	Slope ± SE	Intercept ± SE	R <sup>2</sup>	P	Slope ± SE	Intercept ± SE	R <sup>2</sup>	P
Crown depth (m)	0.06 ± 0.02	8.37 ± 0.86	0.27	0.0019	0.08 ± 0.03	7.88 ± 1.39	0.29	0.0314
Crown area (m <sup>2</sup> )	0.68 ± 0.16	11.07 ± 7.06	0.39	<0.0001	1.73 ± 0.37	-14.58 ± 15.96	0.60	0.0004
Crown volume (m <sup>3</sup> )	6.89 ± 1.36	15.47 ± 61.79	0.45	<0.0001	15.01 ± 3.76	-166.42 ± 160.33	0.53	0.0013
Total leaf area (m <sup>2</sup> )	1.51 ± 1.05	151.70 ± 47.76	0.06	0.16	8.39 ± 2.73	52.18 ± 116.63	0.40	0.0083
Leaf area density (m <sup>2</sup> /m <sup>3</sup> )	-0.009 ± 0.001	1.36 ± 0.88	0.60	<0.0001	-0.013 ± 0.003	1.91 ± 0.19	0.59	0.0005
Foliage contacts	-0.05 ± 0.01	6.75 ± 0.36	0.58	<0.0001	-0.04 ± 0.01	6.97 ± 0.52	0.48	0.0028
Leaf area index (m <sup>2</sup> /m <sup>2</sup> )	-0.06 ± 0.01	8.29 ± 0.46	0.56	<0.0001	-0.07 ± 0.02	10.46 ± 0.92	0.41	0.0077

to determine whether  $\bar{N}$ , LAI, or LAD differed between the two species, and whether they declined with dbh. Analysis of covariance was also used to determine how leaf angles varied with crown position (upper, middle, lower), tree species, and dbh. Covariation between dbh and leaf angle was nonsignificant for both species, so we excluded it from our final analysis of leaf angles. Replicates for this analysis consisted of the average of the 100 measurements taken at each crown position in each tree.

For *A. saccharum* trees with complete cores, we fit regression models that included dbh, tree height, and age as predictors of LAI, as well as reduced models that only included two or one of these variables as a predictor. The fit of the full model was then compared to the reduced models using Akaike's Information Criterion (AIC) to determine whether including two or three variables provided a better fit to the data than any single variable alone, and the model with the lowest AIC was deemed to be the most parsimonious (Burnham and Anderson 1998).

RESULTS

*Crown allometry and leaf angle distributions*

As expected, the depth, area, and volume of tree crowns increased significantly with stem diameter (Table 1). Increases in projected crown area were greater than increases in crown depth, indicating that the increase in crown volume is primarily caused by increasing crown area (Fig. 1). Total leaf area in *B. alleghaniensis* increased significantly with dbh as crown area and volume increased, whereas this pattern was not significant for *A. saccharum* (Table 1).

The mean leaf angle increased from the bottom to the top of the crowns, and the mean leaf angle was significantly greater for *B. alleghaniensis* than for *A. saccharum* (ANCOVA,  $F_{5,139} = 24.08$ ,  $R^2 = 0.47$ ,  $P < 0.0001$ ; Table 2). There was no significant trend of leaf angle with tree dbh in either species (ANCOVA,  $P > 0.05$ ).

*Size- and age-related variation in  $\bar{N}$ , LAI, and LAD*

For both tree species, there was a strong relationship between the number of foliage contacts ( $\bar{N}$ ) and dbh (ANCOVA,  $F_{2,48} = 31.39$ ,  $R^2 = 0.58$ ,  $P < 0.0001$ ; Fig.

