
Structural Phenology of the Leaf Community in the Canopy of a *Liriodendron tulipifera* L. Forest in Maryland, USA

Geoffrey G. Parker and Donna J. Tibbs

ABSTRACT. We measured the vertical dynamics of leaf area in a tall, tulip poplar (*Liriodendron tulipifera*)-dominated, deciduous forest on the Maryland coastal plain over three growing seasons (one intensively) using nondestructive, ground-based observations. Leaf area index (LAI) and leaf area density (LAD) were calculated by vertical level, time, and species; the time-integrated duration of leaf display (leaf area extent, LAE) was estimated by species and vertical level. In this stand LAI rises rapidly in the spring, declines slightly during the growing season, and then rapidly in the fall. In the intensively studied year, total LAI peaked at $7.1 \text{ m}^2\text{m}^{-2}$, LAE was $1259 \text{ m}^2\text{m}^{-2}\text{day}$, and the length of the canopy season (time from half-maximum LAI at leaf-out to the half-maximum at decline) was 191 days. The maximum growing season LAI, the date of leaf emergence, and the LAE differed among years, ranging $0.61 \text{ m}^2\text{m}^{-2}$, 14 days, and $261 \text{ m}^2\text{m}^{-2}\text{day}$, respectively. However, the timing of leaf fall was more consistent, ranging only 6 days. Each species differs in its height distribution, density, and timing of foliar display. In the canopy, leaf number, area, and duration are the bases of species importance; these differ substantially by species from typical importance values derived from stem-based attributes (density, basal area, biomass). FOR. Sci. 50(3):387–397.

Key Words: Canopy cover, foliage-height profile, leaf area index, spring ephemerals.

THE CANOPY OF A FOREST consists of the foliage, twig, epiphyte, and reproductive tissues of all crowns in the stand (Parker 1995, Moffet 2000). Canopy structure is the three-dimensional arrangement of those parts. Considerations of canopy structure generally focus on one or more of its spatial dimensions, describing structural status at an instant or short interval of time (Brokaw and Lent 1998, Bongers 2001). However, canopies are not static—they alter during forest development (e.g., Aber

1979, Brown and Parker 1994), change seasonally (e.g., Ford and Newbould 1971, Gholz et al. 1991), and respond to disturbances such as windstorms (e.g., Boucher 1990, Brokaw and Gear 1991), fires (e.g., Pyne 1982), and pest outbreaks (e.g., Campbell and Sloan 1977). Thus, canopy structure needs to be studied at multiple time scales.

Bulk properties and local characteristics of canopies can be affected by changes in structure at each of these time scales (e.g., Fritschen 1985). Furthermore, both temporal

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Acknowledgments: Larry Atkinson, Bob Bless, Donn Burkness, Donna Dwiggin, Ned Hall, Martha Melendez, John O'Neill, George Raspberry, Ed Schmitt, and Gretchen Seielstad helped collect, sort, and weigh leaves. Dan Shepherd made observations on change in autumnal coloration. Peter Stone advised on programming. Discussions with Martin Brown and Michael Lefsky helped refine some of the ideas. Partial support was provided by the Scholarly Studies and Environmental Sciences Programs (Grant Nos. 123E5001 and 85-320057) of the Smithsonian Institution.

Manuscript received April 15, 2002, accepted April 15, 2003.

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and spatial details of structure influence the extrapolation of functional attributes from physiological (e.g., leaf and minute) to ecosystem (e.g., whole canopy and hour/day) scales (e.g., Baldocchi 1993). Therefore, explicit consideration of both temporal and spatial aspects of structure are important for understanding and extrapolating canopy function.

The long history of plant phenological studies (e.g., Sparks and Carey 1995) has been dominated by observations of the timing and duration of bud-break, flowering, and fruiting events (e.g., Rathcke and Lacey 1985, DeKroon et al. 1991, Lechowicz 1995). A focus on the seasonality of leaf area is relatively recent (Lieth 1973, Taylor 1974, Lechowicz 1984, Bullock and Solis-Magallanes 1990, Koike 1990, Kikuzawa 1995). Advances in remote sensing allow quantification of changes in canopy reflectance at large spatial scales (e.g., Justice et al. 1985), often with temporal resolution for detecting events such as the vernal progression of leaf-out in the temperate zone (e.g., Schwartz 1994, Schwartz and Crawford 2002). Recently, increasing attention has been directed to the functional implications of the presence of foliage for whole-canopy radiative and aerodynamic properties (Sakai et al. 1997, Wilson and Baldocchi 2000) and regional weather (Fitzjarrald et al. 2001).

Quantification of whole-canopy structural dynamics has been attempted in monospecific stands (Ford and Newbould 1971, Gholz et al. 1991). Assessments of structural changes in mixed-species forests have generally involved measures summarizing variation across species and vertical position, such as the canopy cover or the leaf area index (LAI). We are not aware of studies of canopy dynamics that quantify vertical and species distributions. Without such information, the contribution of species to the aggregate canopy dynamics cannot be assessed.

Here we examine the growing season dynamics of canopy structure of a tall, fully deciduous forest on the Maryland coastal plain. The objectives were to: (1) examine the leaf area density, duration, and vertical structure for all species contributing significant leaf area, (2) compare the importance of species indicated by information on the distribution and display of canopy elements with that derived from observations on stems, and (3) assess between-year variation in phenological characteristics of the canopy and consider its implications for the growth of some species and whole-stand production.

Methods

Study Site

The study stand is a tall, mixed deciduous forest with a basal area dominated by *Liriodendron tulipifera*, located about 10 km SSE of Annapolis, Maryland (38°53' N, 76°33' W). The forest, of the "tulip poplar" association (Brush et al. 1980, Eyre 1980), is almost completely deciduous. The stand originated about 1887, following abandonment of a large pasture, and typifies the mature development stage of this forest type (Brown and Parker 1994). The composition of the forest and the vertical organization of the

canopy in part of this stand was reported by Parker et al. (1989). In this study area, there have been investigations on population dynamics of several herbs (Snow and Whigham 1989, DeKroon et al. 1991) and on understory response to gap formation (Whigham and O'Neill 1988, Whigham et al. 1993).

