Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production


Abstract

The seasonal phenology of the leaf area index (LAI) is a major determinant of net ecosystem production in deciduous forest ecosystems. This study describes seasonal and inter-annual differences in LAI in a boreal aspen-hazelnut forest in central Saskatchewan, Canada, between 1994 and 2003, and relates the differences in LAI to annual net ecosystem production (F_NEP). A robust method is developed to fill gaps in the annual LAI cycle from systematic but sparse measurements using associated radiation and temperature indices. The ratio of the photosynthetically-active radiation reflectance to the shortwave reflectance is shown to have a particularly distinct LAI signature.

Optical estimates of the fully-leafed LAI agreed well with measurements from autumn litterfall and showed moderate inter-annual variability for the trembling aspen overstory (mean ± S.D. of 2.44 ± 0.30) and the hazelnut understory (1.98 ± 0.44). Two features of the annual LAI cycle differed among years—the timing of leaf emergence in spring, which varied by up to four weeks, and the fully-leafed value for LAI, which varied between 3.66 and 5.22. The timing of leaf senescence in autumn was nearly constant among years. The seasonal cycles of F_NEP and LAI were tightly coupled and the correspondence between their respective inter-annual differences was remarkable, particularly during leaf emergence in spring. Annual F_NEP was positively correlated with the canopy duration and the annual maximum LAI, with increases in annual F_NEP of 6.9 g C m\(^{-2}\) for each additional day in full leaf and 83 g C m\(^{-2}\) for each additional unit of LAI.

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Keywords: Leaf area index; Net ecosystem production; Boreal deciduous forest; Inter-annual variability

1. Introduction

The seasonal cycle of leaf area index (LAI) in deciduous forest ecosystems is dynamic and has a major influence on the global carbon, water and radiation balances. The timing of leaf emergence and senescence are major determinants of net ecosystem production (F_NEP) in boreal and temperate deciduous forests (Goulden et al., 1996; Black et al., 2000; Barr et al., 2002; Saigusa et al., 2003). Leaf emergence and senescence also affect climate at the regional scale.

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through their impact on the partitioning of available energy between sensible and latent heat (Schwarz, 1992; Margolis and Ryan, 1997; Hogg et al., 2000). Because of its influence on the exchanges of heat and mass between deciduous forest ecosystems and the atmosphere, the annual LAI cycle must be properly characterized in land surface process and ecosystem carbon budget models (Goetz et al., 1999; Liu et al., 1999; White et al., 1999).

Multi-year tower flux studies are producing new insights into the functioning of forest ecosystems and their response to climate variability and change. These studies show that the primary climatic controls on the carbon and water balances of deciduous forest ecosystems are often mediated through leaf phenology (Goulden et al., 1996; Black et al., 2000; Wilson and Baldocchi, 2000). In temperate and boreal deciduous forests, leaf phenology controls the length of the carbon uptake period which in turn is strongly correlated with annual $F_{\text{NEP}}$ (Baldocchi et al., 2001; Carrara et al., 2003; White and Nemani, 2003). In boreal deciduous forests, annual $F_{\text{NEP}}$ is strongly correlated with spring temperature, with warm springs hastening leaf emergence and increasing $F_{\text{NEP}}$ (Black et al., 2000). Because the seasonal $F_{\text{NEP}}$ cycle peaks shortly after leaf emergence, early leaf emergence has a greater impact on annual $F_{\text{NEP}}$ than late leaf senescence (Chen et al., 1999). Inter-annual climatic variability also affects $F_{\text{NEP}}$ via annual maximum LAI, with diminished LAI in years following drought or other stresses (Hogg et al., 2003). While several studies have shown that inter-annual (Goulden et al., 1996; Black et al., 2000) and inter-site (Baldocchi et al., 2001) differences in growing-season length affect $F_{\text{NEP}}$, few have analyzed in detail the dependence of the surface carbon, water and radiation balances on the seasonal LAI cycle (Black et al., 2000). The data from flux-tower studies, many of which began in the 1990s, are just now becoming long enough to allow analysis of the complex, interacting climatic and biophysical controls on $F_{\text{NEP}}$.

This study analyzes nine years of measurements from the Old Aspen tower-flux site in central Saskatchewan, Canada. The Old Aspen site was established in 1993 as a part of the Boreal Ecosystem–Atmosphere Study (BOREAS, Sellers et al., 1997). It has continued since 1997 as part of the Boreal Ecosystem Research and Monitoring Sites (BERMS) program (http://berms.ccrp.ec.gc.ca) and since 2002 as part of the Fluxnet-Canada Research Network (http://www.fluxnet-canada.ca/). A primary goal of the BERMS and Fluxnet-Canada programs is to measure seasonal and inter-annual variability in the carbon, water and energy balances of Canadian forests and to characterize the critical climatic controls. The Old Aspen site is located at the southern edge of the Canadian boreal forest, near the aspen parkland, a transitional zone between the prairie grass- and cropland to the south and the boreal forest to the north (Bird, 1961). The site’s dominant tree species, trembling aspen, is the most extensive deciduous species in the western Canadian boreal forest (Peterson and Peterson, 1992). Recent observations of aspen dieback in the aspen parkland link tree mortality to the dual stresses of insect defoliation and drought and suggest a decline in site productivity under a warmer and drier climate (Hogg et al., 2003).

The primary objectives of this study are to characterize the seasonal and inter-annual differences in LAI in a boreal aspen-hazelnut forest and to relate these to differences in $F_{\text{NEP}}$. A secondary objective is to develop a method to construct the annual LAI cycle from systematic but sparse measurements, based on associated radiation and temperature indices.

2. Measurements and data

2.1. Site description

The Old Aspen site (53.7°N, 106.2°W) is a mature deciduous forest at the southern edge of the Canadian boreal forest in Prince Albert National Park, Saskatchewan, Canada. The forest canopy has two distinct layers: a 22-m trembling aspen overstory (Populus tremuloides Michx. with ~10% balsam poplar (Populus balsamifera L.), and a 2-m hazelnut understory (Corylus cornuta Marsh with sparse alder (Alnus crispa (Al.) Pusch). The forest regenerated after a natural fire in 1919, and had a 1998 stand density of ~830 stems ha$^{-1}$. The soil is an Orthic Gray Luvisol with an 8–10 cm deep surface organic layer overlying a loam to sandy clay loam mineral soil. The terrain is generally level. Mean annual air temperature and precipitation at the nearest long-term weather stations are 0.5 °C and 406 mm, respectively.
Table 1
Inter-annual variability in several climatic variables, net ecosystem productivity, gross ecosystem photosynthesis and ecosystem respiration at the BERMS Old Aspen site

<table>
<thead>
<tr>
<th>Year</th>
<th>Mean annual air temperature (°C)</th>
<th>Annual precipitation (mm)</th>
<th>Canopy duration (days)</th>
<th>(\sum D) (°C days)</th>
<th>(F_{\text{NEP}}) (g C m(^{-2}))</th>
<th>(P) (g C m(^{-2}))</th>
<th>(R) (g C m(^{-2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>1.2</td>
<td>466</td>
<td>114</td>
<td>1404</td>
<td>206</td>
<td>1323</td>
<td>1117</td>
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<tr>
<td>1995</td>
<td>0.6</td>
<td>390</td>
<td>103</td>
<td>1241</td>
<td>54</td>
<td>1216</td>
<td>1162</td>
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<tr>
<td>1996</td>
<td>–0.1</td>
<td>494</td>
<td>108</td>
<td>1524</td>
<td>127</td>
<td>1330</td>
<td>1203</td>
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<tr>
<td>1997</td>
<td>2.6</td>
<td>413</td>
<td>116</td>
<td>1625</td>
<td>265</td>
<td>1402</td>
<td>1137</td>
</tr>
<tr>
<td>1998</td>
<td>3.3</td>
<td>547</td>
<td>137</td>
<td>1293</td>
<td>119</td>
<td>1269</td>
<td>1149</td>
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<tr>
<td>1999</td>
<td>3.0</td>
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<td>118</td>
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<td>1046</td>
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<td>235</td>
<td>126</td>
<td>1300</td>
<td>144</td>
<td>1032</td>
<td>888</td>
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<tr>
<td>2002</td>
<td>0.9</td>
<td>286</td>
<td>108</td>
<td>1548</td>
<td>104</td>
<td>1057</td>
<td>954</td>
</tr>
<tr>
<td>2003</td>
<td>2.0</td>
<td>261</td>
<td>117</td>
<td>1398 ± 158</td>
<td>168 ± 96</td>
<td>1252 ± 136</td>
<td>1084 ± 103</td>
</tr>
<tr>
<td>1994–2003</td>
<td>1.9 ± 1.2</td>
<td>396 ± 103</td>
<td>117 ± 9</td>
<td>1398 ± 158</td>
<td>168 ± 96</td>
<td>1252 ± 136</td>
<td>1084 ± 103</td>
</tr>
</tbody>
</table>

(Prince Albert Airport, 53°13′N, 105°40′W, 428 m elevation, 1942–1990 climatic normals) and 0.3 °C and 456 mm, respectively (Waskesiu Lake, 53°55′N, 106°04′W, 552 m elevation, 1934–1990 climatic normals). The climate at the Old Aspen site during the study period (1994–2003) was on average 1.5 °C warmer and slightly drier than the climatic normals (Table 1). The study years included two significant climatic features: contrasting spring temperatures, with warm springs in 1998 and 2001 and cool springs in 1996 and 2003, and a prolonged drought that began in July 2001 and extended throughout 2002 and 2003.

