

LEAF PHENOLOGY IN RELATION TO CANOPY CLOSURE IN SOUTHERN APPALACHIAN TREES¹

OMAR R. LOPEZ,^{2,3,5} KRISTA FARRIS-LOPEZ,² REBECCA A. MONTGOMERY,⁴ AND THOMAS
J. GIVNISH²

²Department of Botany, University of Wisconsin, Madison, Wisconsin 53706 USA; ³Smithsonian Tropical Research Institute, Center for Tropical Forest Science, Unit 0948, APO AA 34002 USA; and ⁴Department of Forest Resources, University of Minnesota, St. Paul, Minnesota 55108 USA

Leaf phenology varies markedly across tree species of temperate deciduous forests. Early leafing in spring may increase light capture and carbon gain prior to canopy closure, allowing saplings to survive in understory sites deeply shaded in midsummer. We quantified sapling leaf phenology for 18 tree species and seasonal variation in understory light availability at three sites along a ridge–slope–cove landform gradient in the Great Smoky Mountains National Park. Early leafing species (e.g., *Aesculus flava*, *Carpinus caroliniana*) broke bud an average of 24 d before late leafers (e.g., *Magnolia fraseri*, *Nyssa sylvatica*). Canopy closure occurred 14–18 d earlier and summer understory light was on average 63–74% lower on intermediate and mesic sites than on the xeric site. Early leafing species intercepted 45–80% of their growing season photon flux before canopy closure vs. 8–15% for late leafers. However, earlier leafing increased exposure to freezing temperatures by 5.5% per week near the mean time of bud break. Early leafing is strongly correlated with midsummer shade, risk of freezing temperatures, and distribution on mesic sites across a “main spectrum” of 15 deciduous species. Differences in leaf phenology and resultant impacts on spring carbon gain may help determine tree shade tolerance and distribution in southern Appalachian forests.

Key words: bud break; canopy closure; early leafing; environmental gradient; freezing; leaf flush; light gains; photon flux density; shade tolerance.

Shade tolerance—the ability to survive and grow in shaded microsites—is a key factor determining the distribution of plant species and growth forms across spatial and successional gradients (Horn, 1971; Givnish, 1988; Canham et al., 1994, 2006; Kobe, 1996, 1999; Pacala et al., 1993; Montgomery and Chazdon, 2002; Reich et al., 2003; Kneeshaw et al., 2006). Ecophysiological studies aimed at explaining differences among species in shade tolerance have focused mainly on differences in (1) static and dynamic photosynthetic light responses at the leaf level (e.g., Björkman, 1981; Chazdon, 1988; Givnish, 1988; Lei and Lechowicz, 1990; Ellsworth and Reich, 1992; Kitajima, 1994; Walters and Reich, 1999; Valladares et al., 2000; Montgomery and Chazdon, 2002; Givnish et al., 2004); (2) leaf susceptibility to photoinhibition and other forms of photodamage (Powles and Björkman, 1981; Kursar and Coley, 1999; Adams et al., 2004; Valladares et al., 2005); (3) canopy geometry and self-shading (Horn, 1971; Percy and Yang, 1996, 1998; Valladares and Percy, 1999; Naumburg et al.,

2001); and (4) resource allocation to photosynthetic vs. non-photosynthetic tissues (Givnish, 1988; Givnish et al., 2004; Montgomery, 2004; Kneeshaw et al., 2006). Much less attention has been focused on the role of leaf phenology—that is, the timing of leaf flush, expansion, photosynthetic activity, and senescence—in determining shade tolerance.

Early leafing by plants in the forest understory permits photosynthesis for a period of time under brightly lit conditions before the canopy closes (Harrington et al., 1989; Givnish, 1990, 2002; Uemura, 1994; Gill et al., 1998; Seiwa, 1998; Komiyama et al., 2001a, b; Augspurger and Bartlett, 2003; Tomita and Seiwa, 2004; Augspurger et al., 2005; Augspurger, 2008). Saplings of early leafing trees (e.g., *Aesculus flava*, *Carpinus caroliniana*, *Halesia tetraptera* var. *monticola*) in temperate, deciduous forests might fix large amounts of carbon before the forest canopy closes, providing a “spring carbon subsidy” that could permit such plants to persist in moist, fertile sites that are densely shaded in midsummer (Givnish, 1992, 2002; Augspurger, 2008). In contrast, saplings of late-leafing deciduous species (e.g., *Nyssa sylvatica*, *Quercus rubra*), whose leaves are expanded close to or after canopy closure would not gain such a subsidy and thus should lack shade tolerance based on their time of leafing. In addition, the advantage of a spring carbon subsidy should be less on drier, less fertile sites that permit substantial light to penetrate the canopy. Late leafers might gain an advantage in midsummer photosynthesis under brightly lit conditions (i.e., in gaps), based on their possession of large xylem vessels with high hydraulic conductance and on the tendency for leaf-level photosynthetic rates to be positively correlated with stomatal conductance, transpiration rates, and stem hydraulic conductance (e.g., see Wong et al., 1979; Sobrado, 1993; Brodrigg and Feild, 2000; Sperry, 2000; Santiago et al., 2004; Franks, 2006). Although late leaf senescence is often correlated with early leaf expansion across species (Lechowicz, 1984), any “fall subsidy” is much less likely than the spring

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⁵ Author for correspondence (e-mail: prioria@yahoo.com); Smithsonian Tropical Research Institute, Center for Tropical Forest Science Unit 0948, APO AA 34002 USA

subsidy for the same species, given the greater likelihood of drought or reductions in leaf area (e.g., due to herbivory or previous drought) in late summer or early fall.

Several authors have now shown that early leaf expansion can result in substantial increases in light capture and carbon gain (Harrington et al., 1989; Gill et al., 1998; Seiwa, 1998; Tomita and Seiwa, 2004; Augspurger et al., 2005) by individual tree and shrub species during spring in temperate, deciduous forests. These increases in light capture and carbon gain can positively influence growth and survival (Augspurger, 2008). Consequently, avoidance of canopy shade via early leafing appears likely—albeit paradoxically—to serve as a mechanism to increase shade tolerance in some species. Essential to this proposed mechanism is the observed tendency for saplings to leaf earlier than adults of the same species (Gill et al., 1998; Augspurger et al., 2005). Studies to date have generally focused on only one or a few species, have not examined how the significance of the time of leafing for carbon capture would vary along environmental gradients and, most importantly, have not addressed how the difference in timing of leafing relates to understory light availability and affects the magnitude of the “spring subsidy.”

Such analyses are necessarily complex. Evaluating the importance of early leafing to whole-season carbon capture of tree saplings requires the measurement of (1) sapling leaf phenology; (2) seasonality of canopy transmittance and understory photon flux density (PFD: $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$); (3) static and dynamic photosynthetic light responses; (4) respiration rates and construction costs of leaves and associated organs; (5) shade tolerance, defined as survival rate as a function of PFD; (6) risks associated with early leafing (e.g., probability of killing frost); (7) stem hydraulic conductance; and (8) how each of these parameters or functions vary with species and environmental conditions.

Here we present the first steps of such an analysis, focusing on 18 common species along the ridge–slope–cove landform gradient characteristic of mid elevations in the Great Smoky Mountains National Park (Whittaker, 1956) and reporting on variation in sapling leaf phenology in relation to the timing and extent of canopy closure in a mesic, concave cove; intermediate slope; and xeric, convex ridge. Our overarching hypothesis is that early leafing provides a carbon subsidy that allows early leafers to persist on microsites that are densely shaded in midsummer and excludes late leafers from such sites. In this paper, we test two specific hypotheses. First early leafing will result in an increase in light capture during spring. Second, saplings of early leafing deciduous species will dominate moist, fertile sites that favor dense canopies, while late leafers will dominate less fertile, drier, more open canopies sites (Givnish, 2002). In testing these hypotheses, we address five main questions: (1) How do species differ quantitatively in sapling leaf phenology (i.e., timing of bud break and leaf drop, rate of leaf expansion, and leaf longevity)? (2) To what extent are different components of sapling leaf phenology correlated across species? (3) How do sites differ in the timing and extent of canopy closure? (4) How does the proportion of light incident on leaves during the spring phase (i.e., before canopy closure) vary with sapling phenology and the timing and extent of canopy closure? And (5) how do various components of sapling leaf phenology correlate with the distribution of adults of that species along the landform gradient and with the timing and extent of canopy closure at the point along that gradient where each species is most abundant? Our data shed light on each of these questions and provide new insights into the possible causes of differences among temperate deciduous tree species in shade tolerance and distribution along landscape gradients.