Leaf Area Profile

The relative vertical distribution of leaf area was measured on 23 occasions (from Apr. 14 to Dec. 7) before, during, and after the growing season of 1994 using the method of MacArthur and Horn (1969), as modified by Aber (1978) and Parker et al. (1989). In 1988 and 1991, there were 17 and 12 observations, respectively. A 200-mm telephoto lens calibrated to measure distances was used to generate a distribution of the heights of the nearest surface above the observer to within 1-m resolution. This method provides the relative distribution of total leaf area by height; it does not yield the actual leaf area (Brown and Parker 1994). Leaf species identity and the type of tissue (leaf, bark, bud, flower, and seed) were recorded as well as the vertical height of interception. In 1994, a total of 915 observations were taken at a total of 61 fixed positions at each sampling. The positions were the grid intersections and cell centers of a 125 × 125-m grid centered on the site of a meteorological tower. In the other years (1988 and 1991), 360 observations were taken per sampling at 24 locations within a circular plot in the center of the grid. In the autumn of 1992, observations were also made on the progress of autumn coloration in the same grid. In that study, the percentage of foliage that was green, pigmented, or brown was noted at each location, at each 5-m interval of height.

The Forest Floor and Ground Layers

At each sampling period in 1994, we noted the composition of the canopy level below the camera height (i.e., between 0 and 1 m) and of the forest floor. At each sampling location, three plumb lines were dropped and the height, tissue, and species of contact within that layer noted. We also noted the character of the forest floor (soil, woody litter, or leaves) and, when applicable, the species of litter. The mean number of contacts over all 183 sampling points was an estimate of LAI in the 0–1-m layer.

Total LAI

Leaves were regularly retrieved from 24 litter collectors, weekly in the fall abscission period (Sept. 1 - Dec. 15) and monthly otherwise. LAI was obtained as the mean of the leaf area collected per litter collector divided by its aperture. Species leaf areas were obtained from leaf masses per basket using species-specific equations of the sort described in Parker et al. (1989). Leaf areas were summed by species to yield total collector leaf areas. The litterfall LAI combined with the relative profile provided the height distribution of actual LAI. The amount of leaf area per height level is also a measure of the leaf area density (LAD, m²m⁻³).

LAI-cover Relation

The relation between LAI and leaf cover (C_1 , the fraction of the zenith obscured by leaves) developed during the

litterfall season was used to estimate canopy LAI for other periods. Leaf cover was obtained from the optical profile observations. The canopy LAI on a date in the litterfall season was obtained as the total LAI of leaves fallen during the complete litterfall period minus the cumulative LAI fallen to that date.

The resultant relation between C_1 and LAI (termed the overlap relation) was described with the following expression:

$$C_1 = a_0 + a_1 (1 - e^{-a_2 * LAI}) \quad (1)$$

where the parameters a_0 , a_1 , and a_2 reflect the intercept, asymptote, and initial slope of the relation. PROC NLIN of the Statistical Analysis System (SAS Institute 1990a and 1990b) was used to fit the nonlinear model. LAI during leaf expansion and the mid-growing season was then estimated from the cover measurements by inverting Equation 1, that is,

$$LAI = -\frac{1}{a_2} \ln\left(\frac{a_1 + a_0 - C_1}{a_1}\right) \quad (2)$$

Adjustments to LAD

Some estimates of LAD were adjusted to account for the likely presence of leaves not directly observed. Occasionally, leaves of a species usually observed at one height were not seen. Such differences are most likely due to sampling errors than to short-term turnover of leaf area. In the optical point quadrat method, each observation of a leaf can represent a large amount of foliar area, especially in the upper levels. Thus, small variations in sampling can imply large differences in LAD. Dates having no LAD compared with both adjacent dates for the same species and height level were replaced with interpolated values. When this increased the overall LAI on that date, all values were adjusted to sum

to the known LAI. These adjustments tended to smooth the LAD dynamics but did not alter the LAI.

Leaf Area Extent (LAE)

For 1994, the time integral of LAI (LAE in $m^2m^{-2}day$), was estimated for each species and interval of vertical height across the entire growing season using the trapezoidal rule (Press et al. 1992). The LAE for a species was estimated as the sum across all canopy levels; the stand LAE is the sum of all species LAE. LAE for 1988 and 1991 was estimated by integrating the LAI(t) curve. Because sampling errors may affect the estimate of species presence, we estimated the times of foliar appearance and disappearance as the date when modeled LAI first reached half the peak LAI for each species. Similarly, the time of foliar disappearance was the date when LAI declined to half the peak value.

Time-Height Sections of LAD

A representation of the vertical distribution of leaf area throughout the growing season was produced for each major species and for all species combined by contouring values of equal LAD (m^2m^{-3}). Grid points were interpolated with an inverse-square estimator, and the contour lines in the diagrams were smoothed using a cubic spline (Golden Software, Inc. 1999).

Results

Stem Composition of the Forest

Carpinus, *Fagus*, and *Cornus* are most numerous, together accounting for more than 82% of the stems (Table 1). However, the basal area is dominated by *Liriodendron* (49.2%), *Carya* (14.1%), *Quercus* (12.8%), and *Fagus* (10.6%). The largest trees are *Quercus coccinea*, *Q. velutina*, *Q. alba*, and *Liriodendron tulipifera*.

Table 1. Total density and basal area of live stems greater than 2.5 cm dbh in the 1.56-ha stem-mapped permanent plot at the SERC tower during 1994. The species are sorted by importance value (IV), the sum of percent density and percent basal area.