2.2. Leaf area index (LAI)

Our notation uses \(L_a\), \(L_h\) and \(L\) for the overstory (mostly trembling aspen), understory (mostly hazelnut) and total LAI, respectively; \(L_{a\alpha}\), \(L_{h\alpha}\) and \(L_{\alpha}\) for the mean fully-leafed (annual maximum) values of \(L_a\), \(L_h\) and \(L\), respectively; and \(\lambda_{a\alpha}\) and \(\lambda_{h\alpha}\) for the normalized ratios \(L_{a\alpha}/L_{a\alpha}\) and \(L_{h\alpha}/L_{h\alpha}\), respectively. The values of \(L_{\alpha}\), \(L_{a\alpha}\) and \(L_{h\alpha}\) were calculated as the mean of all measurements during the period at full leaf, i.e., from complete foliation (defined according to the cumulative degree days (Eq. (5)) as the period exceeding 300 °C days for aspen and 400 °C days for hazelnut) to the beginning of leaf senescence (defined here only using a fixed date of 15 September).

We measured \(L_a\) and \(L_h\) near the flux tower with a plant canopy analyzer (PCA) (model LAI 2000, LI-COR Inc., Lincoln, NE, USA). The \(L_a\) measurements used the “two-instrument” mode, with the above-canopy instrument mounted on the flux tower. One measurement was made at each sampling location below the aspen canopy. The \(L_h\) measurement used the “one-instrument” mode, with one measurement above and three measurements below the hazelnut canopy at each sampling location. The measurements were made on a flexible schedule between April and October. Approximately half were during leaf emergence in spring. Six to fifteen measurements were made in all years but 1996, when a single measurement was made in midsummer. In 1994, most measurements were taken during daytime periods with uniformly overcast cloud cover. In 1996–2003, most measurements were taken during the first hours after sunrise and before sunset. On most days, the procedure was repeated three times and the results were averaged. The sampling locations changed between 1994–1996 and 1997–2003 but the effect on measured LAI was negligible. In 1994 and 1996, \(L_a\) was measured at two points, 10-m apart and \(L_{h\alpha}\) was measured at six points approximately 20-m apart (Blanken et al., 1997; Chen et al., 1997). In 1997–2003, \(L_a\) and \(L_h\) were measured at 10-m intervals along a 50-m transect. Several comparative tests in summer 1997 and 1998 of these transects and an extended 300-m transect (with measurements every 10 m) showed that the 1994–1996 and 1997–2003 transects were spatially representative and gave similar results.

The values for \(L_{h\alpha}\) were estimated from the raw PCA output (\(L_{he,\alpha}\), where the subscript ‘e’ denotes effective) as (Chen et al., 1997):

\[
L_h = \frac{L_{he}}{\Omega_{h}} - L_{hw}
\]
where $L_{bw}$ is the effective hazelnut stem and branch area index (0.33) and $\Omega_a$ is the hazelnut leaf clumping index (0.98). The values for $L_a$ were estimated from the raw PCA output ($L_{ae}$) as (Kucharik et al., 1998; Leblanc and Chen, 2001)

$$L_a = \frac{\varepsilon L_{ae} - \delta B_{ae}}{\Omega_{ae}} - S_a$$  \hspace{1cm} (2)

where $\varepsilon$ is an empirical correction for blue-light scattering under non-ideal light conditions, $B_{ae}$ is the effective (hemi-surface) aspen branch area index (0.44), $\Omega_{ae}$ is the aspen leaf clumping index at a zenith angle of $35^\circ$ (0.69), $S_a$ is the (hemi-surface) aspen stem area index (0.40), and $\delta$ is the fraction of $B_{ae}$ that is exposed to gaps in the canopy (see below). For the leafless canopy ($L_a = 0$), Eq. (2) with the given parameter values gives $L_{ae}$ of 0.72 which is in good agreement with the PCA measurements of 0.74 ± 0.04 before leaf emergence and 0.72 ± 0.05 after leaf fall. The value for $\varepsilon$ in Eq. (2) is 1.0 for diffuse light conditions (i.e., under uniform overcast skies or near dawn or dusk). For daytime periods with non-overcast skies, Leblanc and Chen (2001) give

$$\varepsilon = \frac{a_1 + a_2 e^{s/\lambda_a} - a_4 (\frac{62 - \theta_s}{90 + \theta_s})^2}{1 + a_5 (\frac{62 - \theta_s}{90 + \theta_s})^2 L_{ae}}$$  \hspace{1cm} (3)

where $a_1$ to $a_5$ are empirical constants (0.756, 0.0206, 0.0278, −40 and 10, respectively) and $\theta_s$ is the solar zenith angle (°). Except for a few periods in 1994, the PCA measurements were during periods with $\varepsilon \sim 1.0$. For non-ideal conditions, 1.00 < $\varepsilon$ < 1.2. The value for $\delta$ in Eq. (2) varies with $\lambda_a$ and may be approximated from the characteristic, fully-expanded, leaf width ($r_0$ = 25 mm) and the typical length of exposed branch ($l = 1.9$ mm), following Kucharik et al. (1998), as

$$\delta = \frac{(l + (1 - \lambda_a^{0.5}) r_0)}{l + r_0}$$  \hspace{1cm} (4)

LAI was also measured using leaf litter collections from bucket traps. The buckets were 20 cm tall with an inner diameter of approximately 20 cm and small holes to allow drainage. During the summer of 1996, we installed 12 bucket traps within each of two aspen clones covering an area of about 20 m × 20 m and situated within 100 m of the flux tower. Litter collections were made annually each October. A second litter collection was necessary in spring 2003 because the leaves had not completely abscised in October 2002. In 1994 only, we used litter-trap measurements (total of 20 traps) from a similar aspen stand 1 km east of the flux tower. The litter samples were oven-dried (50 °C) and the dry leaf litter from the trees (overstory) and shrubs (understory) was then sorted by species and weighed. For each species, litterfall was first expressed on a ground area basis (kg m⁻²) and then LAI was estimated using specific leaf areas of 11.5 m² kg⁻¹ (dry mass) (trembling aspen), 12.4 m² kg⁻¹ (balsam poplar), 23.5 m² kg⁻¹ (hazelnut), and 16.1 m² kg⁻¹ (other understory shrubs). These specific leaf areas were based on re-hydrated leaf litter samples from 1993 and 1994.

Because LAI was measured too infrequently to fully characterize inter-annual differences in leaf emergence, we reconstructed the daily time series of $L_a$ and $L_{bw}$ from empirical models that were fit using the PCA measurements. The procedure is described in Section 3.1. The models used cumulative degree (°C) days, shortwave reflectance, photosynthetically-active radiation (PAR) reflectance, and canopy PAR transmittance as the independent variables.

### 2.3. Temperature and radiation

Air temperature was measured at the 18-m height within the aspen canopy using a temperature/humidity sensor (model HMP35CF, Vaisala Oyi, Helsinki, Finland) in a 12-plate Gill shield (model 41002-2, R.M. Young Co., Traverse City, MI, USA). Canopy temperature was estimated from the upwelling longwave radiation as measured by a precision pyrgeometer (model PIR, The Eppley Laboratory Inc., Newport, RI, USA) at a height of 31 m (10 m above the canopy), using a surface longwave emissivity of 0.98.

We calculated cumulative, growing-season, degree days $\sum D$ on a daily basis as:

$$\sum D = \sum_{d=d_i}^{d_f} \max(T_a - 5^\circ C, 0^\circ C)$$  \hspace{1cm} (5)

where $d$ is the day of the year, $d_i$ and $d_f$ are the initial and final values of $d$ for growing-season degree-day accumulation, and $T_a$ is the mean of the daily minimum and maximum air temperatures. We identified $d_i$ for each year in two ways. When soil temperature data were
available (e.g., for the study period at the Old Aspen site), $d_i$ was identified as the first day in spring when daily mean soil temperature at 20-cm depth exceeded $-0.2^\circ C$, coinciding with the end of snowmelt. When soil temperature data were not available (e.g., for the historic analysis at Prince Albert Airport), $d_i$ was identified as the final day of the first three-day period in spring when mean daily air temperature exceeded $5.0^\circ C$ on all three days. On average, the second method began degree day accumulation two weeks later than the first method; however, the resultant differences in $\sum D$ were small. The value for $d_f$ was identified as the first day after 1 August when daily minimum canopy temperature fell below $0.0^\circ C$.