MATERIALS AND METHODS

Species and study sites—This investigation was conducted in Great Smoky Mountains National Park (GSMNP), a world heritage and biosphere reserve site in Tennessee and North Carolina, USA. GSMNP lies along an ancient northeast-southwest axis of the southern Appalachians, uplifted 200–300 Mya (King et al., 1968; Schulz et al., 2000) and now the center of tree diversity in eastern North America (Whittaker, 1956; Wood, 1970). In the Great Smokies, tree species distributions and diversity are strongly associated with elevational and aspect gradients across which several environmental conditions change, including temperature, humidity, soil moisture, insolation, temperature, evaporative demand, and soil fertility (Whittaker, 1956). At a given elevation, species distributions are strongly correlated with a landform gradient extending from north-facing, concave mesic coves, through open slopes of intermediate soil moisture and fertility, to south-facing, convex dry, infertile ridges (Whittaker, 1956). The environmental gradient in soil depth and moisture availability from ridge to cove implied by Whittaker has been corroborated by direct environmental measurements at the Coweeta Experimental Forest nearby (Yeakley et al., 1998; Elliott et al., 1999). Of the common tree species that occur between 760–1370 m a.s.l., we selected 16 deciduous and two evergreen species for intensive study, stratified by taxonomic affinity, ecological distribution, timing of leaf flush, and apparent degree of shade tolerance (Table 1). Nomenclature throughout follows APG II (2003) and Weakley (2007).

Species selection was made prior to selection of our specific field research sites using data in Robert Whittaker's (1956) classic paper on the vegetation of the Great Smoky Mountains. We first computed the sum of total abundance (% stems) for each tree species across all stations (e.g., landform positions) of the mesic–xeric gradients studied by Whittaker (1956, tables 2 and 3) in elevational bands at 760–1070 and 1070–1370 m a.s.l., and then ranked each species by total abundance at each elevational band. Of the most abundant 20 species in each elevational band, we excluded “duplicate” species in each genus (or sub-

TABLE 1. Stratification of study species based on preliminary estimates of their ecological distribution (Distrib., 1 = mesic, 2 = submesic, 3 = subxeric, 4 = xeric [Whittaker, 1956]) and shade tolerance (Shade, 1 = least tolerant and 5 = most tolerant), relative time of leafing (1 = earliest, 3 = latest [Niinemets and Valladares, 2006; see Materials and Methods, *Species and study sites*]), and maximum stature (C = canopy, S = subcanopy).

Species, Family (APG II)	Distrib.	Shade ^a	Leafing	Stature
<i>Acer rubrum</i> , Sapindaceae	1,2,3,4	3.44	2	C
<i>Acer saccharum</i> , Sapindaceae	1	4.76	1	C
<i>Aesculus flava</i> , Sapindaceae	1	4.14	1	C
<i>Betula lenta</i> , Betulaceae	1,2,3	2.58	2	C
<i>Carpinus caroliniana</i> , Betulaceae	1,2	4.58	1	S
<i>Carya cordiformis</i> , Juglandaceae	1	2.07	1	C
<i>Cornus florida</i> , Cornaceae	1,2	4.87	1	S
<i>Fagus grandifolia</i> , Fagaceae	1	4.75	2 ^b	C
<i>Halesia tetraptera</i> var. <i>monticola</i> , Styracaceae	1	3.11	1	C
<i>Ilex opaca</i> , Aquifoliaceae	1,2	4.28	1 ^c	S
<i>Liriodendron tulipifera</i> , Magnoliaceae	1,2	2.07	2	C
<i>Magnolia fraseri</i> , Magnoliaceae	1,2,3	3.06	3	C
<i>Nyssa sylvatica</i> , Nyssaceae	3,4	3.52	3	C
<i>Oxydendrum arboreum</i> , Ericaceae	2,3	2.70	3	C
<i>Quercus prinus</i> , Fagaceae	2,3,4	2.85	3	C
<i>Quercus rubra</i> , Fagaceae	1,2,3	2.75	3	C
<i>Tilia americana</i> var. <i>heterophylla</i> , Malvaceae	1	3.98	2	C
<i>Tsuga canadensis</i> , Pinaceae	1,2	4.83	1 ^c	C

^aPeet and Loucks (1977) shade tolerance rankings; 0–10 scale was transformed to 1–5 for comparison; *Acer saccharum* = 5.0, *Tilia americana* = 3.8, *Carya cordiformis* = 4.4, *A. rubrum* = 2.6, *Quercus rubra* = 1.0.

^bMid elevation red beech

^cInitiation of photosynthetic activity in evergreen species; actual time of leafing much delayed.

genus in *Quercus*) that share the same general time of leafing (early, mid, late) and apparent shade tolerance (described later) with one or more congeners. We did this to minimize a well-known potential bias in comparative studies, involving the inclusion of closely related species that are (often) ecologically similar.

The issue of “duplicate” species involved the following taxa: (1) *Acer pensylvanicum*, *A. saccharum*, and *A. spicatum* all share high shade tolerance and early leafing; (2) *Betula allegheniensis* and *B. lenta* share moderate tolerance and mid to late leafing; (3) *Quercus alba* and *Q. prinus* of subg. *Quercus* share shade intolerance and late leafing; (4) *Quercus rubra* and *Q. coccinea* of subg. *Erythrobalanus* share shade intolerance and late leafing; and (5) *Pinus pungens* and *P. rigida* also share shade intolerance and late leafing. We studied the more common species in each pair, except for *B. lenta*, which we chose to increase knowledge of this common but little-studied species that is sister to *B. allegheniensis* (Järvinen, 2004). We included (6) *A. rubrum* because its mid leafing and moderate shade tolerance contrast with *A. saccharum*; *A. rubrum* is thus not a duplicate species, and it is also the most common tree species at mid elevations in the Great Smokies and nearby ranges (Whittaker, 1956; Bolstad et al., 2001).

Finally, we had to exclude a few species originally planned for study because they had become rare or inaccessible on our study sites since Whittaker's (1956) survey. These included *Castanea dentata* (mostly vanished due to chestnut blight); *Carya glabra* (a shade-intolerant, gap-phase species, with many large individuals seen, but few saplings with foliage readily accessible and thus suitable for our studies); *Robinia pseudoacacia* (for reasons similar to those given for *C. glabra*); and *Hamamelis virginiana* (which has apparently undergone a previously unreported decline since the 1950s). We substituted *Carya cordiformis* for *C. glabra*; its somewhat greater shade tolerance made it possible to locate saplings suitable for study. We substituted *Carpinus caroliniana* for *Hamamelis*, which it resembles in shade tolerance, early leafing, ecological distribution, and stature. We were unable for logistical reasons to complete a survey of leaf phenology in *Pinus pungens*, so this species (whose shade intolerance, late leafing, and occurrence on xeric sites are shared with several other species already included) was struck from the analysis. Our species differ in stature (Table 1) from subcanopy to canopy trees. Although our study necessarily focused on juvenile trees, it should also have relevance to the ecology of larger individuals. A recent analysis of >50 tropical tree species suggests that physiological traits of adults are strongly related, if not determined, by the environment of the juvenile (Poorter, 2007). Those results suggest that the forest understory environment represents a strong selective filter, through which all species must pass, regardless of adult stature.

Initial stratification of leaf phenology was based on qualitative observations (T. Givnish) in GSMNP between 1990 and 2000. Degree of shade tolerance was scored on the traditional five-point scale (1 = very shade-intolerant, 5 = very shade-tolerant) using data collated from Peet and Loucks (1977) and Niinemets and Valladares (2006). Time of leafing was not used to infer shade tolerance in either study. The indices from Peet and Loucks (1977) reflect the relative abundance of species in understories vs. canopies, while those from the Niinemets and Valladares (2006) meta-analysis largely reflect the responses to questionnaires compiled by Baker (1949). We recognize that any qualitative index of shade tolerance can suffer from multiple shortcomings, including variation in a species' performance across different microsites, geographic locations, and plant sizes (see Givnish, 1988; Beckage et al., 2000; Bond, 2000), or more importantly, lack of a quantified relationship of growth or survival to light level (sensu Kobe et al., 1995; Pacala et al., 1993; Montgomery and Chazdon, 2002) on which operational measures of shade tolerance can then be based. The shade tolerance indices listed in Table 1 were used to ensure that species with saplings of high, intermediate, and low tolerance were included in our study; subsequent analyses involving carbon balance and sapling survival under different canopy conditions will inevitably refine and quantify these initial rankings.

Three sites representing mesic coves on concave, north-facing sites; intermediate slopes; and xeric ridges on convex, south-facing sites and their corresponding forest communities were chosen for study in the Tennessee portion of GSMNP. Mesic and xeric sites were located along the Brushy Mountain Trail (35°41'06"N, 83°24'32"W, elevation 880 m a.s.l.) in the Greenbrier area, while the intermediate site was situated on an open, southeast-facing slope along the Bullhead trail (35°40'08"N, 83°29'34"W, elevation 910 m a.s.l.) near Twin Creeks. All sites were located in mature to old-growth stands, in a portion of GSMNP where canopy disturbance is rare, and consequently, large canopy gaps are essentially absent. We chose sites that were relatively easily accessible for a wide variety of phenological, physiological, and ecological studies, and that collectively included substantial numbers of saplings of the species under study. Our focal sites (each ca. 1 ha) spanned a small elevational range (880–

910 m a.s.l.) to minimize the effect of elevation and highlight the impact of landform and slope aspect. The use of a single site for each landform category may limit the generality of our results. However, the composition of these sites accords with the general patterns documented along landform gradients by Whittaker (1956) and the need for repeated access to sites for related physiological studies prevented our sampling a greater number of sites.