Species	n	%	Basal area		IV
			m^2ha^{-1}	%	
<i>Liriodendron tulipifera</i>	128	6.61	26.53	49.21	55.82
<i>Carpinus caroliniana</i>	789	40.75	1.64	3.04	43.79
<i>Fagus grandifolia</i>	458	23.66	5.69	10.56	34.22
<i>Cornus florida</i>	345	17.82	1.18	2.19	20.01
<i>Carya tomentosa</i>	67	3.46	4.96	9.20	12.66
<i>Liquidambar styraciflua</i>	49	2.53	3.67	6.81	9.34
<i>Quercus alba</i>	19	0.98	3.94	7.31	8.29
<i>Carya glabra</i>	25	1.29	2.64	4.91	6.20
<i>Quercus velutina</i>	11	0.57	2.44	4.53	5.10
<i>Nyssa sylvatica</i>	17	0.88	0.54	1.00	1.88
<i>Quercus coccinea</i>	2	0.10	0.48	0.90	1.00
<i>Acer rubrum</i>	3	0.15	0.03	0.06	0.21
<i>Quercus rubra</i>	3	0.15	0.03	0.05	0.20
<i>Quercus michauxii</i>	2	0.10	0.003	0.01	0.11
7 others ^a	18	0.92	0.125	0.23	1.15
Sums	1936	100	53.91	100	200
per hectare rate	1,239		34.50		

^a In order of importance: *Ulmus americana*, *Ilex opaca*, *Vitus* sp., *Fraxinus americana*, *Albizia julibrissin*, *Amelanchier arborea*, and *Sassafras albidum*.

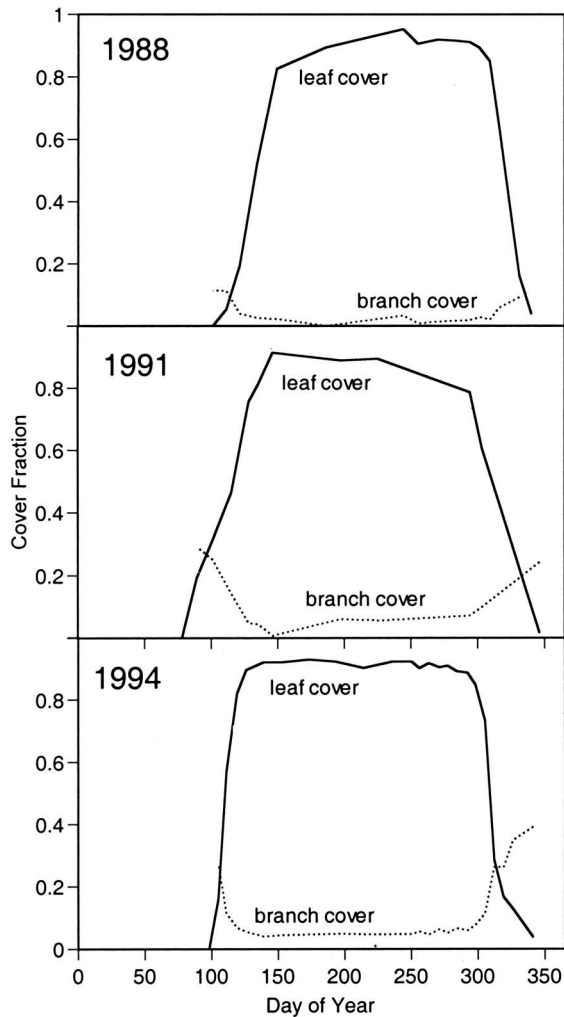


Figure 1. Dynamics of leaf (C_l) and branch (C_b) cover during the growing seasons of 1988, 1991, and 1994.

Change in Leaf and Branch Cover

There is a marked seasonal change in the cover of leaves (C_l) and branches (C_b) (Figure 1). In each year, maximum mid-season C_l exceeds 0.9. Branch cover was highest, as much as 0.39, when leaves were absent, but least, 0.04–0.06, in the middle of the growing season. C_l and C_b are inversely correlated in each year (the Pearson correlation coefficient, r , was -0.92 in 1988; -0.94 in 1991; and -0.98 in 1994). Branches are hidden by leaves from view from below.

Foliar Overlap During Leaf Abscission

The relation between LAI and leaf cover during the abscission period is positive but nonlinear (Figure 2). Note that cover rises almost linearly when $LAI \approx 1.0$. The slope of the relation declines progressively at high LAI; above $LAI \approx 5.0$, cover changes very little.

For 1994, the equation predicting LAI from C_l is

$$LAI = -2.3849 \ln(1.077 - 1.101C_l) \quad (3)$$

which derives from Equation 2. The fitted values of the parameters for each year are listed in Table 2.

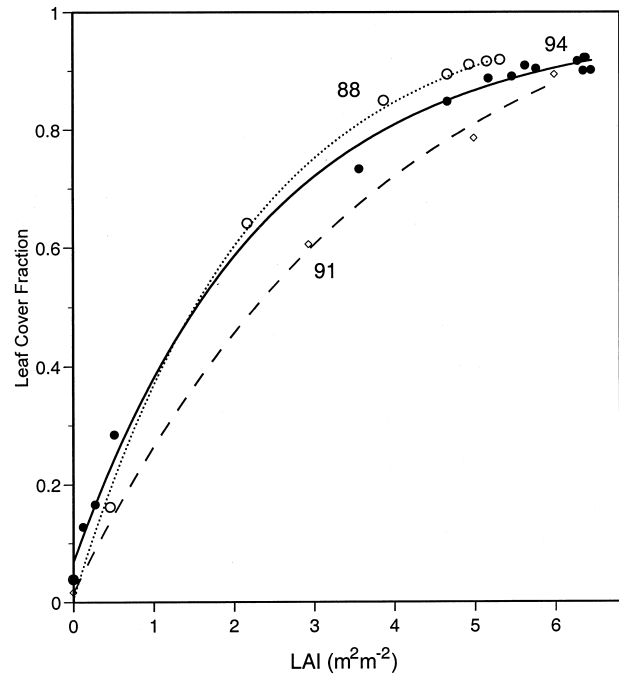


Figure 2. LAI-cover relationship during the abscission period in 1988, 1991, and 1994.

Table 2. Coefficients of the negative exponential function (Equation 1) describing the relation between autumnal leaf cover and leaf area index (the overlap function) for each year of measurement and for all years combined.

Year	a_0	a_1	a_2	R^2 ^a	n
1988	0.00863	1.0081	0.44486	0.999	10
1991	0.01784	1.1018	0.25410	1.00	4
1994	0.06995	0.90830	0.41930	0.999	15
All	0.03192	0.94769	0.42019	0.997	29

^a Coefficient of determination is estimated from nonlinear least-squares regression as $SS_{\text{model}}/SS_{\text{total}}$.