The upwelling and downwelling flux densities of shortwave radiation in W m$^{-2}$ were measured above the forest canopy using paired pyranometers (model CM11, Kipp & Zonen, Delft, The Netherlands). The upwelling and downwelling PAR flux densities, which we will denote as $Q_i$ and $Q_f$ in $\mu$mol (photons) m$^{-2}$ s$^{-1}$, were measured with paired quantum sensors (model LI190SA, LI-COR Inc., Lincoln, NE, USA). The downward-facing radiometers were mounted on a boom, 4 m to the south of the tower and 10 m above the canopy. The downwelling PAR flux density was also measured below the aspen and hazelnut canopies, at 4.0 m (two locations) and 0.2 m (one location), respectively. Afternoon data were excluded for one of the 4-m PAR sensors when the flux tower partially shaded the sensor. We computed five daily radiation indices: shortwave reflectance $\rho_s$ (1994, 1996–2003), PAR reflectance $\rho_p$ (1996–2003), the ratio $\rho_p/\rho_s$ (1996–2003), and PAR transmittances through the aspen ($\tau_a$, 1996–2003) and hazelnut ($\tau_h$, 1997–2003) canopies. The annual cycles of these indices were calculated using a moving window for periods with solar elevations above 20° and atmospheric shortwave transmittances above 0.3. The window size was based on a fixed number of non-missing data rather than a fixed period of time (48 half-hour points for $\rho_p$ and $\rho_p/\rho_s$ and 96 half-hour points for $\rho_s$, $\tau_a$ and $\tau_h$, moved in increments of 12 points). The latter windows were wider because the data were noisier. For each window, the mean radiation indices were calculated from the mean fluxes. Daily values were then computed by linear interpolation between windows.

2.4. Carbon, water and heat fluxes

We will denote net ecosystem production, gross ecosystem photosynthesis and ecosystem respiration as $F_{NEP}$, $P$, and $R$, respectively. Eddy-covariance measurements of the CO$_2$ flux density were made from above a twin scaffold tower at 39 m, approximately twice the height of the forest canopy. The surface flux was calculated as the sum of the eddy flux, measured at 39 m, and the rate of change of storage in the air column below the flux measurement level. Continuous flux measurements were made from February to September 1994 and beginning in March 1996. The flux system consisted of a tri-axial sonic anemometer (model R2 or R3, Gill Instruments Ltd., Lymington, Hampshire, UK) in combination with a closed path, thermostated, infrared gas analyzer (model LI6262, LI-COR Inc.) operated in absolute mode. A diaphragm pump was used to draw air into the IRGA at a flow rate of 10.1 min$^{-1}$, through a short (4 m), 4-mm inner diameter, heated Synflex 1300 tube (Saint-Gobain, Performance Plastics, Wayne, NJ). The data acquisition system included an analog-to-digital converter (model DAQbook 200, IOtech Inc., Cleveland, OH) and a computer. Additional details of the EC system are given in Black et al. (1996) and Chen et al. (1999).

The surface CO$_2$ flux provides a direct measurement of the net ecosystem exchange ($F_{NEE}$)—the net exchange rate of CO$_2$ between the ecosystem and the atmosphere. If we neglect the loss of carbon via groundwater flow, which is negligibly small at this site, $F_{NEE}$ provides a direct measure of the net ecosystem production ($F_{NEP} = -F_{NEE}$). $F_{NEP}$ results as the difference between carbon gains by gross ecosystem photosynthesis ($P$) and carbon losses by ecosystem respiration ($R$) and is positive for a carbon sink.

The procedure to estimate annual $F_{NEP}$ and to partition $F_{NEP}$ into components for $P$ and $R$ is described in Appendix A. The procedure has been adopted as the standard by the Fluxnet-Canada Research Network and differs from that used in previous reports of $F_{NEP}$ at the Old Aspen site (Black et al., 2000; Arain et al., 2002; Griffiths et al., 2003, 2004) in two respects: it uses a moving-window approach to estimate the seasonal variation of time-varying parameters from the empirical $R$ and $P$ relationships; and the empirical $R$ relationship is a logistic rather than an exponential function. The
estimates of $F_{\text{NEP}}, R$ and $P$ reported here differ slightly from our earlier estimates, with increases in mean annual $F_{\text{NEP}}, R$ and $P$ of 11, 21 and 33 g C m$^{-2}$ y$^{-1}$, respectively. However, the differences do not affect the interpretation of inter-annual variability in $F_{\text{NEP}}$ or its attribution to differences in $R$ and $P$.

We isolated the seasonal onset, rise and fall of photosynthesis from the $F_{\text{NEP}}$ time series based on the parameter $P_x$ in the rectangular hyperbolic model (Ruimy et al., 1995; Lee et al., 1999; Hollinger et al., 1999; Luo et al., 2000; Saigusa et al., 2002; Griffis et al., 2003):

$$F_{\text{NEP}} = \frac{aP_xQ}{\alpha Q + P_x} - R$$  \hspace{1cm} (6)

where $P_x$ is the photosynthetic capacity ($P$ at light saturation) and $\alpha$ is the quantum efficiency. The temporal variation in $P_x$ was estimated using a flexible moving window of 240 measured (not-missing) data points. Eq. (6) gave a more distinct signature of the seasonal photosynthesis cycle than Eq. (A.6).

3. Results and discussion

3.1. Empirical LAI relationships

3.1.1. Degree days

Cumulative degree days ($\sum D$) are a major determinant of leaf emergence and expansion (Lechowicz, 1984; Hunter and Lechowicz, 1992; Kramer, 1995).

Fig. 1 plots normalized LAI as a function of $\sum D$. The best simple empirical model as identified by TableCurve (Jandel Scientific) is

$$\lambda^D_a = 0.5 \text{erfc} \left( \frac{-\ln(\sum D/a_1)}{a_2} \right)$$  \hspace{1cm} (7)

$$\lambda^D_h = 0.5 \text{erfc} \left( \frac{-\ln(\sum D/h_1)}{h_2} \right)$$  \hspace{1cm} (8)

where the superscript $D$ denotes modeled estimates from Eqs. (7) and (8), erfc is the complementary error function, the values of $a_1$ and $a_2$ are 130 $\circ C$ days and 0.394, respectively, the values of $h_1$ and $h_2$ are 232 $\circ C$ days and 0.259, respectively, and the coefficients of determination ($r^2$) are 0.97 (Eq. (7)) and 0.96 (Eq. (8)). Table 2 gives threshold values of $\sum D$ by phenological stage. The aspen canopy reached 10 and 90% of $L_a$ at $\sum D$ of 81 and 217 $\circ C$ days, respectively. The hazelnut canopy reached 10 and 90% of $L_h$ at $\sum D$ of 173 and 333 $\circ C$ days, respectively. Among common boreal and temperate deciduous tree species, trembling aspen is one of the earliest to leaf out and the latest to senesce (Lechowicz, 1984), which may account for its broad geographic distribution in the boreal forests of North America (Peterson and Peterson, 1992). The observed, leaf-emergence dates were predicted reasonably well by the chilling-day/degree-day scheme of Botta et al. (2000) except for the two years with late leaf emergence. However, leaf emergence was insensitive to the number of chilling days. Thus, the chilling-day requirement may be more useful for predicting spatial differences in the leaf-emergence date over broad geographic areas (Botta et al., 2000) than for predicting inter-annual variability in leaf emergence at fixed locations, particularly boreal locations where the chilling-day requirement is always met.

3.1.2. Radiation indices

The seasonal LAI cycle produced characteristic changes in reflected and transmitted radiation (Fig. 2). Leaf emergence caused a dramatic decline in $\rho_a$ and a rise in $\rho_h$, with the ratio $\rho_a/\rho_h$ dropping from $\sim 0.60$ above the snow-free, leafless canopy to $\sim 0.20$ above the fully-leafed canopy. Leaf emergence also caused a characteristic decline in the PAR transmittance through the aspen and hazelnut canopies, from $\sim 0.41$ to $\sim 0.18$ for $\tau_a$ and $\sim 0.81$ to $\sim 0.13$ for $\tau_h$. 