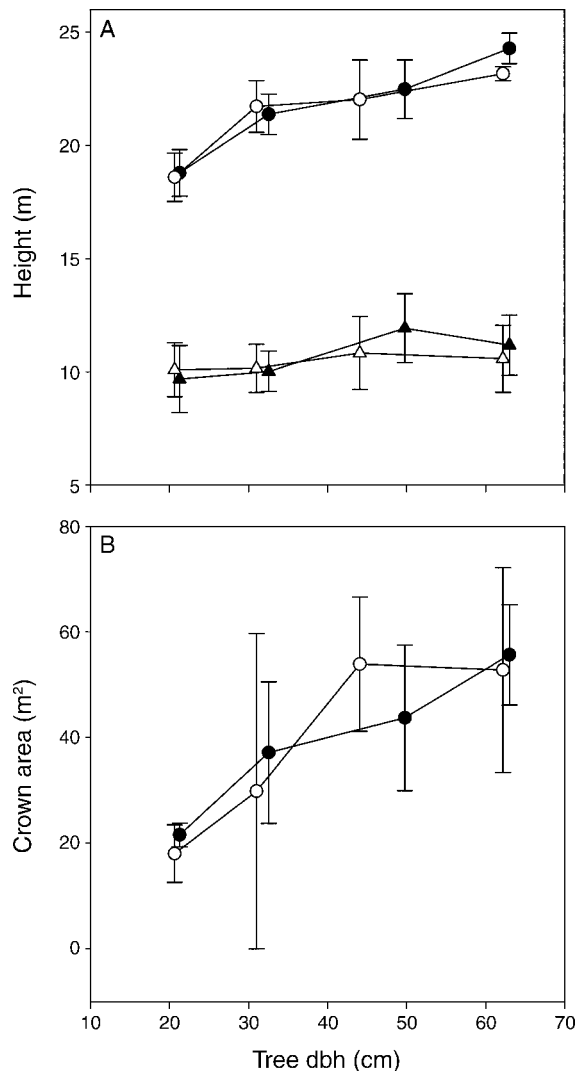


FIG. 1. (A) Tree height (circles) and height to live crown (triangles), and (B) crown area as a function of diameter at breast height (dbh) for *Acer saccharum* (solid) and *Betula alleghaniensis* (open). Points are mean values calculated from 25% of the data.

Note: crown depth is calculated as the difference between tree height and the height to crown.



PLATE 1. (Left) View from above canopy showing boom and line, and (right) detail of line and foliage of *Betula alleghaniensis*. Photo credits: C. A. Nock.

2A, Table 1). In *A. saccharum*,  $\bar{N}$  declined linearly by ~40% as diameter increased from 15 to 72 cm dbh (Fig. 2A). The same pattern was evident for *B. alleghaniensis*, although the decline was less pronounced (Fig. 2A). On average,  $\bar{N}$  was greater for *B. alleghaniensis* than for *A. saccharum* at a given dbh (ANCOVA, species effect,  $F_{2,48} = 4.37$ ,  $P = 0.0421$ ; Fig. 2A).

The results for leaf area index were similar to those for  $\bar{N}$ : LAI of both species decreased by ~40% as dbh increased (ANCOVA,  $R^2 = 0.65$ ,  $F_{2,48} = 43.48$ ,  $P < 0.0001$ , Fig. 2B, Table 1). Values of LAI were higher on average for *B. alleghaniensis* than for *A. saccharum* (ANCOVA, species effect,  $F_{1,48} = 34.84$ ,  $P < 0.0001$ ; Fig. 2B), although the difference between species was smaller than the difference between small and large trees.

The decrease in LAI corresponded to a decrease in leaf area density (LAD), which decreased by ~50% as dbh increased (ANCOVA,  $R^2 = 0.65$ ,  $F_{2,48} = 43.26$ ,  $P < 0.0001$ ; Fig. 2C, Table 1).

Patterns with age were similar to those for dbh:  $\bar{N}$ , LAI, and LAD all declined significantly with age in *A. saccharum* (Fig. 2D–F). The magnitude of decline with respect to age was similar to that observed with respect to size (compare Fig. 2D–F to Fig. 2A–C). However, the AIC comparisons revealed that regression models including age as the sole predictor of LAI were more parsimonious than models including any combination of dbh and tree height (Appendix B).

#### Predicted light transmission

For *A. saccharum*, the percentage of light transmission estimated using the SAIL model increased exponentially with size, from <1% at 20 cm dbh to 4% at 70 cm dbh (Fig. 3). Estimated transmission also increased

exponentially with size for *B. alleghaniensis*, but did not exceed 2% at 70 cm dbh (Fig. 3).

#### DISCUSSION

Our results indicate that intra-crown LAI declines substantially as trees mature, and that this decline is of similar magnitude in the two species studied. In the case of *A. saccharum*, the observed decline in LAI was most parsimoniously explained by tree age rather than tree size. Also, in *A. saccharum*, estimates of light transmission for large/old trees suggest that large declines in LAI result in significant increases in through crown light transmission. These results have important implications for current understanding of age-related patterns of tree growth and development, and suggest that LAI decline may represent an important and previously undocumented source of heterogeneity in light availability, and potentially forest community dynamics.