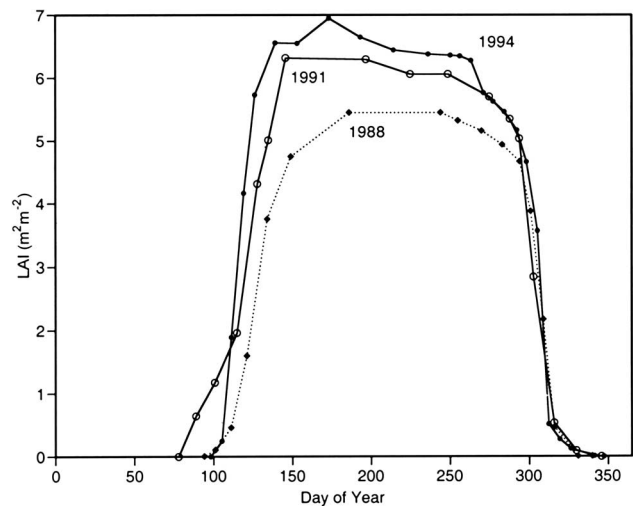


Figure 3. Dynamics of total LAI over the growing season in 1988, 1991, and 1994.

Dynamics of LAI

The change in total LAI in this canopy throughout the growing season of 1994 (day of the year 105–341) was dramatic (Figure 3). The dates of half-expansion and half-decline were estimated to fall on days 114 and 305, respectively (Table 3). The expansion date nearly coincides with the onset at this location of spring, day 112, estimated from weather records by Fitzjarrald et al. (2001, Figure 6). Also, this 191-day interval is similar to the 181-day growing season length estimated for this region in Lull (1968). Vernal foliar expansion was more rapid (approximately $0.30 \text{ m}^2\text{m}^{-2}\text{day}^{-1}$ on day 114) than was the autumnal decline (about $0.13 \text{ m}^2\text{m}^{-2}\text{day}^{-1}$ on day 305).

Temporal differentiation between the species is apparent when LAI change is examined (Figure 4). First to appear are several herbaceous, ground-layer species that emerge by day 105, persist for several months, and decline rapidly by midsummer. *Podophyllum* is the most prominent species of the spring ephemerals until day 183, when it begins to decline. *Arisaema*, *Claytonia*, and *Cardamine* also emerge

early but persist only briefly (Table 3). *Smilacina* emerges later but also does not last. Together, these five species account for 96% of the LAD in the ground layer. Note that *Sanguinaria*, *Tipularia*, *Chaemophila*, and *Cynoglossum*, though present within the study area, were not contacted during the survey.

Of the woody species, *Liriodendron tulipifera* expands first, followed by *Fagus grandifolia*, *Carya tomentosa*, and *Carpinus caroliniana*. At the end of the growing season, *Nyssa sylvatica*, *Quercus falcata*, and *Carya glabra* leaves are dropped first, followed by *Cornus*, *Carpinus*, and *Liquidambar*. The last leaves to fall were of other *Quercus*, *Liriodendron*, *Fagus*, and *Carya tomentosa*.

The first species to change color in the autumn were *Rhus radicans* and *Nyssa*, followed by *Cornus* and *Liriodendron*. Peak coloration fell on day 303. Species generally dropped their leaves in the order they turned color. The delay between the pattern of leaf greening and litterfall was about one week. Though some *Fagus* leaves persist into winter, this component represents a small fraction (<5%) of beech foliage and much less for the entire canopy.

Table 3. Leaf area extent and dates of half-emergence and half-loss for all species, grouped by lifeform.

Species	LAE ($\text{m}^2\text{m}^{-2}\text{day}$)	Date on	Date off
Trees			
<i>Fagus grandifolia</i>	366.49	112	307
<i>Liriodendron tulipifera</i>	181.47	108	308
<i>Carya tomentosa</i>	174.21	115	307
<i>Carpinus caroliniana</i>	149.72	116	298
<i>Cornus florida</i>	111.63	119	297
<i>Liquidambar styraciflua</i>	71.38	119	299
<i>Quercus alba</i>	43.50	124	310
<i>Quercus velutina</i>	41.31	120	305
<i>Carya glabra</i>	30.97	128	291
<i>Quercus falcata</i>	19.53	131	290
<i>Nyssa sylvatica</i>	19.03	126	291
<i>Quercus coccinea</i>	12.64	119	305
<i>Quercus rubra</i>	0.34	*	*
Total trees	1,222.22	14	305
Vines			
<i>Rhus radicans</i>	8.79	134	282
<i>Lonicera japonica</i>	3.62	133	285
<i>Campsis radicans</i>	0.50		*
Total vines	12.91	132	284
Shrubs (<i>Lindera benzoin</i>)	0.59		*
Herbs			
<i>Podophyllum peltatum</i>	12.23	112	163
<i>Arisaema triphylla</i>	5.05	117	201
<i>Smilacina racemosa</i>	2.36	163	208
<i>Claytonia virginica</i>	1.41	102	116
<i>Cardamine diphylla</i>	1.18	102	153
<i>Solidago caesia</i>	0.15	*	*
<i>Clintonia umbellulata</i>	0.13	*	*
<i>Viola</i> sp.	0.32	*	*
<i>Urtica dioica</i>	0.04	*	*
<i>Galearis spectabilis</i>	0.04	*	*
<i>Duchesnea indica</i>	0.05	*	*
Unknown herbs	0.25	*	*
Total herbs	23.21	103	169
Total	1,258.94	114	305