![Fig. 1. The influence of cumulative degree days on normalized aspen LAI ($\lambda_a$, closed symbols) and hazelnut LAI ($\lambda_h$, open symbols) during spring leaf emergence, as measured by the LAI 2000 plant canopy analyzer. The curves are described by Eqs. (7) and (8).](image-url)
Table 2
Timing of key phenological events

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<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>Start of spring greenup</td>
<td>Decline in $p_{\rho}/p_{\rho}$ below pre-leaf-out threshold (~0.60)</td>
<td>05/26</td>
<td>05/10</td>
<td>04/26</td>
<td>05/03</td>
<td>05/04</td>
<td>04/30</td>
<td>05/27</td>
<td>05/03</td>
<td>05/09 ± 12</td>
<td>69 ± 11</td>
<td></td>
</tr>
<tr>
<td>10% aspen LAI</td>
<td>$L_{v} &gt; 0.01 L_{a}$, (Eq. (10))</td>
<td>05/11</td>
<td>05/27</td>
<td>05/12</td>
<td>04/28</td>
<td>05/04</td>
<td>05/05</td>
<td>05/27</td>
<td>05/05</td>
<td>05/11 ± 10</td>
<td>81 ± 10</td>
<td></td>
</tr>
<tr>
<td>Earliest detectable photosynthesis</td>
<td>$P_{s}$ significantly &gt; 0</td>
<td>05/09</td>
<td>06/03</td>
<td>05/29</td>
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<td>05/13</td>
<td>05/12</td>
<td>05/29</td>
<td>05/16</td>
<td>05/17 ± 11</td>
<td>115 ± 26</td>
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<tr>
<td>Hazelnut leaf emergence</td>
<td>Decline in $t_{h}$ below pre-leaf-emergence threshold (~0.60)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10% hazelnut LAI</td>
<td>$L_{h} &gt; 0.1 L_{a}$, (Eq. (11))</td>
<td>06/02</td>
<td>06/09</td>
<td>06/02</td>
<td>05/20</td>
<td>06/03</td>
<td>06/06</td>
<td>05/27</td>
<td>06/12</td>
<td>05/27</td>
<td>06/02 ± 7</td>
<td>217 ± 4</td>
</tr>
<tr>
<td>90% aspen leaf emergence</td>
<td>$L_{v} &gt; 0.9 L_{a}$, (Eq. (10))</td>
<td>06/04</td>
<td>06/13</td>
<td>06/04</td>
<td>05/22</td>
<td>06/04</td>
<td>06/07</td>
<td>05/27</td>
<td>06/08</td>
<td>05/27</td>
<td>06/03 ± 7</td>
<td>230 ± 23</td>
</tr>
<tr>
<td>Earliest moderate photosynthesis</td>
<td>$P_{s}$ &gt; 40th percentile</td>
<td>06/22</td>
<td>06/12</td>
<td>05/27</td>
<td>06/12</td>
<td>06/16</td>
<td>06/07</td>
<td>06/14</td>
<td>06/06</td>
<td>06/11 ± 8</td>
<td>298 ± 39</td>
<td></td>
</tr>
<tr>
<td>End of green-up</td>
<td>$p_{\rho}/p_{\rho}$ reaches growing-season minimum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Earliest near-maximum photosynthesis</td>
<td>$P_{s}$ &gt; 80th percentile</td>
<td>06/26</td>
<td>06/19</td>
<td>06/17</td>
<td>05/25</td>
<td>06/11</td>
<td>06/11</td>
<td>06/09</td>
<td>06/18</td>
<td>06/07</td>
<td>06/12 ± 9</td>
<td>316 ± 67</td>
</tr>
<tr>
<td>90% hazelnut LAI</td>
<td>$L_{h} &gt; 0.9 L_{a}$, (Eq. (11))</td>
<td>06/13</td>
<td>06/19</td>
<td>06/10</td>
<td>05/30</td>
<td>06/16</td>
<td>06/24</td>
<td>06/10</td>
<td>06/23</td>
<td>06/14</td>
<td>06/14 ± 8</td>
<td>333 ± 18</td>
</tr>
<tr>
<td>Start of senescence</td>
<td>$P_{s}$ &lt; 40th percentile</td>
<td>09/11</td>
<td>09/06</td>
<td>08/31</td>
<td>09/22</td>
<td>09/08</td>
<td>09/19</td>
<td>09/12</td>
<td>09/21</td>
<td>09/23</td>
<td>09/14 ± 8</td>
<td>n/a</td>
</tr>
<tr>
<td>Start of senescence</td>
<td>Significant increase in $p_{\rho}/p_{\rho}$</td>
<td>09/18</td>
<td>09/18</td>
<td>09/13</td>
<td>09/11</td>
<td>09/11</td>
<td>09/11</td>
<td>09/11</td>
<td>09/17</td>
<td>09/17 ± 2</td>
<td>n/a</td>
<td></td>
</tr>
<tr>
<td>Start of hazelnut senescence</td>
<td>Significant increase in $t_{h}$</td>
<td>09/18</td>
<td>09/14</td>
<td>09/18</td>
<td>09/18</td>
<td>09/18</td>
<td>09/18</td>
<td>09/19</td>
<td>09/19</td>
<td>09/17 ± 2</td>
<td>n/a</td>
<td></td>
</tr>
<tr>
<td>End of senescence</td>
<td>$P_{s} = 0$</td>
<td>09/25</td>
<td>09/25</td>
<td>09/21</td>
<td>10/02</td>
<td>09/27</td>
<td>09/30</td>
<td>10/05</td>
<td>09/28</td>
<td>09/28</td>
<td>09/25 ± 4</td>
<td>n/a</td>
</tr>
<tr>
<td>End of hazelnut senescence</td>
<td>Plateau in $t_{h}$ above 0.60</td>
<td>09/24</td>
<td>09/24</td>
<td>09/23</td>
<td>09/21</td>
<td>09/23</td>
<td>09/25</td>
<td>09/28</td>
<td>09/24</td>
<td>09/24 ± 2</td>
<td>n/a</td>
<td></td>
</tr>
<tr>
<td>End of senescence</td>
<td>Plateau in $p_{\rho}/p_{\rho}$ above 0.50</td>
<td>10/13</td>
<td>09/28</td>
<td>10/05</td>
<td>09/26</td>
<td>10/03</td>
<td>09/30</td>
<td>10/18</td>
<td>10/05</td>
<td>10/05 ± 7</td>
<td>n/a</td>
<td></td>
</tr>
</tbody>
</table>
Leaf senescence reversed these changes but the reversal was sometimes only partial; note, for instance, the spring-to-autumn difference in $t_a$ that was caused by the decline in the mean solar zenith angle and the persistence of a low value for $t_a$ in October 2003 when the leaves failed to abscise from the canopy.

Although the reflectance ratio $\rho_p/\rho_s$ integrated LAI from both aspen and hazelnut canopies, it was dominated by the aspen overstory which leafed out before the hazelnut understory and partially covered it. As a result, there was a strong functional relationship during leaf emergence between $L_a$ and $\rho_p/\rho_s$ (Fig. 3):

$$L_a^\rho = \max \left( 0, a_0 + a_1 \left( \frac{\rho_p}{\rho_s} \right) + a_2 \left( \frac{\rho_p}{\rho_s} \right)^2 \right)$$

(9)

where the superscript $\rho$ denotes modeled estimates from Eq. (9). The least-squares estimates for $a_0$ to $a_2$ were $-2.69$, $-3.91$, and $3.43$ ($r^2 = 0.96$). Of the four radiation indices that tracked $L_a$ ($\rho_s$, $\rho_p$, $\rho_p/\rho_s$, and $t_a$), the reflectance ratio $\rho_p/\rho_s$ had the clearest and most distinct $L_a$ signature and was most tightly coupled to seasonal $L_a$ cycle. It was particularly useful during leaf emergence. It had three minor shortcomings for predicting the seasonal $L_a$ cycle: it was not constant during the fully-leafed period but rose slightly as the summer advanced; it was sensitive to differences in water stress among years; and its autumn rise sometimes extended beyond the leaf senescence period, perhaps because leaf abscission sometimes lagged leaf senescence. The fully-leafed values of $\rho_p/\rho_s$, including the subtle but characteristic summer rise, were similar for all years but 2003, when the mean value was 0.262 compared with 0.219 for 1996–2002. This 19% increase in $\rho_p/\rho_s$ was caused by a 12% increase in $\rho_p$ (from 0.033 to 0.037) and a 6% drop in $\rho_s$ (from 0.151 to 0.142). The increase may reflect the low $L_a$ value in 2003 or it may show a change in canopy optical properties during the 2001–2003 drought. Aber et al. (2002) observed a similar drought-induced change in the reflectance of a temperate deciduous forest in Kansas, with the change in reflectance lagging the drought by one to two years.