Prior studies have shown that the LAI of even-aged stands undergoes a gradual and persistent decline after

TABLE 2. Mean leaf angle by crown position for *Acer saccharum* and *Betula alleghaniensis*.

Crown position	<i>A. saccharum</i> leaf angle (°)			<i>B. alleghaniensis</i> leaf angle (°)		
	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE
Upper	31	33 <sup>d</sup>	0.4	16	47 <sup>c</sup>	0.6
Middle	31	30 <sup>bd</sup>	0.3	16	38 <sup>a</sup>	0.5
Lower	30	28 <sup>b</sup>	0.3	16	33 <sup>ad</sup>	0.5
All	92	30	0.2	48	40	0.3

Note: Means with the same letter are not significantly different at the alpha = 0.05 level (ANCOVA,  $F_{5,139} = 24.08$ ,  $R^2 = 0.47$ ,  $P < 0.0001$ ); *n* is the number of branches used to calculate the mean branch angle (100 leaves were measured on each branch).

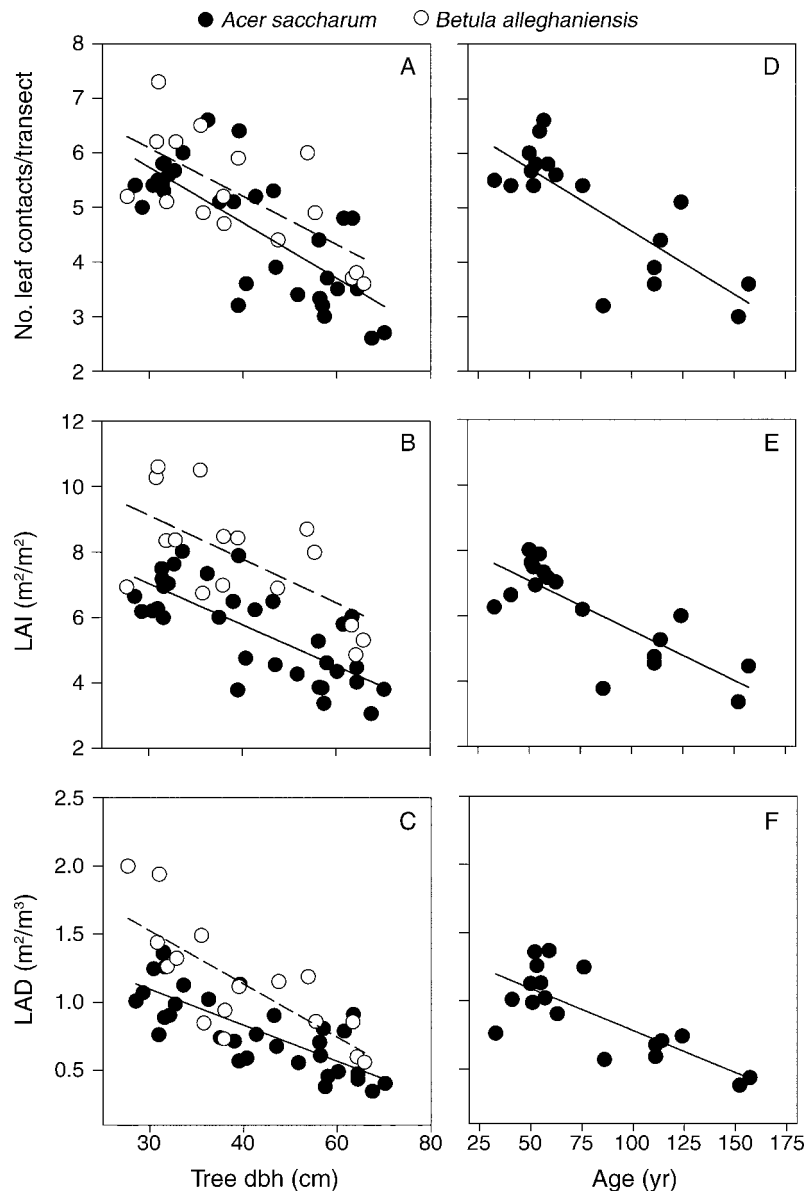


FIG. 2. Relationships between dbh and (A) mean number of leaf contacts ( $\bar{N}$ ), (B) leaf area index (LAI), and (C) leaf area density (LAD) for *Acer saccharum* and *Betula alleghaniensis*. Panels D–F show the relationships between the same independent variables and tree age for the subset of *Acer saccharum* trees that were aged.