* Not readily calculated

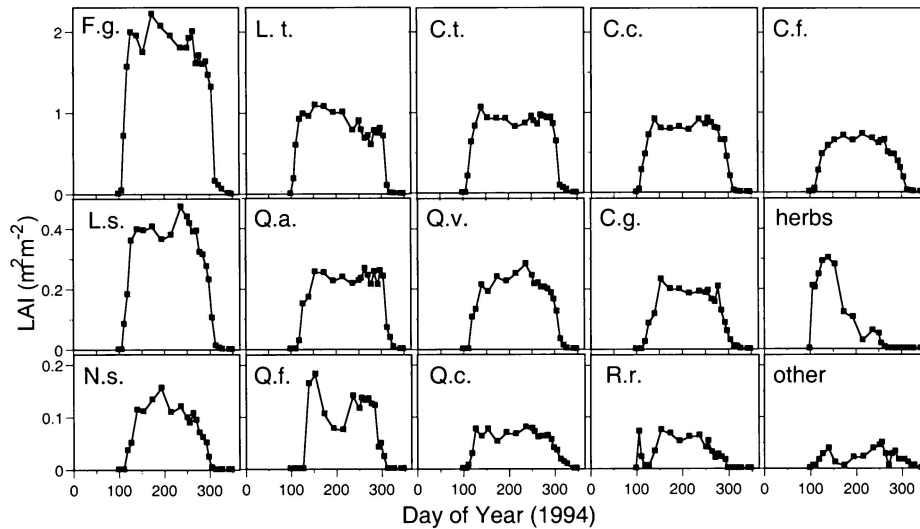


Figure 4. Dynamics of LAI for each species in the stand. Note that the vertical axis differs for each row of panels. Species depicted are *Fagus grandifolia* (F.g.), *Liriodendron tulipifera* (L.t.), *Carya tomentosa* (C.t.), *Carpinus caroliniana* (C.c.), *Cornus florida* (C.f.), *Liquidambar styraciflua* (L.s.), *Quercus alba* (Q.a.), *Quercus velutina* (Q.v.), *Carya glabra* (C.g.), *Nyssa sylvatica* (N.s.), *Quercus falcata* (Q.f.), *Quercus coccinea* (Q.c.), *Rhus radicans* (R.r.), and minor species (other).

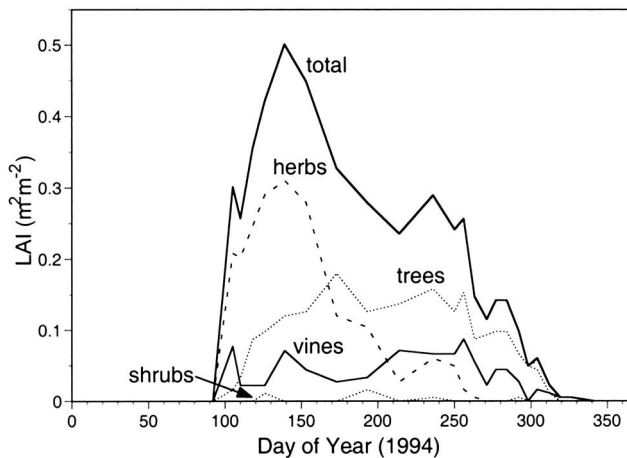


Figure 5. Dynamics of the ground layer, showing the change in LAI of different life-forms.

Mean Foliar Height

Despite the large seasonality in LAI, the mean leaf height (weighted by the LAD at each height), was relatively constant throughout the growing season, ranging from 14 to 17 m. In early canopy expansion, when the ephemerals in the ground layer (0–1 m) are abundant, the mean height is somewhat lower. Initially, the highest concentration of stand LAI is in this layer (from more than 50% on day 105, declining rapidly to less than 5% after day 153). After the upper canopy (initially *Liriodendron tulipifera*) emerges, mean heights for individual species varied little throughout the season. At the end of the growing season, mean height declines again, this time reflecting the tendency of lower *Fagus* leaves to be retained.

Foliar dynamics were most pronounced in the ground layer. Figure 5 shows the LAD in this zone for several

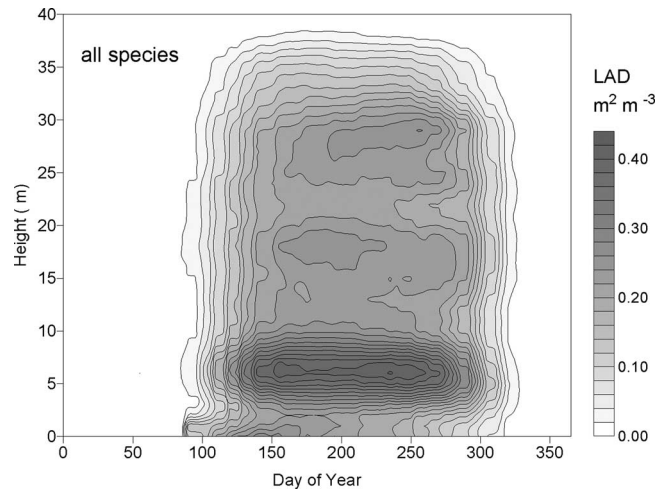


Figure 6. Time-height section of total leaf area density across the growing season. Contour units are $0.02 \text{ m}^2 \text{ m}^{-3}$.

different life forms. Note the progression from early dominance by herbs to shrubs and trees.

Temporal and Vertical Patterns

The vertical distribution of LAD throughout the growing season in this stand has two height maxima: a pronounced understory peak and a broad overstory maximum (possibly itself the combination of two minor maxima) (Figure 6).

The temporal-vertical distribution of LAD clearly shows that some species are restricted to the overstory (e.g., *Liriodendron tulipifera* and *Quercus* spp.) and others to the understory (e.g., *Cornus florida* and *Carpinus caroliniana*); and, still others (e.g., *Liquidambar styraciflua* and *Fagus grandifolia*) to the mid-canopy (Figure 7).