Another reflectance index that is commonly related to forest LAI is the normalized difference vegetation index (NDVI, Blair and Baumgardner, 1977; Badwar et al., 1986). Satellite-derived estimates of NDVI have been used extensively to observe the green up and brown up of terrestrial ecosystems and to map LAI in time and space (Spanner et al., 1994; Cihlar et al., 1997; Liu et al., 1997), to validate models of LAI phenology at regional scales (Bondeau et al., 1999), to input seasonal LAI phenology into models of net primary production (Goetz et al., 1999; Liu et al., 1997).
1999) and to monitor the occurrence and severity of drought (Peters et al., 1991; Aber et al., 2002). Huemmrich et al. (1999) computed a broadband estimate of NDVI based on the up- and down-welling flux densities of shortwave radiation and PAR at the Old Aspen site and showed a clear delineation of the seasonal LAI cycle. Note that the broadband NDVI is directly related to the reflectance ratio (NDVI = \( \frac{\rho_d}{\rho_s} \)). We prefer the use of \( \frac{\rho_d}{\rho_s} \) to broadband NDVI because it is simpler and does not require assumptions about the factors to convert \( Q_d \) and \( Q_s \) from photon flux density to energy flux density.

Fig. 4 shows the relationship between LAI and PAR transmittance (\( \tau \)) during spring leaf emergence, for the aspen (closed symbols) and hazelnut (open symbols) canopies. The curves are described by Eq. (10).

\[
L_h^\tau = \max(0, a_0 + a_1 \tau_h^{3/2})
\]  

where the superscript \( \tau \) denotes modeled estimates from Eq. (10) and the least-squares estimates for \( a_0 \) and \( a_1 \) were 2.00 and -4.26, respectively (\( r^2 = 0.90 \)).

### 3.2. Measured LAI

Fig. 5 shows measured aspen and hazelnut LAI (Eqs. (1) and (2)) by day of year. The aspen canopy leafed out in May, two to four weeks before the hazelnut canopy. Both canopies senesced in late September. The data clearly show an early leaf emergence in 1998 and a late leaf emergence in 2002 but are too infrequent to fully characterize inter-annual differences in the timing of leaf emergence and senescence. Within each year, the fully-leafed LAI appears to be constant between leaf emergence and senescence.

Table 3 summarizes inter-annual differences in the fully-leafed LAI values for aspen and hazelnut and compares independent measurements by PCA and litter traps. The PCA measurements of \( L_{ax} \) had greater inter-annual variability than the litter-trap measurements but similar means and annual rankings. The PCA and litter-trap measurements of \( L_{hx} \) had similar inter-annual differences and annual rankings but the PCA measurements were on average 21% higher than the litter-trap measurements. This difference may be due to a bias in our estimate of the hazelnut specific leaf area. Middleton et al. (1997) reported aspen and hazelnut specific leaf areas of 12.9 and 27.1 m\(^2\) kg\(^{-1}\), respectively, for fresh leaf tissue collected at the same site in early to mid September 1994, compared with our estimates of 11.5 and 23.5 m\(^2\) kg\(^{-1}\) for rehydrated leaves collected after leaf fall. Because the specific leaf area increases during senescence, our estimate of the hazelnut specific leaf area appears to be anomalously low. This would account for the PCA — litter-trap difference in the estimates for \( L_{hx} \).

The mean, fully-leafed PCA value for \( L_{ax} \) was 4.43 ± 0.56, with an inter-annual range of 3.66–5.22 or 35% of the mean. The \( L_{ax} \) values varied significantly among years, with low values in 1994 and 1996, a
Table 3
Fully-leafed LAI for the aspen and hazelnut canopies, as measured by the PCA (mean ± standard deviation) and litter traps

<table>
<thead>
<tr>
<th>Year</th>
<th>Aspen Litterfall</th>
<th>Hazelnut Litterfall</th>
<th>Total Litterfall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PCA Litterfall</td>
<td>PCA Litterfall</td>
<td>PCA Litterfall</td>
</tr>
<tr>
<td>1994</td>
<td>2.34 ± 0.32</td>
<td>2.46a</td>
<td>2.82 ± 0.46</td>
</tr>
<tr>
<td>1996</td>
<td>2.34</td>
<td>2.34</td>
<td>1.32b</td>
</tr>
<tr>
<td>1997</td>
<td>2.51 ± 0.05</td>
<td>2.36</td>
<td>1.88 ± 0.41</td>
</tr>
<tr>
<td>1998</td>
<td>2.53 ± 0.12</td>
<td>2.59</td>
<td>1.46 ± 0.18</td>
</tr>
<tr>
<td>1999</td>
<td>2.52 ± 0.17</td>
<td>2.62</td>
<td>1.96 ± 0.22</td>
</tr>
<tr>
<td>2000</td>
<td>2.82 ± 0.24</td>
<td>2.80</td>
<td>2.08 ± 0.20</td>
</tr>
<tr>
<td>2001</td>
<td>2.89 ± 0.32</td>
<td>2.75</td>
<td>2.33 ± 0.04</td>
</tr>
<tr>
<td>2002</td>
<td>2.10 ± 0.21</td>
<td>2.39</td>
<td>1.89 ± 0.12</td>
</tr>
<tr>
<td>2003</td>
<td>1.95</td>
<td>1.96</td>
<td>2.08 ± 0.10</td>
</tr>
<tr>
<td>Mean</td>
<td>2.44 ± 0.30</td>
<td>2.47 ± 0.25</td>
<td>1.98 ± 0.44</td>
</tr>
</tbody>
</table>

For 1994 only, the litter plots were 1-km SE of the flux tower.
For 1996 only when no PCA hazelnut LAI measurements were made, the PCA value is estimate is based on litterfall, adjusted for the PCA – litter-trap difference.

gradual increase between 1996 and 2000, a plateau from 2000 to 2001, and a drop in 2002 and 2003 to below the 1994 value. The L_{hx} values were unusually high in 1994 and low in 1996. Some of the observed inter-annual differences in L_{ax} and L_{hx} fall within the PCA measurement uncertainty but the consistency between the PCA and litter-trap measurements suggests that they were real. Inter-annual variation in aspen LAI has been linked to defoliation and drought events in the previous year. Hogg (1999) modeled the effect of insect defoliation on trembling aspen dieback and reported high inter-annual variability in LAI, caused primarily by intermittent defoliation events, with a gradual recovery of annual L_a in the years following defoliation. He concluded that over-winter reserves of non-structural carbohydrates are critical to leaf emergence of boreal deciduous tree species the following spring.

During the selection of the Old Aspen site in 1992, a partial defoliation of the aspen canopy by large aspen tortrix (Choristoneura conflictana Walker) was observed (E.H. Hogg, personal communication). This could account for the low L_{ax} and high L_{hx} in 1994; defoliation of the aspen would reduce PAR interception, photosynthesis and non-structural carbohydrate storage in the aspen overstory and increase PAR interception, photosynthesis and non-structural carbohydrate storage in the hazelnut understory. Although the data do not show a direct response of L_a or L_{ax} to P from the previous year, the general increase in L_{ax} between 1994 and 2001 may show post-defoliation recovery during a period of low water stress and relatively high P (Table 1). The 2001–2003 decline in L_{ax} is almost certainly related to the extended drought that began in summer 2001 (Table 1). Abiotic stresses, such as drought, typically cause diminished LAI in the following year (Le Dantec et al., 2000). There are two possible mechanisms: a drought-induced reduction in the annual carry-over of non-structural carbohydrates (Hogg, 1999) and reduced leaf water potential during leaf emergence, the direct result of low soil moisture or the indirect result of drought-induced cavitation during the previous year (Tyree et al., 1994). It is interesting that no concomitant decline in L_{ax} was observed during the 2001–2003 drought. We have not accounted for the low L_{hx} in 1996.

3.3. Filling gaps in the annual LAI cycle

To fill in the annual LAI cycle, we estimated daily values of L_{ax}^* and L_{h}^* based on the empirical relationships from Section 3.2. The superscript ‘*’ denotes the daily estimates from Eqs. (11) and (12). The values were estimated separately for five periods each year, corresponding to the pre-leaf-emergence, leaf-emergence, fully-leafed, leaf-senescence, and post-senescence periods. Before leaf emergence and after leaf senescence, L_{a}^* and L_{h}^* were set to zero. During the leaf-emergence and fully-leafed periods, L_{a}^* was estimated as

\[
L_{a}^* = (1 - \lambda_{a}^{D})L_{a}^{0} + \lambda_{a}^{D}L_{ax}
\]  

(11)
where $L_{ax}$ is the measured, PCA value (Table 3). Eq. (11) blends the degree-day-based estimates ($D_n^{la}$) from Eq. (7) with the radiation-based estimates $L_n^p$ from Eq. (9); ($D_n^{la}$) is weighted by $\lambda_n^D$ (Eq. (7)) and $L_n^p$ is weighted by $(1 - \lambda_n^D)$. Because $\lambda_n^D$ varies from zero before leaf emergence to one for complete foliation, Eq. (11) weights the radiation-based estimates $L_n^p$ heavily at low $L_n$ and the degree-day estimates ($D_n^{la}$) heavily at high $L_n$. It also constrains $L_n^a$ to $L_{ax}$ following leaf emergence. Similarly, $L_n^h$ during the leaf-emergence and fully-leaved periods was estimated as

$$L_n^h = (1 - \lambda_n^h) L_n^a + \lambda_n^D L_n^h$$

(12)

based on the $L_n^h$ estimates ($D_n^{lh}$) from Eq. (8) and $L_n^a$ from Eq. (10). Eqs. (11) and (12), which combine the radiation and degree-day models, outperformed the individual radiation and degree-day models (Eqs. (7)–(10)) for both aspen and hazelnut LAI. Eqs. (11) and (12) were particularly effective during the leaf-emergence and full-leaf periods.