Leaf phenology—In late winter 2002, we extensively searched our focal sites for saplings of our study species. Individuals chosen for phenological measurements were selected prior to bud break, <3 m tall, and scattered widely in our focal sites. Buds chosen were readily accessible from the ground and scattered around the periphery of the canopy of each individual on undamaged healthy twigs. To avoid confounding effects of sapling position on leaf phenology, we choose individuals with the same aspect. During the early spring (ca. 1 March) of 2002 and 2003, 1–3 apical buds were tagged using colored telephone wires on each of 10–12 individuals per species. After leaf flush, one target leaf per bud was marked and censused at intervals of 3–5 days until the leaf had completed expansion. At each census, opening of bud scales (= bud break), appearance of leaves, leaf number per bud, and leaf blade length (cm) were recorded. After full leaf expansion was reached, the census frequency was decreased to approximately once a month, and only the total number of leaves was recorded. In autumn, the census interval was increased again to intervals of 3–5 days, and percentage green leaf tissue and total number of leaves per bud were recorded until more than 90% of the leaves had died (i.e., desiccated), disappeared (i.e., fallen or completely eaten), or discolored (i.e., turned pale yellow). In addition to direct observation of leaf length and the dates of bud break, complete leaf expansion, and leaf fall, we used our census data to calculate (1) date of 50% leaf expansion; (2) the rate of expansion at 50% leaf expansion; (3) date of 50% leaf fall, which we calculated as the time at which 50% of the leaves had fallen or discolored; and (4) functional leaf longevity, the number of days between 50% expansion and 50% leaf fall. Phenological data for leaf expansion and leaf fall phenophases were expressed as leaf ratios: a leaf length ratio — leaf blade length at census date divided by the final leaf length at full expansion; and a leaf area ratio — green leaf area at census date divided by total leaf area before leaf fall.

Quantification of light environment, landform distribution, and probability of freezing temperatures—At each site, we deployed 32 gallium arsenide photodiodes (GAsPs, Hamamatsu, Newark, New Jersey, USA) previously calibrated with a Li-Cor SA-190 Quantum and a Li-Cor 1000 data logger (Li-Cor, Lincoln, Nebraska, USA). Sensors were placed on steel stakes at 1.2 m height every 5 m along a single transect at the center of each site. This array allowed us to characterize the amount of light penetrating to saplings below canopy at three different sites, in a way that would not reflect differences in sapling height among sites. Each sensor was connected to a relay multiplexer M-416 controlled by a CR21X data logger with an SM-64 data storage module (Campbell Science, Logan, Utah, USA). Average photon flux density (PFD: $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) for each sensor was logged every 10 s during daylight hours during the 2002 and 2003 growing seasons. Each data logger was powered by a 12 V lead-acid battery and protected from bears and boars using an electrified barrier. Batteries and data storage modules were replaced at roughly 3-week intervals.

To characterize midsummer light environments experienced by individual saplings of each species, we shot hemispherical canopy photographs over each census plant during summer 2003, using a tripod-mounted Nikon Coolpix 995 digital camera with 180° fisheye lens converter. All canopy photographs were taken under overcast sky conditions, with the camera oriented north and leveled. We set the black–white threshold for each hemispherical photograph by determining the lower edge of the right-hand (brighter) peak in its luminosity histogram in Photoshop 7.0 (Adobe Systems, San Jose, California, USA); this procedure corrects for differences in overall brightness among photographs and greatly increases repeatability. We used this threshold in the program Hemiview v.2.1 (Delta-T devices, Cambridge, UK) to estimate the proportion of visible sky (Vsky), the indirect site factor (ISF, proportion of indirect radiation penetrating the canopy), and the corresponding direct site factor (DSF) (Rich, 1990). It is important to recognize that these photographs do not fully represent the distribution of each species, given that our selection of individuals was not stratified across a full light gradient from large gaps (essentially nonexistent at our study sites, due to infrequent canopy disturbance in GSMNP) to densely shaded understories, nor were individuals sampled across an extensive landscape. Nevertheless, even this limited sample provides important insights into species distributions and possible ties of phenology to light regime, given that shade-intolerant species will perforce not be found in the microsites most densely shaded in midsummer.

Species distributions along the landform gradient were quantified by calculating the average site position of each species along Whittaker's (1956) 13-step, mesic-xeric gradient at 760–1070 m a.s.l. (see Table 2 in Whittaker, 1956), weighted by its share of stem density, and then converting to a scale in which the most mesic sites received a score of 0 and the most xeric sites a score of 100. We used this elevational band for the analysis because it encompasses the range of elevation in our study sites (e.g., 880–910 m a.s.l.). We calculated the average date of 50% leaf expansion (based on our measurements) for all deciduous taxa at each station on Whittaker's gradient, weighting each species by its stem density in his Table 2. This calculation assumes no variation in time of leafing across the gradient within each species and is designed to illustrate how differences in the distribution and relative timing of leafing of individual species alone would influence the average time of leafing. Because no data were provided in Whittaker's Table 2 for the distribution and abundance of *Carpinus caroliniana* and *Carya cordiformis*, our calculations excluded these species. However, calculations that used the distribution of *Hamamelis* for *Carpinus*, and that of *Carya glabra* for *C. cordiformis* yielded similar results (O. Lopez, R. Montgomery, and T. Givnish, unpublished data).

We estimated freezing probabilities as a sigmoid function (described in *Statistical analysis*) of Julian date (January 1 = 1) using minimum daily temperatures in a 56-yr record from Asheville NC, about 90 km ESE of our study sites (35°26'10"N, 82°32'30"W, 700 m a.s.l.). This approach ignores variation in frost probability due to site convexity. At a given elevation, the likelihood of nightly freezing may be less on convex ridge sites (which permit cold-air drainage) than on concave cove sites (which receive cold-air drainage from above).

Statistical analysis—Site factors—We averaged daily PFD across all functioning sensors at each site using two years of data and calculated the daily standard error for PFD based on the number of such sensors. Due to bear and boar activity, occasionally sensors were damaged or destroyed resulting in no data for the damaged sensors in the time between damage and repair (usually <1 wk). To estimate the date of canopy closure, we used linear regressions relating PFD to date during the linear decline of PFD in the spring, then calculated the date at which the model PFD would equal the average PFD during June (the time of maximal canopy cover). Average spring and summer PFD were calculated using the daily PFD values before and after canopy closure, respectively. The probability of a spring freeze was estimated by fitting the sigmoid function (see Lockhart, 1983) $f(x) = a/(1 + \exp^{-(x - x_0)/b})$ (Eq. 1) to the proportion of years for each date x (January–June) for which the daily minimum temperature was $\leq 0^\circ\text{C}$, based on the 56-yr record from Asheville, North Carolina.

Species factors—ANOVA and Tukey–Kramer honestly significantly different (HSD) tests were used to determine whether interspecific differences in various components of light environment and leaf phenology were statistically

significant. For each species \times site combination, we estimated the proportion of growing-season PFD gained before canopy closure by integrating average understory PFD between 50% sapling leaf expansion and canopy closure on a given site, then dividing it by the integral of average PFD between 50% leaf expansion and 50% leaf loss.

We used principal component analysis (PCA) to distill our numerous inter-correlated variables into a few explanatory factors (McCune and Grace, 2002). The objective was to determine the number of significant dimensions of variation among a series of phenological and habitat traits that are, in many cases, closely correlated with each other. The resulting orthogonal principal components were then used to examine the relationships among ecological distributions, leaf phenology, and environmental characteristics across species. Variables in the PCA included bud break, dates at full leaf expansion and complete drop, leaf longevity, dates of 50% leaf expansion and leaf drop, rates of expansion at 50% leaf expansion, Vsky, ISF, DSF, proportion of PFD intercepted before canopy closure, and the probability of freezing temperatures at or after bud break. The Julian date of complete leaf fall for evergreen species was set arbitrarily at 365.

All data were analyzed with the statistical software JMP v 3.2.1. (SAS Institute, Cary, North Carolina, USA). We related time of leafing to position along Whittaker's mesic-xeric gradient using Pearson correlations and least mean squares (LMS) regressions. Time of leafing was characterized by the date of bud break and the date of 50% leaf expansion. One-tailed t tests were used when a specific sign in the relationship was predicted a priori; two-tailed tests were used otherwise. We used standard, phylogenetically unstructured analyses throughout, given that (1) the angiosperm species under study are distributed widely across 11 families and seven orders, with estimated times of divergence between families of 47–143 My based on the maximum-likelihood analysis of Wikström et al. (2001); (2) the closest within-family relatives were chosen to be phenotypically divergent rather than convergent; and (3) extensive ecological character evolution and reversal can occur in woody plants even over short periods of 5–10 My (Givnish et al., 2004; see also Ackerly and Reich, 1999; Givnish et al., 2005).

RESULTS

Light environment across sites—Understory PFD ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) was high and temporally variable on each site in spring before canopy closure, averaging 8.7 ± 0.7 $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ on the xeric site, 7.5 ± 0.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ on the intermediate site, and 6.1 ± 0.5 $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ on the mesic site (Fig. 1). These differences were significant ($F_{1,30} = 9.32$,

TABLE 2. Summary of phenological parameters for each tree species studied. Values are means for leaves from 10 to 12 plants per species for the 2003 growing season; similar rankings were obtained from a less complete survey in 2002. Where given, error estimates are ± 1 SE across individuals. All dates are given on basis of Jan 1 = 1; all other units are specified.