Leaf Area Extent (LAE)

The time-integrated display of leaves in this stand over the growing season was estimated to be $1258.9 \text{ m}^2 \text{ m}^{-2} \text{ day}$

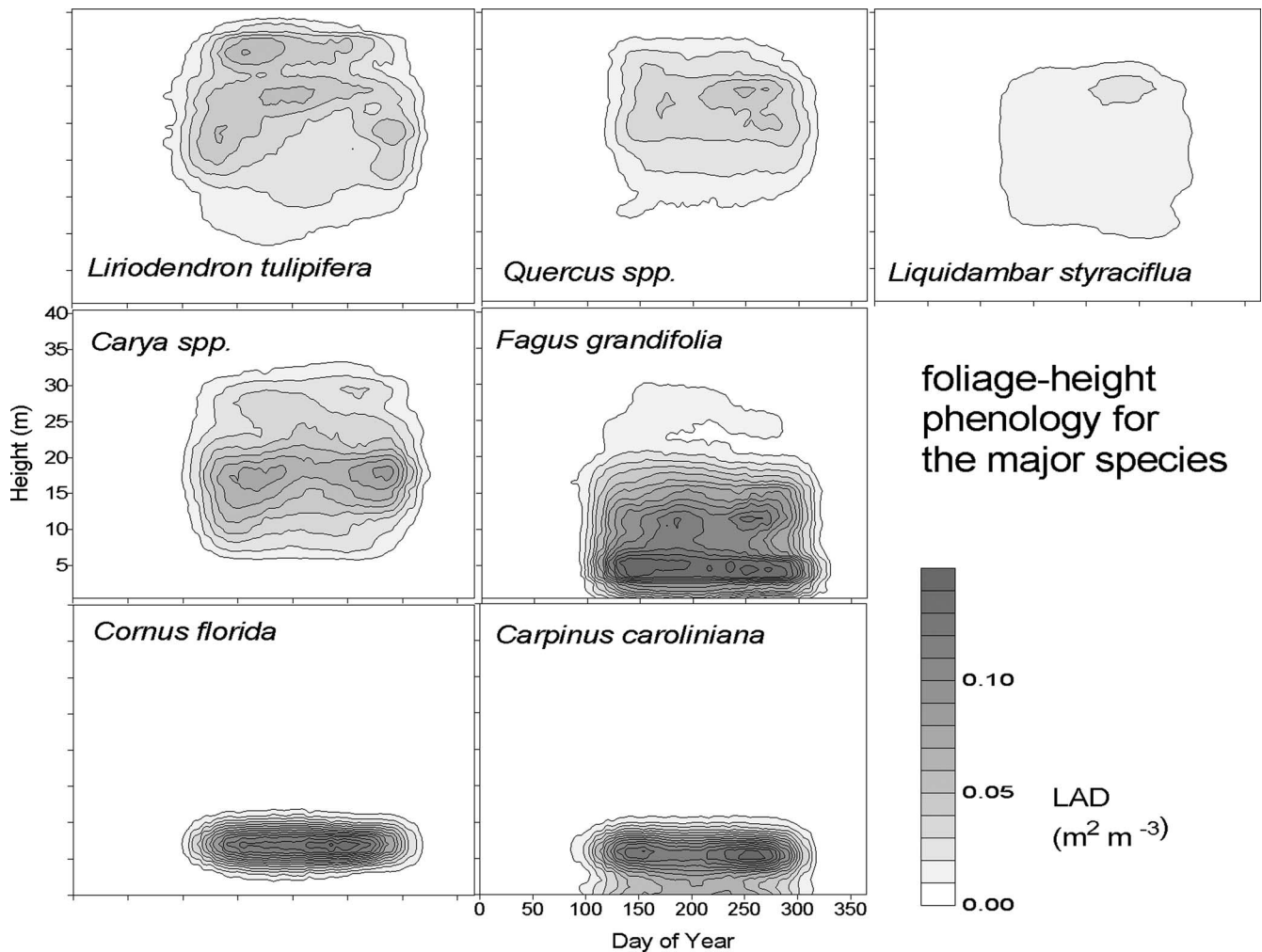


Figure 7. Time-height section of leaf area density for the dominant species across the growing season. Contour units are $0.01 \text{ m}^2 \text{ m}^{-3}$.

(Table 3). This sum was unevenly distributed among species, ranging from 366.5 for beech to 0.3 for one of the oaks. LAE values for most tree species were between 20 and $200 \text{ m}^2 \text{ m}^{-2} \text{ day}$ (Table 3). For 1988 and 1991, the LAE of trees was estimated to be 939 and $1131 \text{ m}^2 \text{ m}^{-2} \text{ day}$, respectively.

The pattern of LAE over the growing season is very similar to that of LAI in the midsummer (combined from the six sampling periods from days 153 to 250) both across species and vertically within the stand. The contribution of each of the canopy species to the total LAE is remarkably similar to the midsummer LAD (Table 4). Furthermore, except for the high LAD in the 0–1-m layer, the vertical distribution of LAE is quite similar to the midsummer profile of foliage area with height ($L(h)$, Figure 8).

Discussion

Prediction of LAI

To predict LAI during leaf expansion from C_1 , we assumed the relation between C_1 and LAI was independent of whether the canopy was expanding or eroding. To validate this assumption without direct measurements of LAI outside the abscission period is difficult. However, the similarity of

relative vertical foliage profiles in spring and autumn as well as the lack of change in the mean foliar height suggests that the vernal allocation and autumnal loss of leaves is not dependent on height. That is, the accumulation and abscission of leaves proceed as progressive infilling and depletion at all layers.

Though structurally similar from this analysis, the spring and autumn canopies differ in the function of displayed leaves. The small expanding vernal leaves are metabolically active, whereas the autumnal canopy consists of many low activity leaves and others that are inactive but not abscised. Some canopy characteristics (e.g., canopy resistance or roughness) may be similar in spring and fall, but others (e.g., light attenuation, exchange of water vapor and carbon dioxide), will surely differ (e.g., Sakai et al. 1997). In this canopy, there is a lag of about a week between the patterns of litterfall and leaf greenness, i.e., the midpoint of leaf greenness from the midpoint of litterfall is separated by about 7 days (Figure 9). During this period, a leaf has lost some or all of its pigments and is less active per unit area than during the mid-growing season.

The assembly of repeated observations on foliage-height

profiles into a seasonal view of leaf area distribution is straightforward but time-consuming. The consequently low sampling intensity at each interval may produce irregularities in estimates of LAI(*t*) and LAE in tall stands. These deficiencies may be partially overcome with more intensive sampling. We strove to obtain numerous observations (i.e., to average about 30 per height interval chosen), but this effort may not be sufficient for detailed characterization of

structural dynamics. Nonetheless, in the absence of direct methods for making structural measurements within the forest canopy, approaches such as the present offer a solution.