It was more difficult to estimate the decline in LAI during leaf senescence. The PCA measurements, which are based on gap fractions, do not differentiate between green and brown LAI during periods when the leaves have senesced but are not yet abscised. The radiation indices $\rho_s/\rho_p$ (aspen) and $\tau_h$ (hazelnut) marked the onset of leaf senescence in all years but failed in some years to track the decline in photosynthesis during senescence or show when photosynthesis ended. Consequently, we adopted a pragmatic approach for estimating LAI during leaf senescence that used the radiation indices in conjunction with the first occurrence of frost. We identified the onset of leaf senescence as the first day in late summer or early autumn when $\rho_s/\rho_p$ (aspen) and $\tau_h$ (hazelnut) began to rise sharply above the summer values or the daily minimum canopy temperature dropped below 0.0 °C. We identified the end of leaf senescence as the first day in late summer or early autumn when $\rho_s/\rho_p$ exceeded 0.50 (aspen) and $\tau_h$ exceeded 0.60 (hazelnut) or the daily minimum canopy temperature dropped below −2.0 °C. We then estimated the decline in $L_n^a$ and $L_n^h$ during senescence by scaling the radiation-based estimates $L_n^a$ and $L_n^h$ from Eqs. (8) and (9) to match $L_{ax}$ and $L_{ax}$ at the beginning of senescence and decline to zero at the end of senescence. Although the estimates during senescence were questionable in some years, the senescence period was short and its timing was similar among years.

3.4. Annual LAI cycles

Fig. 6 shows the reconstructed, annual cycles of $L_n^a$ and $L_n^h$ for the nine years in this study. Table 2 gives the mean dates for significant phenological events. The most striking feature was the large inter-annual variability in spring leaf-emergence dates, with differences for leaf emergence and expansion of up to four weeks. The inter-annual differences in leaf emergence were tightly coupled to differences in $\sum D$, which also occurred predominantly in spring. Contrast 1998, when $L$ reached 50% of $L_n$ on May 11th, with 1996 and 2002, when $L$ reached 50% of $L_n$ on June 6th and 8th, respectively. The speed of leaf emergence also varied among years. The 10–90% leaf-emergence period averaged 28 ± 9 days but ranged from 17 days in 1997 to 45 days in 2000. Hazelnut leaf emergence lagged aspen leaf emergence by 17 ± 5 days at 10% foliation and 12 ± 3 days at 90% foliation.

Fig. 7 puts the leaf-emergence dates from the nine years of this study in an historic context, based on the daily temperature record from the Prince Albert Airport, 1900 to 2003. The estimates of the 50%-foliation date for total LAI were based on $\sum D = 181$ °C days, with degree-day accumulation beginning on day three of the first three-day period in spring when mean daily air temperature exceeded 5 °C on all
three days. The analysis showed that the study period (1994 and 1996–2003) had historically representative leaf-emergence dates, spanning the 5th to the 87th percentiles. Two of the study years (1998 and 2001) had extreme warm springs and early leaf emergence while two (1996 and 2002) had extreme cool springs and late leaf emergence. Least-squares linear regression showed a small but significant 6-day advance in the estimated 50%-foliation date between 1900 and 2003, which is considerably smaller than the observed range of 22 days in the nine years of this study. The 22-day versus 6-day contrast illustrates the large magnitude of inter-annual climatic variability vis-à-vis the subtler trend of climatic warming.

In contrast to the variable spring leaf-emergence dates, the autumn leaf-senescence dates were similar among years. The autumn rise in $\tau_h$ occurred during a narrow window and showed hazelnut leaf senescence to begin on 14–19 September and end on 21–28 September in all seven years with $\tau_h$ measurements. We will see in Section 3.5 that the $F_{NEP}$ measurements showed an equally distinct window for leaf senescence. The autumn rise in $p_d/p_s$, which was used to identify the aspen leaf senescence period, was a little less distinct, beginning between 11 and 23 September and ending between 26 September and 18 October. The year-to-year similarity in the timing of leaf senescence suggests that senescence is controlled by day length (Bondeau et al., 1999). We believe that an early frost would override the initiation of senescence by day length but there were no early frosts in the study period; the earliest frost, as measured by the canopy temperature, occurred in 1997 on September 19th.

The amplitude and timing of the annual LAI cycle at the Old Aspen site are very similar to those reported for temperate deciduous forests (Greco and Baldocchi, 1996; Schmid et al., 2000; Staebler et al., 2000; Saigusa et al., 2003). The primary difference is in the timing of leaf senescence. At the temperate deciduous forest sites, leaf senescence extends into mid-to-late October and varies in timing among years. At the Old Aspen site, leaf senescence occurs earlier (mid-to-late September), is more rapid (1–2 weeks) and has similar timing each year.

The total LAI at the Old Aspen site is divided almost evenly between the overstory and understory. The viability of the hazelnut understory results from the openness of the aspen overstory, which is both sparse ($L_a \sim 2.5$) and clumped ($\Omega_e \sim 0.69$). Even when fully leafed, the aspen overstory allows a daily mean PAR transmittance of 18% (1997–2003 mean) or a clear-sky transmittance of 26% (Chen et al., 1997). The relatively high PAR transmittance through the aspen overstory sustains substantial rates of understory photosynthesis throughout the growing season (Black et al., 1996; Grant and Nalder, 2000). In contrast, the viability of the understory in other deciduous forest ecosystems results from its phenological adaptation to early leaf emergence and late senescence. For instance, Gill et al. (1998) reported seasonal measurements of photosynthesis from an understory of hardwood saplings and shrubs in a mature, northern beech-maple forest in central New Hampshire. The prime periods for understory carbon sequestration were spring and autumn, before the overstory leafed out and after it senesced and abscised. At the Old Aspen site, it is the aspen overstory that is adapted to early leaf emergence and late senescence (Lechowicz, 1984), with the $L_h$ lagging $L_a$ at leaf emergence and leading it at senescence.

### 3.5. LAI and $F_{NEP}$

Fig. 8 compares the annual cycles of LAI and $F_{NEP}$. The spring rise in $F_{NEP}$ during leaf emergence occurs in close synchrony with $L$, substantiating the earlier conclusion of Black et al. (2000) and Barr et al. (2002) that inter-annual variability in $F_{NEP}$ in boreal
deciduous ecosystems is largely controlled by spring temperature via its influence on the timing of leaf emergence. We identified the onset of photosynthesis in spring on the basis of the $F_{\text{NEP}} - Q_1$ relationship, as the time when $P_\alpha$ (Eq. (6)) became significantly greater than zero. The photosynthesis-onset date varied among years from May 5th to June 3rd and occurred on average eight days after the ecosystem began to green up (Table 2), at a mean $L$ of $1.02 \pm 0.55$. The subsequent spring rise in $F_{\text{NEP}}$ was tightly coupled to the increase in $L$. Three independent phenological indicators converged in late May to late June to mark the end of leaf emergence: the completion of green up (as evidenced by near-minimum $\rho_p / \rho_s$), 90% hazelnut leaf emergence, and near-maximum photosynthesis (Table 2). The mean duration from the beginning of green up to near-maximum photosynthesis at the Old Aspen site was 34 days, compared with 50 days for an oak-sycamore forest in the UK (Morecroft and Roberts, 1999).