Taxon	Date of bud break	Days to full leaf expansion	Date of full leaf expansion	Date of 50% leaf expansion	Expansion rate ($\text{cm}\cdot\text{day}^{-1}$) at 50% leaf expansion	Date of 50% leaf fall	Functional leaf longevity (d)	% PFD before canopy closure
<i>Aesculus</i> ^M	78.0 \pm 0.7	30.5 \pm 1.1	108.5	86.6	1.08 \pm 0.11	202.4	115.8	80.3
<i>Halesia</i> ^M	79.3 \pm 0.9	44.0 \pm 1.0	123.3	108.6	0.24 \pm 0.01	243.9	135.3	37.3
<i>Cornus</i> ¹	81.1 \pm 0.4	58.4 \pm 1.6	139.6	112.2	0.21 \pm 0.02	266.6	154.4	24.1
<i>Carpinus</i> ^M	84.6 \pm 0.8	48.7 \pm 1.0	133.3	115.4	0.12 \pm 0.01	272.3	156.9	17.9
<i>Carya</i> ¹	91.4 \pm 1.0	36.9 \pm 1.9	128.2	112.9	0.40 \pm 0.04	292.7	179.8	21.7
<i>Tilia</i> ^M	94.7 \pm 0.3	29.0 \pm 0.9	123.7	111.8	0.57 \pm 0.04	269.3	157.5	25.6
<i>Oxydendrum</i> ¹	95.2 \pm 0.4	34.9 \pm 1.3	130.1	115.2	0.27 \pm 0.02	278.7	163.5	17.4
<i>Acer rubrum</i> ¹	96.4 \pm 0.9	26.8 \pm 0.6	123.2	116.4	0.43 \pm 0.04	264.2	147.8	16.3
<i>Quercus prinus</i> ^X	96.4 \pm 0.9	24.2 \pm 1.6	120.6	112.5	0.43 \pm 0.04	278.4	165.9	23.0
<i>Acer saccharum</i> ^M	96.7 \pm 0.9	30.5 \pm 1.1	127.2	108.6	0.47 \pm 0.04	283.0	174.3	31.5
<i>Liriodendron</i> ¹	97.1 \pm 0.9	35.9 \pm 1.3	133.0	116.6	0.23 \pm 0.03	281.2	164.6	15.1
<i>Quercus rubra</i> ^X	101.7 \pm 1.3	28.6 \pm 2.1	130.3	114.7	0.51 \pm 0.07	293.7	179.0	17.4
<i>Nyssa</i> ^X	103.1 \pm 0.3	36.3 \pm 1.6	139.4	119.2	0.27 \pm 0.02	261.0	141.7	10.8
<i>Tsuga</i> ^{1E}	104.0 \pm 0.9	38.0 \pm 0.0	142.0	123.0	0.03 \pm 0.00	—	365.0	3.6
<i>Magnolia</i> ¹	105.5 \pm 0.6	36.9 \pm 1.0	142.4	119.5	1.08 \pm 0.04	276.5	157.0	10.1
<i>Betula</i> ¹	106.3 \pm 0.6	30.7 \pm 2.0	137.0	117.3	0.39 \pm 0.03	271.3	154.0	14.6
<i>Ilex</i> ^{1E}	108.3 \pm 2.0	36.0 \pm 1.8	144.3	126.3	0.22 \pm 0.04	—	365.0	1.6
<i>Fagus</i> ¹	108.7 \pm 0.9	13.9 \pm 0.8	122.6	114.2	1.18 \pm 0.11	288.9	174.7	17.8

Notes: ^EEvergreen species, ¹intermediate site, ^Mmesic site, ^Xxeric site; functional leaf longevity = the number of days between 50% expansion and 50% leaf fall

$P < 0.005$ for repeated measures ANOVA applied to daily data); the xeric site received the most light before canopy closure (albeit decreased by the presence of a few evergreen canopy trees), while the mesic site received the least. After canopy closure, understory PFD decreased sharply at all sites (Fig. 1). Although the absolute magnitudes of differences among sites decreased, the relative differences increased, with the xeric site receiving $1.9 \pm 0.2 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$; the intermediate site, $0.5 \pm 0.01 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$; and the mesic site, $0.7 \pm 0.02 \text{ mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. Thus, while understory PFD on the xeric site averaged 43% higher than that on the mesic site in spring, by summer this difference had grown to 280%, reflecting the much greater density of the canopy on the mesic site. All differences among sites in understory PFD after canopy closure were significant ($F_{1,175} = 66.02$, $P < 0.0001$ for repeated measures ANOVA). A dense understory layer of *Acer pensylvanicum* on the intermediate site reduced light levels at sensor level slightly below those on the mesic site. Finally, the canopy closed earliest in the mesic cove (average date = May 7) and latest on the xeric ridge (May 25), with the intermediate site closing at a date between these extremes (May 11). There was thus an 18-d difference among sites in date of canopy closure.

Characterization of species light environment—Species varied significantly in V_{Sky}, ISF, and DSF ($F_{18,231} = 4.61$, 4.23 and 4.85, respectively, $P < 0.0001$, ANOVA; Appendix S1, see Supplemental Data with the online version of this article). Species tended to have the most significant differentiation with respect to V_{Sky}, and the least with respect to DSF (Appendix S1; see online Supplemental Data). *Halesia tetraptera* var. *monticola* tended to occur in the shadiest summer microsites, while *Nyssa sylvatica* occurred in the most sunlit. At the intermediate site, where 12 of 18 study species occurred, DSF differed significantly across species ($F_{11,145} = 2.74$, $P = 0.003$, ANOVA), with *Ilex*, *Oxydendrum*, and *Quercus rubra* occurring in significantly brighter microsites.

Leaf phenology—Species differed significantly in date of bud break ($F_{15,135} = 67.15$, $P < 0.0001$), expansion rates at 50% leaf expansion ($F_{15,135} = 39.75$, $P < 0.0001$), date of leaf fall ($F_{15,135} = 25.24$, $P < 0.0001$), and leaf longevity ($F_{15,135} = 15.24$, $P < 0.0001$; Fig. 2, Table 2). Early leafing *Aesculus flava*, *Halesia tetraptera* var. *monticola*, *Cornus florida*, and *Carpinus caroliniana* broke bud an average of 24 d before late-leafing *Magnolia fraseri*, *Betula lenta*, *Ilex opaca*, and *Fagus grandifolia* (Fig. 2). Most earlier leafers required more time to expand