The measures of canopy structure presented here summarize the variation among horizontal positions. They neither reveal the condition at a given location nor quantify variation of the structural estimates in space. Therefore, the present view of structure is a spatially aggregated average.

Table 4. Mean midsummer (days 153–250) LAI and the full-season LAE for each species, ordered by its percentage of the total LAE.

Species	LAI		LAE	
	m ² m ⁻²	%	m ² m ⁻² day	%
<i>Fagus grandifolia</i>	2.102	29.76	366.5	29.11
<i>Liriodendron tulipifera</i>	1.291	18.28	181.5	14.41
<i>Carya tomentosa</i>	1.078	15.27	174.2	13.84
<i>Carpinus caroliniana</i>	0.847	11.99	149.7	11.89
<i>Cornus florida</i>	0.691	9.78	111.6	8.87
<i>Liquidambar styraciflua</i>	0.361	5.11	71.4	5.67
<i>Quercus alba</i>	0.095	1.35	43.5	3.46
<i>Quercus velutina</i>	0.138	1.95	41.3	3.28
<i>Carya glabra</i>	0.097	1.37	31.0	2.46
Forest floor herbs ^a	0.107	1.51	23.2	1.84
<i>Quercus falcata</i>	0.070	0.99	19.5	1.55
<i>Nyssa sylvatica</i>	0.074	1.05	19.0	1.51
<i>Quercus coccinea</i>	0.036	0.50	12.6	1.00
<i>Rhus radicans</i>	0.053	0.75	8.8	0.70
Other shrubs and vines ^b	0.024	0.34	4.8	0.38
<i>Quercus rubra</i>	0	0	0.3	0.03
Total	7.063	100	1,258.9	100

^a In order of importance: *Podophyllum peltatum*, *Arisaema triphylla*, *Smilacina racemosa*, *Claytonia virginica*, *Cardamine diphylla*, *Viola* sp., *Solidago caesia*, *Clintonia umbellulata*, *Duchesnea indica*, *Urtica dioica*, and *Galearis spectabilis*.

^b *Prunus serotina*, *Lindera benzoin*, *Lonicera japonica*, and *Campsis radicans*.

LAE and LAD

Similarities across species and vertical position between the midsummer LAD and the growing season LAE (Figure 8 and Table 4) suggest that the midsummer LAD(*h*) represents the general characteristics of the full seasonal leaf area extent in this stand. The two distributions do not differ significantly according to a Kolmogorov-Smirnov test (Sokal and Rohlf 1980). Except for the evanescent ground layer herbs, the midsummer partition of LAD by species is similar to the annual foliar display. However, differences in the timing of foliar display will have marked consequences for individual species: the priority of leaf expansion may determine the species share of the overall LAI or LAE. Note that the vertical profiles of LAI and LAE are similar to those obtained by airborne laser altimetry for the same stand the following year (Harding et al. 2001).

Seasonal Differentiation

The vertical distribution of LAD shifted little during the growing season. However, in the early spring, the canopy leaf area was dominated by forest floor herbs *Podophyllum*, *Arisaema*, and *Smilacina* at 0–1 m, causing some depression in mean leaf height. The early vernal dominance of the ground layer ended by day 126, when the full overstory had developed. Nonetheless, well into the growing season, there

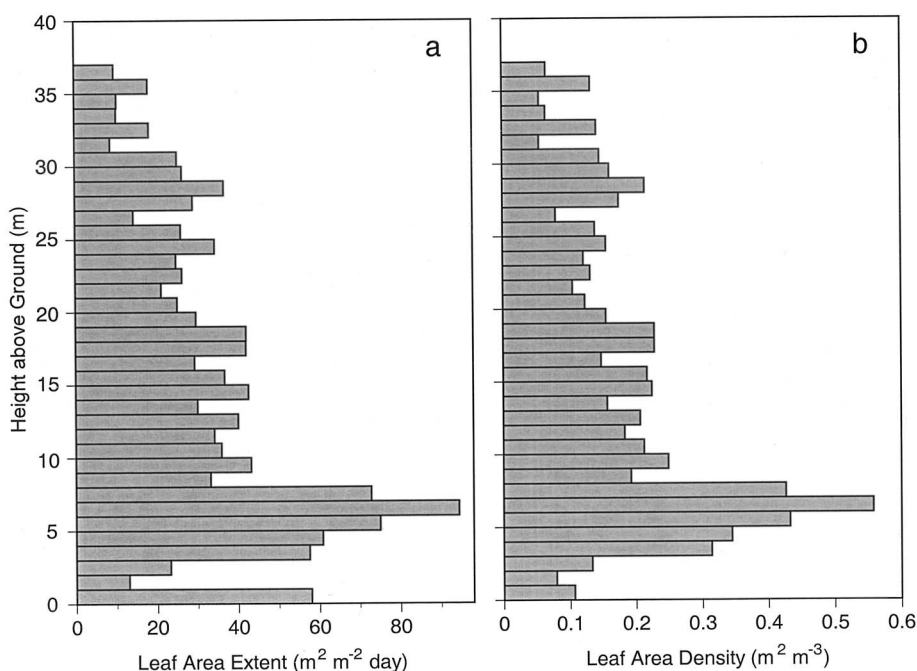


Figure 8. The vertical patterns of full season LAE (a) and mid-season LAD (b).

was a high concentration of leaf area ($>0.25 \text{ m}^2\text{m}^{-3}$) in the ground layer (Figure 5).