In autumn, $F_{\text{NEP}}$ was also coupled to $L$ but with less inter-annual variability than in spring; during most years, $L$ and $F_{\text{NEP}}$ both declined rapidly during a two-week period in late September when the canopy senesced (Fig. 8). The three indicators of leaf senescence (the rise in $\rho_p / \rho_s$, the rise in $r_h$ and the drop in $P_\alpha$) showed similar starting dates in mid September but different ending dates. The rise in $r_h$ showed the completion of hazelnut senescence on 21–28 September, on average five days before $P_\alpha$ dropped to zero and 11 days before the rise in $\rho_p / \rho_s$ showed the completion of aspen senescence. In two years, the autumn rise in $\rho_p / \rho_s$ showed an extension of aspen senescence into mid October, two weeks after photosynthesis had ended. We conclude that the rise in $\rho_p / \rho_s$ during senescence can become decoupled from the decline in photosynthesis in some years and that the most reliable delineator of the senescence period is the autumn decline in $P_\alpha$ (Eq. (6)).

The modeling study of Hogg (1999) showed that a change in the timing of autumn leaf senescence would significantly impact the annual carbon budget of deciduous forest ecosystems. Our observations at the Old Aspen site cannot be used to substantiate this result because the observed inter-annual differences in leaf senescence were small. The primary differences among years occurred in spring. This may be generally true of boreal deciduous ecosystems. It does not appear to be true of temperate deciduous ecosystems, where greater inter-annual variability in the timing of autumn senescence has been observed (Goulden et al., 1996; Staebler et al., 2000; Saigusa et al., 2002).

Annual $F_{\text{NEP}}$ at the Old Aspen site was highly variable among years, ranging from a minimum of $54 \text{ g C m}^{-2} \text{ y}^{-1}$ in 1996 to a maximum of $367 \text{ g C m}^{-2} \text{ y}^{-1}$ in 2001 (Table 1). Our earlier analysis of 1994–1999 showed that the primary climatic control on annual $F_{\text{NEP}}$ was spring temperature (Black et al., 2000). Drought was an important secondary control, although in some years drought had a positive effect on $F_{\text{NEP}}$ because it suppressed $R$ more than $P$ (Griffis et al., 2004). The data from 2000 to 2003, which include years with extreme cool and warm springs and an extended drought, strengthen these earlier conclusions. They also highlight the importance of the phenology of LAI as a primary biophysical control on $F_{\text{NEP}}$. We isolated the critical climatic and biophysical controls on $F_{\text{NEP}}$ using a least-squares multiple linear regression analysis, with annual $F_{\text{NEP}}$ as the dependent variable and ten independent variables, including mean annual air temperature, mean April–May air temperature, mean annual soil temperature, total annual precipitation, total precipitation from the current and previous years, annual cumulative degree days, cumulative degree days on May 31st, $L_x$, $L_{ax}$, and canopy duration (defined, following Norby et al. (2003), as the number of days with $L > 0.5L_x$). The regression analysis was run for all possible combinations of the independent variables. The best regression model was selected as the one that produced the lowest $p$-value (the probability of a type one error). The best regression
model, with a p-value of 0.017 and a coefficient of determination \((R^2)\) of 0.74, had two independent variables, both of which were related to LAI: the canopy duration and \(L_x\). The regression showed increases in annual \(F_{\text{NEP}}\) of 6.9 g C m\(^{-2}\) for each additional day in leaf and 83 g C m\(^{-2}\) for each additional unit of LAI. The positive impacts of canopy duration and \(L_x\) on annual \(F_{\text{NEP}}\) were due to associated increases in \(P\); annual \(R\) was essentially independent of both canopy duration and \(L_x\) (Table 4). Annual \(F_{\text{NEP}}\) was more closely related to these two “LAI” variables than to any of the climatic variables perhaps because their effect was direct; the primary climatic controls on \(F_{\text{NEP}}\) were mediated through LAI. We conclude that climatic factors that control leaf phenology and \(L_x\), such as spring temperature, drought and frost, have a greater impact on annual \(F_{\text{NEP}}\) in boreal deciduous forests than climatic factors that affect \(P\) and \(R\) directly, such as growing-season temperature, soil moisture and cloudiness (Goulden et al., 1996; Barr et al., 2002; Granier et al., 2002; Knohl et al., 2003; Schmid et al., 2003; Griffis et al., 2004).

Previous studies have reported a slightly smaller increase in \(F_{\text{NEP}}\) with increasing growing-season length (GSL). Baldocchi et al. (2001) compared eleven FLUXNET deciduous forest sites, including the Old Aspen site (1994–1998), and found an overall increase of 5.7 g C m\(^{-2}\) in \(F_{\text{NEP}}\) for each additional day in the carbon uptake period. The GSL accounted for 83% of the variance in annual \(F_{\text{NEP}}\). Carrara et al. (2003) reported a gain of 3.5 g C m\(^{-2}\) y\(^{-1}\) for each additional day of GSL, based on five years of measurements above a temperate mixed-wood forest in Belgium. White et al. (1999) reported a 4.9 g C m\(^{-2}\) y\(^{-1}\) increase in annual \(F_{\text{NEP}}\) for each one-day extension to the growing season, based on a modeling study of twelve temperate deciduous forest sites in the north-eastern USA. At the Harvard hardwood forest in central Massachusetts, 1991–2000, White and Nemani (2003) found an increase of 5.4 g C m\(^{-2}\) y\(^{-1}\) in \(F_{\text{NEP}}\) for each additional day in the carbon uptake period. However, further analysis led them to advise against the use of the carbon uptake period as a measure of the GSL in studies of the phenological controls on \(F_{\text{NEP}}\). The GSL is more appropriately defined using measures that are independent of measured \(F_{\text{NEP}}\) such as the frost-free period or the canopy duration. When they repeated the analysis using the canopy duration (defined in their study as the number of days from the onset of leaf emergence to the end of leaf senescence), they found that annual \(F_{\text{NEP}}\) and canopy duration were uncorrelated. The lack of correlation at the Harvard forest substantiated their modeling analysis of temperate deciduous forests in the eastern USA, which showed an extremely weak correlation between annual \(F_{\text{NEP}}\) and canopy duration except for years when the warm-season precipitation was above normal.

Our results from the Old Aspen site are different than those of White and Nemani (2003) and show a significant, positive correlation between \(F_{\text{NEP}}\) and canopy duration. The difference between the two studies may be methodological or it may be real. The definitions for canopy duration are subtly different. Our definition (the number of days with \(L > 0.5L_x\)) may lead to a closer coupling to \(P\) than their definition (the number of days with \(L > 0\)), given the low values for carbon uptake at \(L < 0.5L_x\) and the tight coupling that was observed between \(P_x\) and several independent indices of leaf out and leaf senescence (Table 2). Alternately, the differences may be real and show a fundamental difference between temperate and boreal deciduous forest ecosystems. In general, the observed increases in \(F_{\text{NEP}}\) with increasing GSL at the temperate deciduous forest sites reported above were smaller than at the Old Aspen site and the correlations between \(F_{\text{NEP}}\) and canopy duration were weaker. One important difference between sites is in the timing of

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>(a_0) (g C m(^{-2}) y(^{-1}))</th>
<th>(a_1) (g C m(^{-2}) y(^{-1}) d(^{-1}))</th>
<th>(a_2) (g C m(^{-2}) y(^{-1}))</th>
<th>(R^2)</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(F_{\text{NEP}})</td>
<td>–1003</td>
<td>6.9</td>
<td>83</td>
<td>0.74</td>
<td>0.017</td>
</tr>
<tr>
<td>(R)</td>
<td>747</td>
<td>2.2</td>
<td>18</td>
<td>0.05</td>
<td>0.851</td>
</tr>
<tr>
<td>(P)</td>
<td>–257</td>
<td>9.0</td>
<td>101</td>
<td>0.61</td>
<td>0.060</td>
</tr>
</tbody>
</table>

The regression equation is, e.g., \(F_{\text{NEP}} = a_0 + a_1\delta + a_2L_x\).
inter-annual differences in GSL. At the temperate forest sites, the inter-annual differences in \( F_{\text{NEP}} \) and GSL were split between spring and autumn, whereas at the Old Aspen site, the differences occurred primarily in spring. This is significant because of the asymmetry in the annual \( F_{\text{NEP}} \) cycle; days added to the growing season in spring cause a greater increase in \( F_{\text{NEP}} \) than days added in autumn (Chen et al., 1999). Another potential difference between sites is in the dependence of \( R \) on GSL. At the Old Aspen site, annual \( R \) was independent of canopy duration, strengthening the linkage between canopy duration and \( F_{\text{NEP}} \). This may not be the case elsewhere.