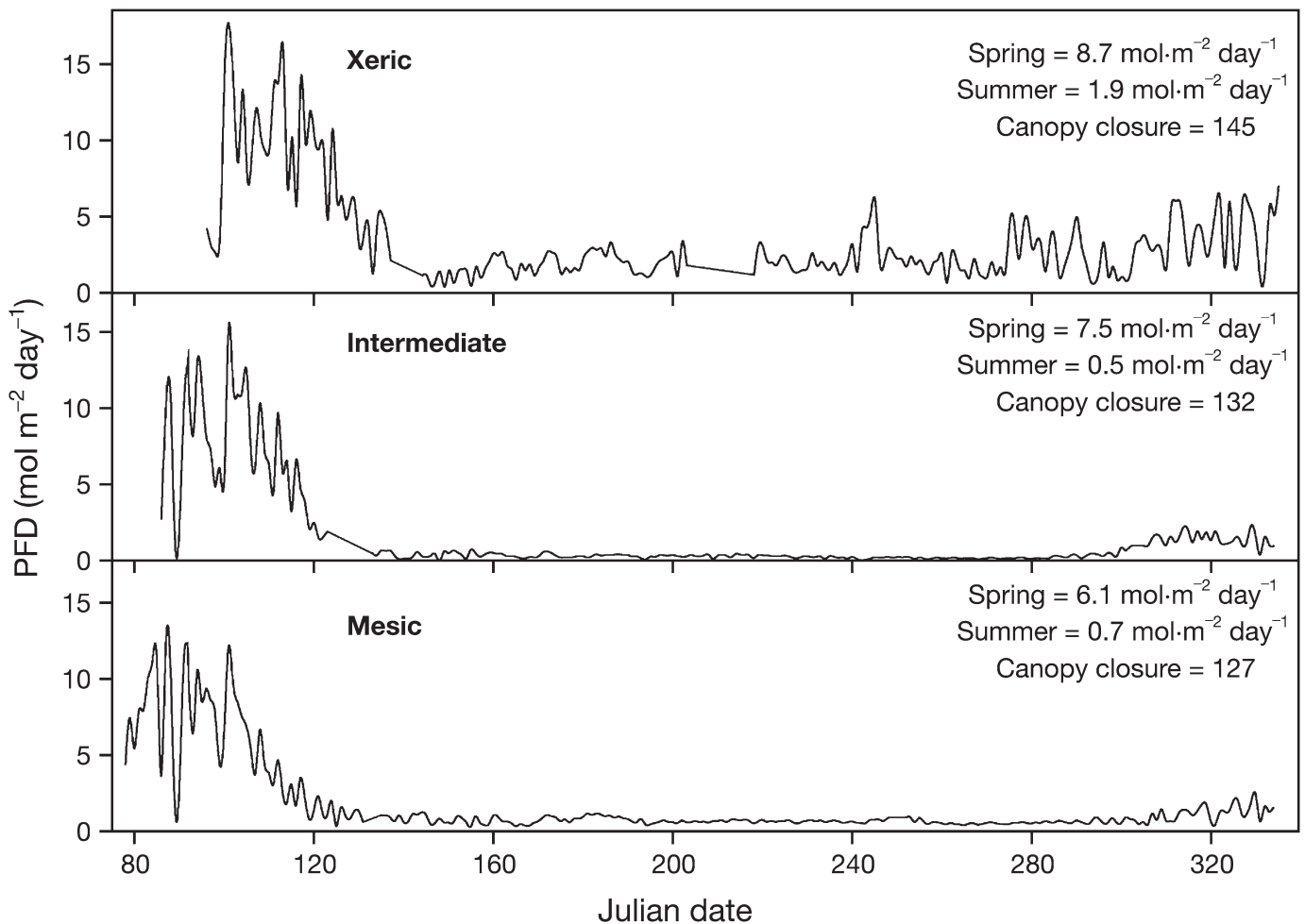
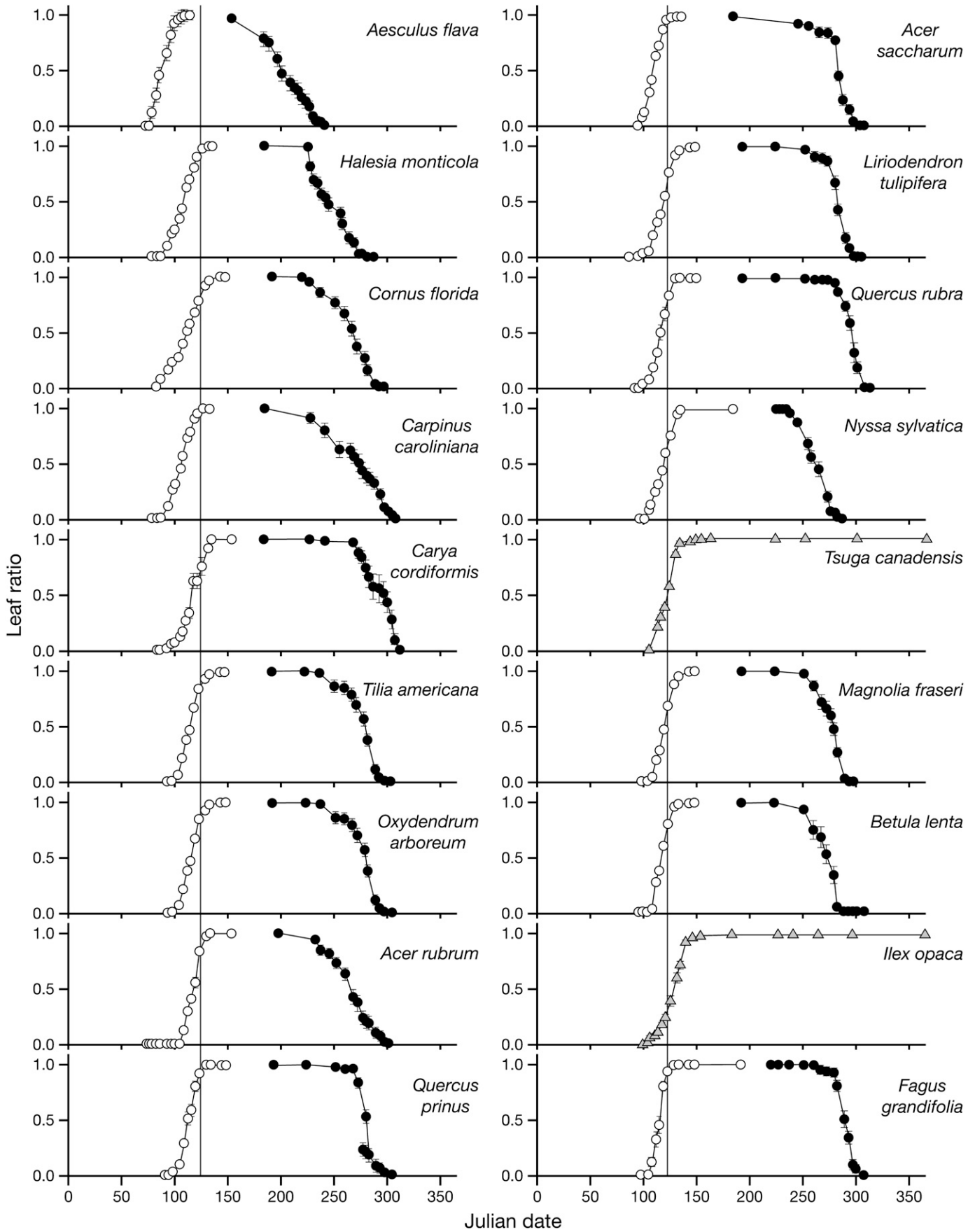


Fig. 1. Seasonal fluctuation in understory photon flux density (PFD: $\text{mol}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) in xeric, intermediate, and mesic sites in Great Smoky Mountains National Park, North Carolina, USA. Data represent two-year average across all functioning sensors for each date at each site. Note the asymmetry in understory light availability in spring before canopy closure (Julian date 80–120) vs. after leaf fall (Julian date 280–330).



their leaves (Fig. 3A), and—except for earliest-breaking *Aesculus*—had lower rates of leaf expansion (Fig. 3B). Leaf expansion rates at 50% leaf expansion varied from 0.03 cm·d⁻¹ in *Tsuga* to 1.18 cm·d⁻¹ in *Fagus* (Table 2). *Fagus* was the last species to break bud but the fastest to achieve full leaf expansion; it required less than 14 d to achieve full expansion, while other species required 36 d on average. *Fagus* lagged the average date of 50% full leaf expansion in other species by less than one day, and reached full leaf expansion 8.3 d before the average of other species, ranking third in the latter regard. Earliest-leaving *Aesculus* had exceptionally rapid leaf expansion among early leafers and tied for second place behind *Fagus* overall (Fig. 3B). Expansion rates at 50% full expansion increased with date of bud break among deciduous species but only when *Aesculus* is excluded as an outlier (Fig. 3B; $r^2 = 0.323$, $P < 0.08$ for 13 df). Date of 50% leaf fall increased significantly with date of 50% full expansion across deciduous species ($r^2 = 0.658$, $P < 0.01$ for 14 df), but this relationship disappeared when *Aesculus* was excluded ($r^2 = 0.295$, $P > 0.25$ for 13 df). Paralleling a pattern documented by Lechowicz (1984), some early leafers (e.g., *Carpinus caroliniana*, *Carya cordiformis*) drop their leaves late, and some late leafers (e.g., *Nyssa*) drop their leaves early. However, there were many exceptions to this rule, and we note that the two earliest leafers (*Aesculus flava*, *Halesia tetraptera* var. *monticola*) were also earliest to shed their leaves, at least at the sapling stage, becoming deciduous 40–78 d before *Carya cordiformis*.

Functional leaf longevity, the time from 50% leaf expansion to 50% leaf drop in deciduous species, ranged from 116 d in *Aesculus flava* to 180 d in *Carya cordiformis*. Leaf longevity increased with date of bud break across deciduous species ($P < 0.04$), but again the significance of this relationship disappeared when *Aesculus* was excluded ($P > 0.2$). Similarly, leaf longevity increased with date of bud break across all deciduous species ($r = 0.52$, $P < 0.05$), but that relationship vanished when *Aesculus* was excluded ($r = 0.32$, $P > 0.2$). Leaf longevity increased significantly with the date of 50% leaf drop across deciduous species, regardless of whether *Aesculus* was included ($y = 0.73x - 40.8$, $r^2 = 0.92$, $P < 0.0001$, two-tailed t test with 14 df) or excluded ($y = 0.98x - 107.7$, $r^2 = 0.94$, $P < 0.0001$). Taken together, these patterns indicate that long leaf lifespan is achieved mainly by delaying leaf fall in autumn, rather than by early leaf flushing in spring.

Phenology, topographic position, and predicted light interception—As expected, across deciduous species, the date of 50% leaf expansion—averaged across species weighted by their abundance—increased toward more xeric sites, indicating that early leafers dominated more mesic sites (Fig. 4). Across deciduous species, earlier leafing placed sapling leaves in a bright understory light environment for a longer period and resulted in higher estimated fractions of total growing season PFD intercepted prior to canopy closure (Fig. 5A: $r^2 = 0.99$, $P < 0.0001$ for 14 df, two-tailed t test; $r^2 = 0.94$, $P < 0.0001$ excluding *Aesculus*). Absolute interception of PFD was also

higher in early leafers over their growing season (Fig. 5B: $r^2 = 0.94$, $P < 0.0001$ for 16 df, two-tailed t test; $r^2 = 0.68$, $P < 0.0001$ excluding *Aesculus*). Early leafing *Aesculus flava* received 80% of its total growing-season PFD before canopy closure, in contrast to late-leaving *Magnolia fraseri* and *Nyssa sylvatica*, which received ca. 10% of growing-season PFD in spring (Fig. 5A). Despite these marked differences, all species achieved considerable light capture before canopy closure (Fig. 5B).