Differentiating Importance

The importance of a species in a community depends on the attribute measured. Hybrid measures are sometimes used that combine two or more distinct attributes (e.g., Curtis 1959, Whittaker 1975). Several measures, based on both stem and foliar attributes, are presented for the woody species in this stand in Table 5. Species with large (*Liriodendron*) or numerous (*Carpinus*, *Cornus*) individuals dominate the stem attributes (first two columns in Table 5),

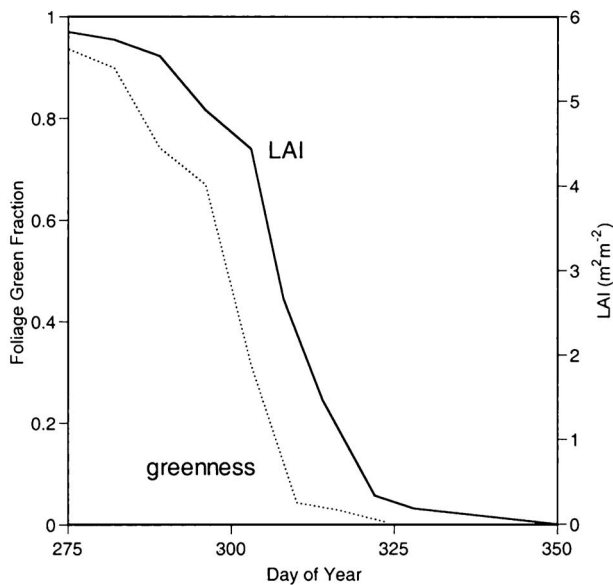


Figure 9. The autumnal dynamics of stand LAI and the percentage of green canopy foliage in 1992.

whereas those with numerous, large, or long-lasting leaves (*Fagus*, *Carya*) control the foliar attributes (last four columns). Species important in the stem attributes were usually not those important in the foliage attributes. In our data set, these classes of measurements were sometimes correlated, which may predominantly reflect the species assembly studied. For example, the species ranking of stem density was similar to that of leaf number (because the commonest species tended to have smallest leaves) as well as peak LAI and LAD (because *Fagus* had numerous small stems). The ranking of basal area predicted that of leaf mass and LAI (because *Quercus* and *Carya* have large leaves).

The stem-based characteristics of the stand reflect long-lived aspects of structure, the stand “armature.” High importance values for stem characteristics indicate the historical success of the species and its individual stems. On the other hand, the leaf-based characteristics reflect a more recent performance: over the current growing season, and possibly also of the previous year.

Phenological Implications

The canopy LAE due to trees varied by $261 \text{ m}^2\text{m}^{-2}\text{day}$ among years. This variation is more than the LAE contributed in 1994 by any single species except *Fagus* (Table 3). Thus, shifts in whole-canopy LAI(*t*) can be similar in magnitude to the annual contributions of individual species.

Particular features of the LAI(*t*) curve, such as the date of leaf-out and the maximum LAI, may differ in their consequences for species performance and stand production. The interaction between canopy phenology and the dynamics of incident radiation is important to consider. For example, the variation in time of leaf-out occurs soon after the spring equinox, when the angle of the sun and incident radiation are increasing rapidly.

Table 5. The percentage importance of each woody species in the forest based on several criteria. The measures based on stems are from Table 1. Those for leaf number and mass were calculated from peak LAI using each species mean leaf area and specific leaf areas. Importance values for peak summer LAI and full-season LAE are from Table 4.

Species	Basis of the measure of importance					
	Stems		Leaves			
	<i>n</i>	Basal area	<i>n</i>	Mass	Peak LAI	LAE
<i>Liriodendron tulipifera</i>	6.6	49.2	12.4	19.7	18.6	14.7
<i>Carpinus caroliniana</i>	40.8	3.0	30.8	8.0	12.2	12.1
<i>Fagus grandifolia</i>	23.7	10.6	30.7	22.8	30.2	29.7
<i>Cornus florida</i>	17.8	2.2	9.1	5.6	9.9	9.0
<i>Carya tomentosa</i>	3.5	9.2	4.5	24.7	15.5	14.1
<i>Liquidambar styraciflua</i>	2.5	6.8	4.6	7.6	5.2	5.8
<i>Quercus alba</i>	1.0	7.3	1.7	2.3	1.4	3.5
<i>Carya glabra</i>	1.3	4.9	0.6	2.2	1.4	2.5
<i>Quercus falcata</i>	0.0	0.0	0.8	1.4	1.0	1.6
<i>Quercus velutina</i>	0.6	4.5	1.4	2.4	2.0	3.3
<i>Nyssa sylvatica</i>	0.9	1.0	1.7	1.1	1.1	1.5
<i>Quercus coccinea</i>	0.1	0.9	0.3	0.0	0.5	1.0
<i>Acer rubrum</i>	0.2	0.1	0	0	0	0
<i>Quercus rubra</i>	0.2	0.1	—	—	—	0.03
8 others ^a	1.0	0.2	1.5	1.3	0.3	0.3
Total	100.0	100.0	100.1	100.1	100.0	100.0

^a *Quercus michauxii*, *Ulmus americana*, *Ilex opaca*, *Vitis* sp., *Fraxinus americana*, *Albizia julibrissin*, *Amelanchier arborea*, and *Sassafras albidum*.

Some species or lifeforms might be disproportionately affected by shifts in leaf-out. A lengthened growing period (such as in 1994) might favor the production of forest floor herbs. A late spring would coincide with higher levels of incident ultraviolet-B radiation, potentially damaging to understory plants (Brown et al. 1994).

If LAE increases through an early leaf-out, then the annual total of photosynthetically active radiation absorbed by leaves would also increase, leading to a rise in stand production (Monteith 1977). If LAE increases mainly through a rise in the maximum LAI (such as in 1991) the total radiation absorbed would change little and production would not necessarily rise.

Conclusions

The organization of the foliage in the canopy of this tall deciduous forest has space-, time-, and species-specific components. These attributes may be variously summarized: for example, LAI is the vertical integral of LAD, and LAE is the temporal analog. Because the distribution and dynamics of the components differ from that of the ensemble, these details are important. Also, such intermediate details are essential to some approaches to scaling structure or functions measured at small scales to large.

The multiple characteristics of canopies have implications for evaluating the influence of individual species. The measure of that influence (e.g., "importance value") must depend on the objective of the comparison. If, for example, stem size is of concern, then *Liriodendron* is dominant, whereas *Fagus* controls the leaf area and its display. Inter-annual variation in the dynamics of LAI, especially the timing of leaf-out, may have important consequences for species performance and whole-stand production.

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