canopy closure (Ryan et al. 1997). Two prior studies have also noted that the intra-crown LAI of small pioneer tree species begins to decrease after a peak early in ontogeny (Shukla and Ramakrishnan 1984, Osada 2005). In contrast, an allometric model developed by King (1999) predicts that intra-crown LAI should increase in the early stages of ontogeny because support costs increase with crown area, but this model applies only to juvenile trees. Thus, there are no model predictions, nor prior observations, which indicate how the intra-crown LAI of canopy-dominant trees changes as they mature.

Here we found that intra-crown LAI decreased by 40% (Fig. 2) even as projected crown area continued to increase (Fig. 1). The pattern was similar in both *A. saccharum* and *B. alleghaniensis*, suggesting that ontogenetic declines in LAI may be a common phenomenon that occurs in many other tree species. The magnitude of the ontogenetic declines in LAI observed, ~40%, is similar to that found in stand-level chronosequence studies (Ryan et al. 1997), suggesting that ontogenetic effects at the individual tree level may be a primary determinant of the widely observed stand-level declines in LAI.

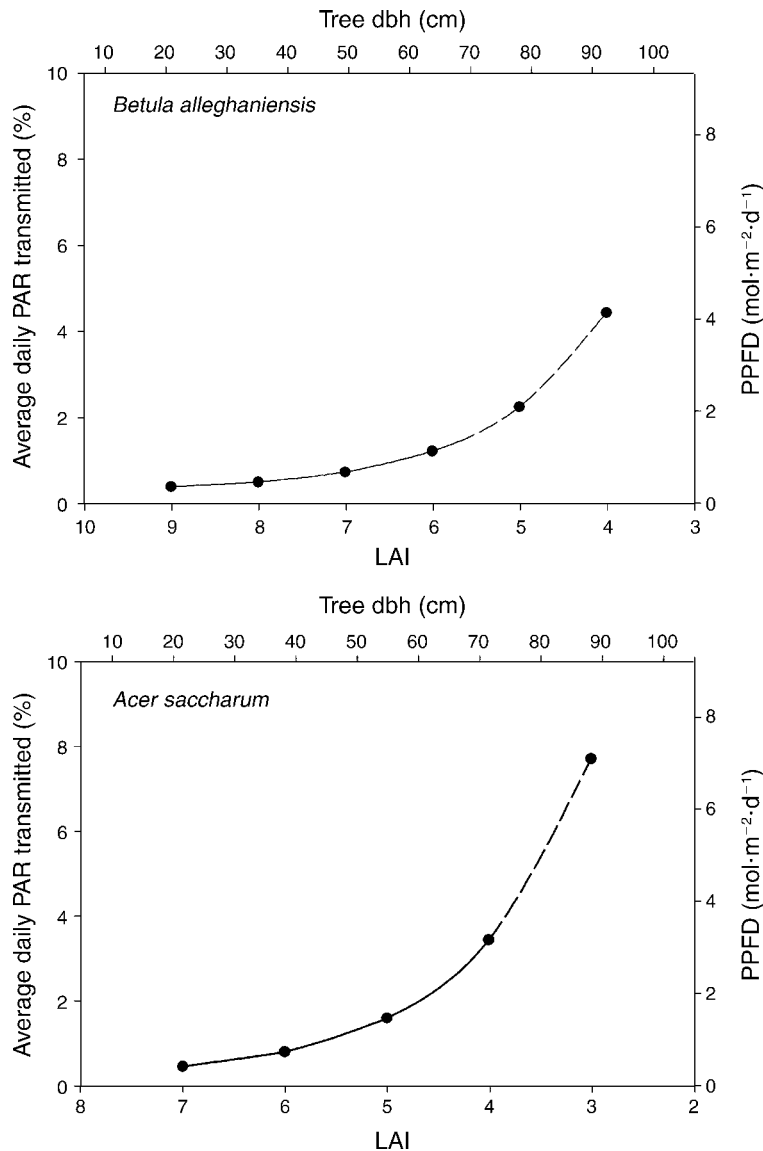


FIG. 3. Predicted light transmission as a function of LAI and dbh for *Acer saccharum* and *Betula alleghaniensis*. The scaling of dbh vs. LAI is based on the regressions presented in Fig. 2. Dashed lines indicate extrapolation of light transmission for large trees present in old-growth stands that were inaccessible and hence not measured, assuming a continued linear decline in LAI. PAR is photosynthetically active radiation; PPFD is photosynthetic photon flux density.