Early leafing and associated gains in potential light capture came with a significantly increased risk of freezing temperatures (Fig. 6; $r^2 = 0.97$, $P < 0.0001$ for 16 df). Based on meteorological data, the probability of freezing temperatures from late winter until the onset of the summer showed a sigmoid pattern, dropping most rapidly between March 1 and April 10 ($y = 0.68/(1 + \exp[-(x - 78.7)/14.9])$; $r^2 = 0.98$, $P < 0.0001$). A 10-d delay in bud break around March 1 (i.e., from March 1 to March 11) reduced the absolute risk of freezing temperatures by 11%.

Species ordination (PCA) in relation to phenology parameters and light environment—Principal component analysis of species phenological and light-environment characteristics produced three significant axes (Fig. 7A). The first axis of these explained 55% of the variance in the data and was positively correlated with the dates of bud break ($r = 0.81$, $P < 0.0001$), 50% expansion ($r = 0.90$, $P < 0.0001$), full expansion ($r = 0.79$, $P < 0.0001$), and (for deciduous species) leaf fall ($r = 0.71$, $P < 0.003$), as well as with functional leaf lifespan ($r = 0.60$, $P < 0.02$; Fig. 7B). In addition, PCA axis 1 was significantly positively correlated with all measures of understory light availability ($r = 0.58$ for Vsky, $r = 0.63$ for ISF, $r = 0.56$ for DSF, $P < 0.05$ in all cases, two-tailed t test; $r = 0.90$ for ISF + DSF, $P < 0.0001$). These correlations resulted in a species gradient along axis 1 from early leafers with relatively short leaf longevity occupying densely shaded microsites (e.g., *Aesculus*, *Halesia*) to evergreens (*Tsuga*, *Ilex*) with late bud break and long leaf longevity and late-leaving, deciduous taxa (*Nyssa*, *Oxydendrum*, *Quercus*) with long leaf longevity in more brightly lit sites (Fig. 7A). This species gradient also showed strong, highly significant correlations of early leafing with % PFD intercepted before canopy closure ($r = -0.90$, $P < 0.0001$) and with a higher risk of an early spring freezing event ($r = -0.83$, $P < 0.0001$). Much of the variation along axis 2, which accounts for 20% of the variance in the trait data, is positively correlated with the proportion of open sky (i.e., Vsky) ($r = 0.73$, $P < 0.0001$) and the amount of indirect sunlight (i.e., ISF) penetrating the canopy ($r = 0.67$, $P < 0.01$), separating species associated with very shaded sites (*Halesia tetraptera* var. *monticola*, *Carpinus caroliniana*, *Acer saccharum*) from those occurring under relatively open canopies (*Nyssa sylvatica*, *Quercus rubra*, *Oxydendrum arboreum*). Axis 3 explains only 11% of the variance among species.

Earliest-leaving and -dropping *Aesculus* and the two evergreen species (in which time of leafing and length of photosyn-

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Fig. 2. Mean leaf ratios as a function of date for 16 deciduous species (circles) and two evergreen species (triangles) common in the southern Appalachians. Leaf ratios are the leaf length ratio (open symbols), i.e., the ratio of leaf length on day of census in relation to maximum leaf length; and the leaf area ratio (closed symbols), i.e., the ratio of green leaf area on day of census to maximum leaf area; see Materials and Methods, *Leaf phenology*. To facilitate interspecific comparisons, a vertical line has been placed at the average dates of canopy closure for the mesic site (May 7); canopy closure occurred on 11 May at the intermediate site and on 25 May at the xeric site.

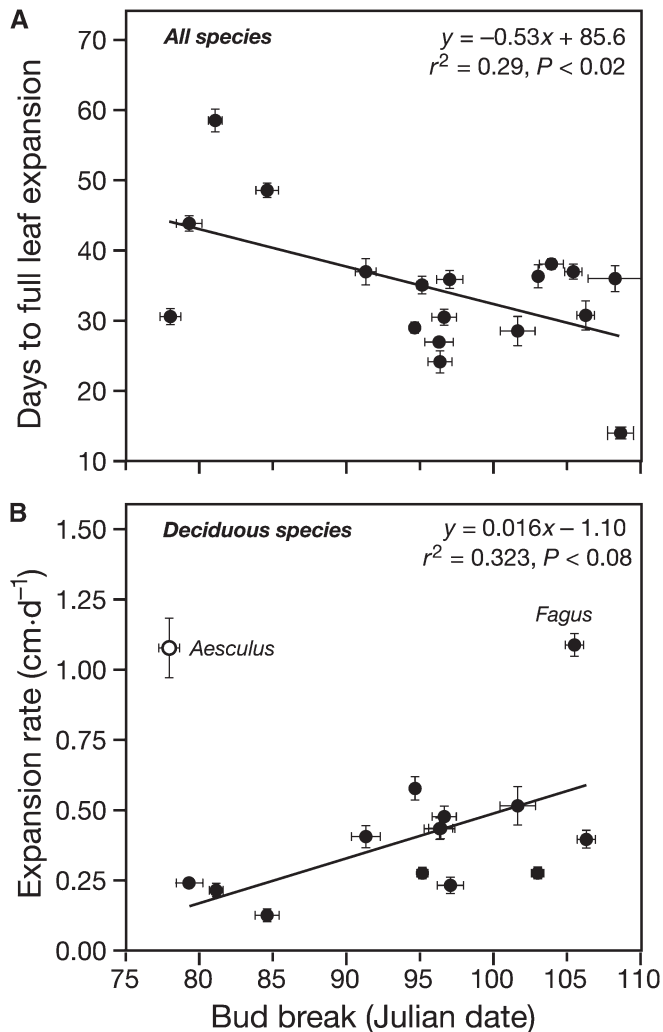


Fig. 3. (A) Number of days (mean \pm SE) needed to achieve full leaf expansion as a function of the mean date of bud break across all study species. Line represents LMS regression ($r^2 = 0.29$; $P < 0.02$ for two-tailed t test with 16 df). (B) Leaf expansion rates ($\text{cm}\cdot\text{d}^{-1}$) as a function of the mean date of bud break for deciduous species; points and error bars represent mean \pm SE for each species. *Aesculus* (hollow dot) was excluded from the regression as an outlier; it has extraordinarily high rates of leaf expansion $1.08 \text{ cm}\cdot\text{d}^{-1}$ given its early leafing.

thetic period are decoupled) are “outliers” in the two-dimensional PCA plot (Fig. 7A). The remaining species occupy a diagonal “main spectrum” from early leafers at lower left, associated with low midsummer light levels and a high probability of freezing temperatures early in the growing season, to late leafers at upper right, associated with more open canopies and a lower risk of freezing temperatures. As expected, most aspects of species’ leaf phenology, ecological distribution, midsummer light environment and exposure to freezing temperatures show strong collinearity along the main spectrum, with early leafing, densely shade summer microsites, and high risk of freezing temperatures varying together (Fig. 7C). Across species along the main spectrum, as the date of 50% leaf expansion increases, there are significant increases in direct radiation (DSF: $r = 0.53$, $P < 0.05$), indirect radiation (i.e., ISF, $r = 0.54$, $P < 0.05$), and percentage open sky (i.e., VSky, $r = 0.64$, $P < 0.01$).

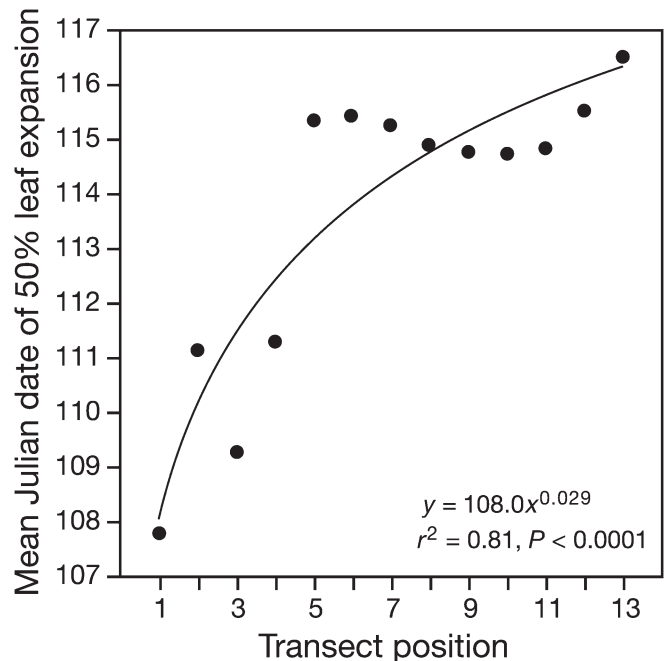


Fig. 4. Weighted average date of 50% leaf expansion across species as a function of landform position ($r^2 = 0.81$; $P < 0.0001$ for two-tailed t test with 11 df). The undulation in average time of leaf expansion seen at top right is caused by the high dominance and sequential replacement of *Acer rubrum*, *Quercus prinus*, and *Nyssa sylvatica* on subxeric and xeric sites, with the *Quercus* having a slightly earlier average date of leafing than the other two.