4. Summary and conclusions

This study describes the inter-annual variability in the phenology of LAI at the BERMS Old Aspen site, 1994 and 1996–2003, and relates inter-annual differences in \( F_{\text{NEP}} \) to the seasonal cycle of LAI. PCA measurements of \( L_x \) agreed well with autumn litterfall collection and showed moderate inter-annual variability for the aspen overstory \( (L_{ax} = 2.44 \pm 0.30) \) and the hazelnut understory \( (L_{ux} = 1.98 \pm 0.44) \). The observed inter-annual variability in annual maximum LAI was small but significant, supporting the conclusion of Le Dantec et al. (2000) that annual maximum LAI in mature forest stands is relatively stable among years; the observed inter-annual variability in \( L_x \) at this site was certainly smaller than the spatial variability in \( L_x \) across the disturbance-dominated, boreal landscape. However, the PCA measurements were too sparse to allow detailed inter-annual comparisons of the timing of leaf emergence and senescence. To enable comparisons of the seasonal LAI cycle among years, we developed a robust method to estimate the annual LAI cycle from sparse measurements. The method estimated daily values of \( L_a \) and \( L_h \) from empirical models that were fit to the PCA measurements, with cumulative degree days, shortwave reflectance, PAR reflectance, and PAR transmittance as the independent variables. The method was designed to fill gaps in the annual cycle and has no predictive value. Its parameters are local. The method performed well during the leaf-emergence and fully-leaved periods and adequately during leaf senescence. The ratio of the PAR to shortwave reflectance, which is related to the broad-band NDVI, had a particularly distinct LAI signature during leaf emergence.

Analysis of nine annual LAI cycles at the BERMS Old Aspen site revealed two primary features that varied among years—the timing of leaf emergence in spring and the value of \( L_x \). The timing of autumn senescence was similar among years. The timing of leaf emergence varied by up to four weeks and was controlled by cumulative degree days. Inter-annual differences in \( L_x \), which varied between 3.66 and 5.22, were related to defoliation and drought stresses in the previous years. Analysis of the historic temperature record showed that the nine years of this study were very representative of historic leaf-emergence dates and included two early and two late leaf-emergence years. A multiple linear regression analysis relating annual \( F_{\text{NEP}} \) to a number of simple climatic and biophysical variables showed that a relatively simple model performed best, with canopy duration and \( L_x \) as the independent variables.

Many studies are showing the importance of climatic warming for northern deciduous ecosystems (Goulden et al., 1996; Frolking, 1997; Myneni et al., 1997; Black et al., 2000; Baldocchi et al., 2001). The greatest seasonal warming in the boreal zone of Canada is occurring in winter and spring (Zhang et al., 2000). Spring warming hastens snowmelt (Jarvis and Linder, 2000) and leaf emergence, lengthens the growing season and may contribute to higher growing-season soil temperatures (Goulden et al., 1998) and lower soil moisture, all of which affect the carbon and water balances. The results of this study substantiate our earlier conclusion that the primary climatic control on annual \( F_{\text{NEP}} \) in boreal deciduous ecosystems is spring temperature (Black et al., 2000) and strengthens the linkage between spring temperature, the timing of leaf emergence, \( P \) and \( F_{\text{NEP}} \). The spring rise in LAI has a large and direct effect on \( P \) whereas \( R \) is controlled primarily by soil temperature and moisture and is largely independent of LAI. A companion paper (Barr et al., in preparation) will explore the relative importance of spring temperature and drought as critical climatic controls on \( F_{\text{NEP}} \), \( P \) and \( R \) at this site.

Acknowledgements

We gratefully acknowledge the work of Dave Wieder, Charmine Hrynkiw and Paula Pacholek, who
Appendix A. Estimating annual $F_{\text{NEP}}, P$ and $R$

The procedure to estimate annual $F_{\text{NEP}}, P$ and $R$ from half-hour measurements of $F_{\text{NEP}}$ first derives $P$ and $R$ from measured $F_{\text{NEP}}$ and then fills gaps in $P, R$ and $F_{\text{NEP}}$ using simple empirical models that are constrained by the measured data. The data are processed one year at a time. The post-processing procedure as described below has been adopted as the standard method for the Fluxnet-Canada Research Network. It makes use of two simple annual empirical relationships determined from measured data. One is between $R$ and soil temperature ($T_s$) at a shallow depth and the other is between $P$ and $Q_1$ above the stand. For each relationship, parameters are first obtained for the annual analysis. One parameter per relationship is then allowed to vary over time with the other parameters held constant; its temporal variation accounts in part for changes in other environmental variables, such as LAI, soil water content and air saturation deficit.

The time-varying parameters are determined using a flexible moving window approach. Within each window, the parameter is calculated as the slope of the linear regression between estimates of $R$ (and $P$) obtained from the annual relationships and $R$ (and $P$) from the measurements (see below). The implementation of the moving window uses a fixed number of measured (non-missing) data points rather than a fixed period of time. The window is 100 data points wide, moved in an increment of 20 points at a time. For each window, the obtained value of the time-varying parameter is assigned to the mean time of the 100 data points (i.e. usually near the centre of the window). The values of the time-varying parameters for each individual half-hour period are then estimated by linear interpolation. These adjusted relationships are then used to fill data gaps. The sensitivity of $R$ and $P$ to $T_s$ and $Q_1$, respectively, is largely determined by the annual relationships, but is modified to some extent by the time-varying parameters within each window period.

The post-processing steps are as follows. First, the net ecosystem exchange ($F_{\text{NEE}}$) is estimated as the sum of the measured eddy ($F_e$) and air-column storage ($S_a$) fluxes,

$$F_{\text{NEE}} = F_e + S_a$$  \hspace{1cm} (A.1)

where

$$S_a = \int_0^{z_{\text{ec}}} \frac{\rho_a}{M_a} \frac{dC}{dr} \, dz$$  \hspace{1cm} (A.2)

where $z_{\text{ec}}$ is the height above ground level of the eddy-covariance measurement, $\rho_a$ is the density of dry air, $M_a$ is the molecular weight of dry air, and $C$ is the CO₂ molar mixing ratio. Two adjustments are applied to $F_{\text{NEE}}$: the nighttime $F_{\text{NEE}}$ data are excluded at low-$u_*$ (here, $u_* < 0.35 \text{ m s}^{-1}$) and an energy-balance-closure adjustment is applied by dividing the measured $F_{\text{NEE}}$ by the fractional energy balance closure (here, 0.873), calculated as the ratio of the sum of the sensible and latent heat fluxes to the available energy flux. $F_{\text{NEP}}$ is then estimated as $-F_{\text{NEE}}$. Small gaps in $F_{\text{NEP}}$ (four half-hour periods or less) are filled by linear interpolation before larger gaps are filled using the procedure outlined below.

Next, measured $R$ is estimated as $R = -F_{\text{NEP}}$ during periods when $P$ is known to be zero, i.e., at night and during both night and day in the cold season (periods when both air ($T_a$) and 2-cm soil ($T_s$) temperatures are less than 0 °C). An empirical, logistic relationship is then fit to the measured $R$ values from the entire year:

$$R = \frac{r_1}{1 + \exp[r_2(r_3 - T_s)\,]}$$  \hspace{1cm} (A.3)
where $r_1$, $r_2$ and $r_3$ are empirical constants. An additional empirical parameter, $r_w(t)$, is introduced into (A.3), resulting in

$$R = f(T_s,t) = \frac{r_w(t)r_1}{1 + \exp[r_2(r_3 - T_s)]}$$  \hfill (A.4)$$

where $r_w(t)$ is allowed to vary in time ($t$). Its value is estimated within a 100-point moving window as the slope of a linear regression (forced through zero) of the modeled $R$ estimates from (A.3) versus measured $R$. The $R = f(T_s,t)$ model (A.4) is used to estimate $R$ during the day and to fill gaps in $R$ at night.

Finally, $P$ is estimated as $F_{NEP} + R$ (daytime) or zero (nighttime and during periods when both $T_s$ and $T_a$ are less than 0°C). An empirical model is fit to the non-zero $P$ data for the entire year:

$$P = \frac{\alpha Q_l P_x}{\alpha Q_l + P_x}$$  \hfill (A.5)$$

where $\alpha$ is the quantum yield and $P_x$ is the photosynthetic capacity ($P$ at light saturation). Both parameters are treated as constants. An additional empirical parameter, $p_w(t)$, is introduced into (A.5), resulting in

$$P = f(Q_l,t) = \frac{p_w(t)\alpha Q_l P_x}{\alpha Q_l + P_x}$$  \hfill (A.6)$$

$p_w(t)$ is allowed to vary in time and is estimated within a 100-point moving window as the slope of a linear regression (forced through zero) of the modeled daytime $P$ from (A.5) versus measured $P$. The $P = f(Q_l,t)$ model (A.6) is used to fill gaps in $P$. Gaps in $F_{NEP}$ are filled using modeled $P-R$ from (A.4) and (A.6).

References


Bondeau, A., Kicklighter, D.W., Kaduk, J., the participants of the Potsdam NPP Model Intercomparison, 1999. Comparing global models of terrestrial net primary productivity (NPP); importance of vegetation structure on seasonal NPP estimates. Global Change Biol. 5 (Suppl. 1), 35–45.