Our intra-crown LAI estimates broadly overlap, but slightly exceed, stand-level estimates obtained using other methods in comparable forests. For example, stand-level LAI estimates of ~6–8 have been reported for other *A. saccharum*-dominated forests (Ellsworth and Reich 1993, Fassnacht and Gower 1997), compared to values as high as 10 for some of the smaller trees in our sample. There are three reasons that individual intra-crown LAI values may be substantially higher than stand-level LAI. First, trees may vary widely in LAI, some well above the stand-level mean, and some below. Second, intra-crown estimates do not include canopy gaps or the spaces between crowns of neigh-

boring trees. Intra-crown LAI may be converted to stand-level LAI (of canopy trees) given the fraction of ground covered by tree crowns: for example, if the fraction of ground covered by tree crowns is 80%, and the intra-crown LAI of all tree crowns is 10, then the stand-level LAI would be eight. This simple calculation shows that even our highest estimates are in approximate agreement with prior stand-level estimates. Finally, many of the smaller trees were sampled in a stand damaged in the 1995 windstorm: this storm may have increased the lateral illumination of the smaller trees crowns, resulting in increased surface area and increased LAI.

*Potential causes of LAI declines*

Our results raise two questions concerning the proximate and ultimate causes of LAI decline: (1) What are the changes in canopy structure that result in the observed decline? (2) Is declining LAI an unavoidable consequence of growing taller (e.g., hydraulic limitation) and older (e.g., senescence), or is it part of an adaptive allocation strategy that favors reproduction, defense, and crown expansion over the maintenance of LAI? We cannot answer these questions definitively, but speculate here on the basis of preliminary observations and previously published studies.

With regard to proximate causes, three types of changes in crown structure could result in declining LAI: (1) a decrease the area of individual leaves, (2) a decrease in the number of leaves per shoot or branch, and (3) a decrease in the density of live branches. Declines in the area of individual leaves late in tree ontogeny have been documented in many tropical tree species (Thomas and Ickes 1995), and such declines are often associated with ramification of branches (Alvarez-Buylla and Martinez-Ramos 1992, Yamada et al. 2000). In addition, previous studies (in this case of long-lived temperate conifers) have shown that as trees age the density of live branches (per meter of trunk) decreases, and the density of dead branches increases (Ishii and Wilson 2001). It is likely that branches that die are not all replaced by new branches, and that LAI and leaf area density decline due to both decreased leaf size and reduced branch density. Preliminary data on *A. saccharum* (J. Caspersen, unpublished data) suggest that changes in leaf size, numbers of leaves per shoot, and branch density all contribute to the observed decline in LAI.

As for ultimate causes, our AIC comparisons reveal that LAI does not vary with tree height independently of tree age, suggesting that the decline is not caused by increased hydraulic resistance associated with increased height (Koch et al. 2004). Whether declining LAI is an unavoidable consequence of aging is more difficult to assess. Our AIC comparison revealed the most parsimonious model to be the one that included age as the sole predictor of LAI, demonstrating that LAI does vary with tree age independently of tree size. Thus, declining LAI may be the result of senescence, but it could also be the result of adaptive allocation strategy that favors reproduction, defense, and crown expansion over the maintenance of LAI. Previous studies have shown that trees increase allocation to reproduction and defense as they grow larger and older (Loehle 1988, Thomas 1996), and our preliminary observations confirm that the production of samaras increases substantially with the size of *A. saccharum* trees (J. Caspersen, unpublished data). Thus, it is reasonable to believe that trees forgo the option of replacing dead branches in order to maximize longevity and reproductive output. At the same time, our results show that trees do not forgo the opportunity to increase total leaf area by expanding their crowns (Table 1, Fig. 1B). This suggests that

expanding the circumference of the crown yields greater photosynthetic returns than maintaining LAI within the crown, or that it is a better long-term competitive strategy.