DISCUSSION

This study documents extensive variation in the time of leafing among saplings of common deciduous tree species growing at mid elevations in the southern Appalachians. Earliest-leafing *Aesculus flava* achieved 50% leaf expansion 33 d before latest-leafing *Magnolia fraseri* and *Nyssa sylvatica* (Fig. 2, Table 2). Such differences in leaf phenology may have profound effects on the ability of saplings to survive in microsites densely shaded in midsummer, by permitting photosynthesis for long periods under brightly lit conditions before the canopy closes (Harrington et al., 1989; Givnish, 1990, 2002; Uemura, 1994; Gill et al., 1998; Seiwa, 1998; Komiyama et al., 2001a, b; Augspurger and Bartlett, 2003; Tomita and Seiwa, 2004; Augspurger et al., 2005).

The ability to survive and grow under canopies of a given density can be a function of several factors, including physiological variation at the leaf level (Björkman, 1981; Givnish, 1988; Percy, 1990; Valladares et al., 1997; Givnish et al., 2004), plant height (Givnish, 1988), canopy geometry (Horn, 1971; Valladares et al., 2002), allocation to root tissue (Givnish, 1988), drought or flooding stress (Valladares and Percy, 2002; Sack, 2004; Sánchez-Gómez et al., 2006; Niinemets and Valladares, 2006; Lopez and Kursar, 2007), seedling inability to penetrate deep litter (Givnish 1998; Metcalfe and Turner, 1998; Sayer 2006), susceptibility to pathogens in shaded or humid microsites (Jenkins and White, 2002; Rackham, 2003; Holzmüller et al., 2006) and leaf phenology (Harrington et al., 1989; Givnish, 2002; Augspurger et al., 2005, Augspurger 2008). The data presented here provide the first step toward

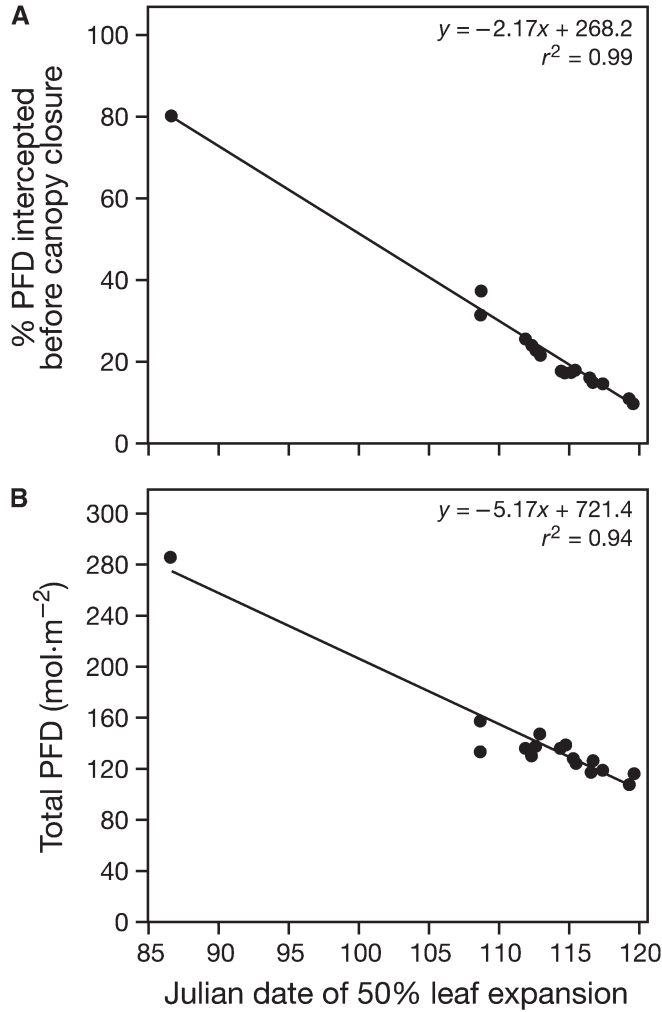


Fig. 5. (A) Percentage of growing-season photon flux density (PFD) intercepted by deciduous saplings before canopy closure as a function of date of 50% full leaf expansion, assuming a mesic canopy and light capture during each species' functional leaf lifespan; line represents LMS regression. (B) Total growing-season PFD intercepted as a function of date of 50% full leaf expansion.

documenting the importance of leaf phenology for shade tolerance across a diverse set of temperate deciduous tree species growing in mature forests in the southern Appalachians. Our data demonstrate that earlier times of leafing increase the total amount of light intercepted by saplings under a given forest canopy, as well as the fraction of light captured before canopy closure (Fig. 4). Our data corroborate and extend work in Illinois on early leafing *Aesculus glabra* and *Acer saccharum* that showed significantly reduced growth and increased mortality when the spring "window of light" was removed using artificial shading (Augsburger, 2008). We expect the benefit of earlier leafing in terms of light capture and early season carbon gain to be greatest on mesic, concave landforms, whose canopy closes earlier and often casts denser shade in midsummer than those on open slopes or xeric, convex ridges (Fig. 1, Table 2). In such sites, we expect that early leafing represents one mechanism underlying differences among species in shade tolerance.

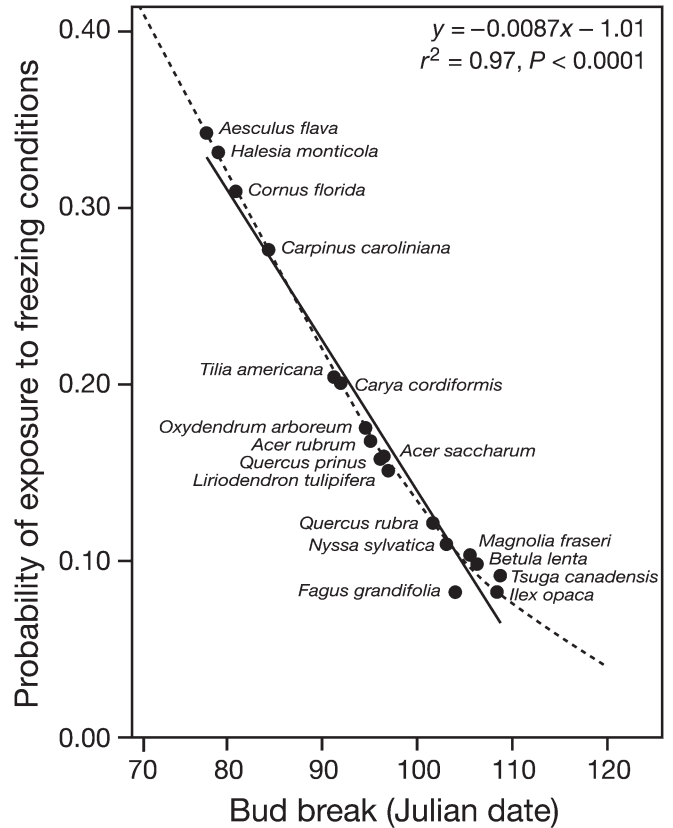
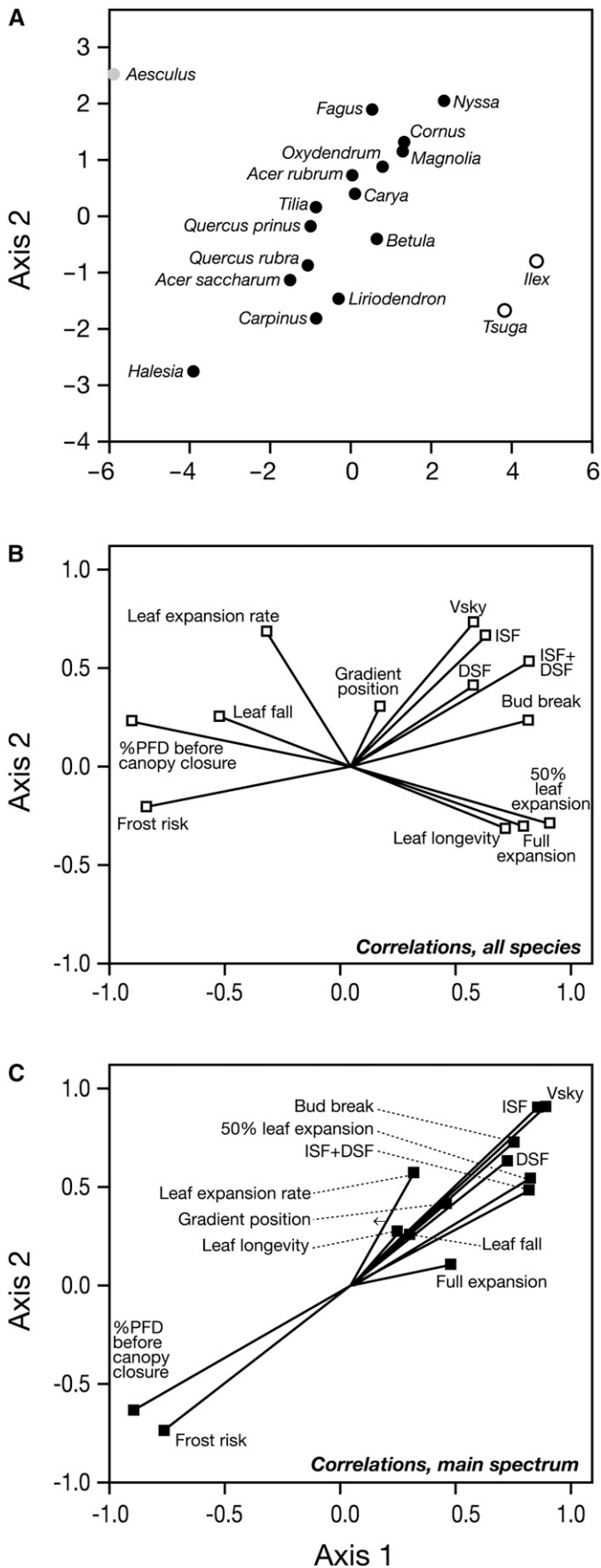


Fig. 6. Probability of exposure to freezing temperatures as a function of date of bud break for a species. Dashed curve is logistic curve; solid line is LMS regression ($r^2 = 0.97$; $P < 0.0001$ for two-tailed t test with 16 df).