*Implications for sub-canopy light regimes*

Whatever the causes may be, ontogenetic declines of the magnitude observed clearly provide an important potential source of heterogeneity in light availability in mature northern hardwood stands. Our results for *A. saccharum* (Fig. 3) show that light transmission varies from <1% for the smallest trees (20 cm dbh) to 4% for the largest trees (72 cm dbh). These estimates broadly overlap, but are somewhat lower than stand-level light transmission estimates obtained using other methods in similar forests. For example, Canham et al. (1994) observed that 2.1% of PAR is transmitted through canopies dominated by *A. saccharum* trees with a mean dbh of 31.5, while our estimate for a 31-cm dbh tree is <1%. As with LAI, this discrepancy exists because our transmission estimates do not include inter-crown spaces or gaps, and so are expected to be lower than PAR transmission at the stand level.

It is widely recognized that heterogeneity in light availability plays an important role in maintaining tree species diversity (Rees et al. 2001). However, research on the interplay between stand dynamics and light dynamics has largely focused on a single source of heterogeneity, namely canopy gaps. As a result, the temporal dynamics of light below the canopy are often characterized as follows: light availability first increases abruptly when a tree falls, then gradually decreases until the next disturbance (Valverde and Silvertown 1997). Indeed, this conceptual model of temporal light dynamics underlies almost all the simulation models that are used to study secondary succession and the maintenance of tree species diversity in forests.

We believe that this conceptual model does not adequately represent the long-term dynamics of sub-canopy light because it neglects another important source of heterogeneity, namely ontogenetic declines in LAI. If ontogenetic declines similar to those described here are common, sub-canopy light availability may only decrease until the horizontal dimensions of the gap are filled, and then gradually increase until the next exogenous disturbance. In the absence of an exogenous disturbance, our results suggest that light may simply continue to increase until the tree eventually dies standing, resulting in a modest and not so sudden increase in light. Of course, the dynamics of light on the forest floor may follow a different pattern if sub-canopy trees or saplings utilize most of the light transmitted by canopy trees.

Even neglecting additional light transmission associated with crown shyness and other canopy gaps, large *A. saccharum* trees were predicted to transmit more light than is required for mid-tolerant species to maintain a positive carbon balance. For example, we estimated the

largest *A. saccharum* tree in our sample (72 cm dbh) transmits  $3.7 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . This is considerably higher than the whole-plant light compensation point for saplings of two of the most common mid-tolerant tree species present at the site, *Fraxinus americana* L. ( $2.3 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) and *Acer rubrum* L. ( $2.6 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ), and even slightly higher than the whole-plant light compensation point of the intolerant species *Betula papyrifera* Marsh. ( $3.1 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) (Baltzer and Thomas 2007). Furthermore, the spaces between large tree crowns would increase the stand-level transmission well above  $4 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . Thus, the observed decline in LAI may be of sufficient magnitude to allow the mid-tolerant species to persist under continuous canopy cover in mature stands, and may thereby help to maintain species diversity in mature forests. However, it is important to note ontogenetic increases in non-photosynthetic biomass (e.g., branches) may partially offset decreases in LAI by intercepting more light as trees grow older, and that the regeneration of mid-tolerant saplings may be retarded by sub-canopy trees of more shade-tolerant species if they utilize most of the light transmitted by canopy trees. Direct observations of patterns of community composition and tree recruitment beneath crowns of trees of varying size and age are needed to assess the possible influence of age-related declines in intra-crown LAI on forest community dynamics.

#### ACKNOWLEDGMENTS

We thank Haliburton Forest and Wildlife Reserve for their support of our research, Trevor Jones for his lift training, and Drew Purves, Julian Norghauer, and Tomasz Gradowski for comments on the manuscript, as well as Ashley Wilson, Agnieszka Sztaba, and Bess Callard for their contributions in the field. This research was supported by the National Science and Engineering Research Council of Canada, the Canadian Foundation for Innovation, and the Sustainable Forest Management Network.

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#### APPENDIX A

Parameterization of the SAIL light model (*Ecological Archives* E089-040-A1).

#### APPENDIX B

Summary of regression models that included dbh, age, and tree height as predictors of LAI for *Acer saccharum*, and reduced models that only included two or one of these variables as a predictor (*Ecological Archives* E089-040-A2).