In eastern North America, the forests of the southern Appalachians are a center of temperate tree diversity. Within these forests, species occur nonrandomly, showing significant species turnover across landform gradients (Whittaker, 1956). Understanding the environmental and functional diversity underlying species distribution patterns within this landscape was a major goal of our research. Our PCA revealed a "main spectrum" of species associated with the landform gradient. At one end of the spectrum are early leafing species that experience low midsummer light levels and occur on moister, more fertile cove forest sites. At the other end of the spectrum are late leafers that experience higher midsummer light levels and occur on drier, more nutrient-poor ridge forest sites.

Three species, *Aesculus*, *Tsuga*, and *Ilex*, fall far from this main spectrum, suggesting that they employ different functional strategies compared to the species of the "main spectrum" (Fig. 7). Rapid leaf expansion and early leaf fall set *Aesculus* apart. These traits parallel the strategy of many spring ephemerals that co-occur with *Aesculus* in cove forests (DePamphilis and Neufeld, 1989; Small and McCarthy, 2002). Cove sites have densely shaded understories in midsummer and our photosynthetic data (not shown) suggest that *Aesculus* operates very close to its light compensation point during midsummer. As such, the returns on continued investment in leaf tissue as the summer progresses are likely small. The evergreen species (e.g., *Ilex*, *Tsuga*) differ from the main spectrum species (and *Aesculus*) in their long lifespans and late production of new



leaves, but are functionally more similar to early leafing taxa as overwintered leaves likely become photosynthetically active before sympatric deciduous species (Givnish, 2002). Within a habitat, evergreens should be *more* shade tolerant than deciduous species, given their longer payback period for leaf construction costs and longer seasonal window of photosynthetic activity. Across habitats, evergreens should be *less* shade tolerant, given their frequent restriction to poor soils and the heavy belowground costs such soils impose (Givnish, 2002).

The spring “window of light” in temperate deciduous forests corresponds to a relatively high solar angle, abundant moisture due to snow deposition, and/or reduced evaporation during winter, and a flush of soil nutrients (Muller and Bormann, 1976; Hutchison and Matt, 1977; Givnish, 2002; Augspurger and Bartlett, 2003), but the corresponding autumn “window” tends to be much darker and drier. Not surprisingly, Harrington et al. (1989) found that two shrub species in Wisconsin oak forests showed little photosynthesis during fall, despite showing high rates of photosynthesis and acquiring up to 35% of their annual carbon input during the spring window. Sapling photosynthesis under leafless canopies should thus be much more energetically productive in spring than in fall.

Early leafing comes with an increased risk of exposure to freezing temperatures (Fig. 6). The risk of freezing temperatures decreases by about 5.5% per week around the time of bud break, corresponding to a relative reduction in risk of 51%. Although it is uncertain how detrimental freezing temperatures might be to buds and leaves of the study species, the costs of replacing leaves damaged by freezing temperatures would be effectively greater on drier, less fertile sites, given the greater investments in roots required to replace nutrients lost in damaged leaves (Givnish, 2002). Thus, even though early spring is the one time of year when moisture is reliably in abundant supply on xeric sites, selection there against loss of leaves to potential late frosts could favor the observed dominance of infertile, dry sites by late leafers.

Early leafing may help some tree species escape damage by late-emerging insect herbivores (Feeny, 1970; Seiwa, 1998; Aizen and Patterson, 1995). However, early leafers—the only woody species with soft, young leaves present in early spring—are exceptionally exposed to vertebrate herbivory. It is likely no accident that the earliest leafers—*Aesculus flava* and its relatives (e.g., *A. sylvatica*, DePamphilis and Neufeld [1989])—typically show almost no leaf damage by any herbivore (T. Givnish, personal observation); buckeyes are highly toxic, protected by high levels of the coumarin glycoside aesculin, and the ground leaves, fruits, and buds of *Aesculus* have been used

← Fig. 7. (A) Principal component analysis of 18 tree species of the southern Appalachians using leaf phenology, light regimes, and probability of freezing temperatures. Evergreen species are indicated by open dots. Earliest-leafing and -dropping *Aesculus* (upper left) and the two evergreen species (lower right) are outliers. Most species (solid dots) occupy a diagonal swath from early leafers at lower left (associated with low midsummer light levels, mesic sites, and high risk of freezing temperatures) to late leafers at upper right (associated with greater canopy openness, xeric sites, and lower probability of freezing temperatures). (B) Joint plot showing the direction and magnitude of the correlation (r) between each parameter and scores on each axis of the PCA. (C) Same as previous graph, but for saplings of main-spectrum species only; note the near collinearity of most factors, indicating gradient from early leafing, dark midsummer light environments, and distribution on mesic sites at lower left, to the inverse set of these conditions at upper right.

as fish poisons (Russell et al., 1997). Late leafers (e.g., *Quercus*) commonly occur on xeric sites and typically have young leaves that rapidly expand, tough adult leaves, and high concentrations of condensed tannins (Forkner et al., 2004; Matsuki and Koike, 2006), as expected among plants exposed to herbivorous insects in a nutrient-poor habitat.

Ecologists have long recognized that seasonal variation in understory light availability tracks cycles in solar angle, cloudiness, and canopy closure (Salisbury, 1916; Anderson, 1964; Hutchison and Matt, 1977; Hashimoto and Aoki, 1996). Landform position also affects understory light availability: our ridge stand received 16% more understory PFD before canopy closure than did a forested open slope, and 43% more than did a mesic, concave cove. Presumably, much of the observed variation in understory PFD among sites is due proximally to site differences in canopy density; there is a strong increase in leaf area index—measured via litterfall—in moving from ridges to coves in nearby Nantahala National Forest (Bolstad et al., 2001). However, site differences in insolation due to landform position, convexity, and shading by the surrounding landscape should also play an important role in determining solar input and evaporative demand (e.g., see Dubayah and Rich, 1995; Wang et al., 2006). Landform position—associated with a variety of environmental factors, including moisture supply, evaporative demand, soil thickness, soil fertility, fire frequency, leaf area index, and rate of tree growth (Whittaker, 1956; Helvey and Patric, 1988; Elliott et al., 1999, 2002; Bolstad et al., 2001; Boerner, 2006)—is also correlated with time of canopy closure, with canopy trees leafing earlier on more mesic sites (Fig. 1). Earlier and more complete canopy closure on more mesic stands should not only favor early leafing in saplings on such sites, but also favor herbs over shrubs (as observed by Whittaker [1956]), based on expected differences between life-forms in whole-plant light compensation points (Givnish, 2002). The greater density of foliage on more mesic sites—and lower light penetration to the groundlayer (Fig. 1 and see also Bolstad et al., 2001; Fig. 7 for our study species)—may thus be an important driver of tree species distributions, in addition to any direct effects of soil conditions on the context-specific survival, growth, and competitive ability of such species. Simply put, dense early leafing canopies on mesic sites may help exclude late-leafing, less shade tolerant trees and permit only early leafing, more shade-tolerant tree species to persist. The more open canopies and higher costs associated with leaf replacement due to late frosts on xeric sites should work against early leafing tree species and favor dominance by late leafers. Differences in leaf phenology thus appear to play a key role in determining not only the shade tolerance of individual species, but also differences in their distributions at the landscape and community levels.

Avoidance of canopy shade via early leafing appears to be an important, albeit paradoxical, mechanism to persist in shady environments and thereby affect the ecological distribution in tree species of southern Appalachian forests. This study shows that 10–80% of growing season photon flux density arrived prior to canopy closure; that time of leafing has a larger effect on light capture on mesic sites, whose canopies close rapidly and achieve dense coverage, than on xeric sites with more open and slowly closing canopies; that earlier leafing is associated with species occupying more densely shaded microsites; and that earlier leafing is significantly correlated with tree sapling distribution on more concave landforms. These results suggest a close tie of shade tolerance to time of leafing, although this tie should be confirmed with more rigorous metrics of growth and

survival as a function of PFD (see Kobe, 1996, 1999; Pacala et al., 1993; Montgomery and Chazdon, 2002). Moreover, future research is needed to quantify the gains in photosynthesis, whole-plant growth, and competitive ability associated with differences in time of leafing and time of canopy closure, based on seasonality in static and dynamic photosynthetic light responses, photosynthetic limitation by hydraulic conductance, and habitat-specific shifts in phenology and biomass allocation. Such research would contribute to our understanding of the role of leafing phenology as a determinant of shade tolerance.

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