

**LEAF ECONOMIC TRAITS FROM FOSSILS SUPPORT A WEEDY
HABIT FOR EARLY ANGIOSPERMS¹**

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Many key aspects of early angiosperms are poorly known, including their ecophysiology and associated habitats. Evidence for fast-growing, weedy angiosperms comes from the Early Cretaceous Potomac Group, where angiosperm fossils, some of them putative herbs, are found in riparian depositional settings. However, inferences of growth rate from sedimentology and growth habit are somewhat indirect; also, the geographic extent of a weedy habit in early angiosperms is poorly constrained. Using a power law between petiole width and leaf mass, we estimated the leaf mass per area (LMA) of species from three Albian (110–105 Ma) fossil floras from North America (Winthrop Formation, Patapsco Formation of the Potomac Group, and the Aspen Shale). All LMAs for angiosperm species are low (<125 g/m²; mean = 76 g/m²) but are high for gymnosperm species (>240 g/m²; mean = 291 g/m²). On the basis of extant relationships between LMA and other leaf economic traits such as photosynthetic rate and leaf lifespan, we conclude that these Early Cretaceous landscapes were populated with weedy angiosperms with short-lived leaves (<12 mo). The unrivalled capacity for fast growth observed today in many angiosperms was in place by no later than the Albian and likely played an important role in their subsequent ecological success.

Key words: Albian; angiosperms; Cretaceous; evolution; leaf economics spectrum; leaf mass per area; paleobotany; paleoecology; riparian habitats.

Angiosperms today comprise ~90% of plant species, but many aspects of their origin and early radiation are poorly known (Taylor et al., 2009). The earliest angiosperm fossils are rare, Late Valanginian (139–136 Ma, timescale after Gradstein et al., 2004) pollen from Israel (Brenner, 1996). The Lower Aptian to Lower Cenomanian (125–96 Ma; Hochuli et al., 2006) Potomac Group sequence from the United States mid-Atlantic coast contains some of the earliest angiosperm megafossils and provides critical constraints on their ecology. In this sequence, angiosperms become increasingly abundant through time in riparian facies (e.g., stream channels, levees, crevasse splays), while conifers and Bennettitales dominate in quiet, nutrient-limited swamp environments where plants likely experienced little physical disturbance (Hickey and Doyle, 1977; Upchurch et al., 1994). Further, some of the Potomac taxa are possibly herbaceous based on their relatively low leaf-rank, cordate ba-

ses, and fragile appearance (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Upchurch et al., 1994). Because fast-growing, weedy plants typically dominate in highly disturbed riparian corridors today, and because extant herbs typically employ a fast growth strategy (Grime, 2001), sediment and fossils from the Potomac support the proposal that many early angiosperms were fast-growing, weedy shrubs and herbs (Wettstein, 1907; Stebbins, 1965, 1974; Bond, 1989) that first became ecologically important in disturbed, streamside environments (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Taylor and Hickey, 1992, 1996; Wing et al., 1993).

The interpretations of growth strategy from Potomac Group fossils have provided key insights into the ecophysiology of early angiosperms (Doyle and Hickey, 1976; Hickey and Doyle, 1977). However, it is not clear whether the attendant relationships between growth rate and streamside environments held in the past, especially early in angiosperm evolution. Further, the geographic extent of a fast growth strategy at this early stage in angiosperm evolution is poorly known.

Growth strategy and the leaf economics spectrum—Growth rate cannot be measured directly from fossils, but intensity of resource use covaries with a large number of leaf traits that reflect fundamental trade-offs. This coordinated trait array is sometimes called the leaf economics spectrum (Wright et al., 2004). Plants with rapid resource acquisition (the “fast-return” end of the spectrum) typically have a high mass-based photosynthetic and respiration rate, high concentration by mass of nitrogen and phosphorus, short leaf lifespan, and low leaf dry mass per area (LMA) (Reich et al., 1997; Westoby et al., 2002; Díaz et al., 2004; Wright et al., 2004). The reverse is true for plants at the “slow-return” end of the spectrum: plants investing in a high LMA have slower photosynthetic rates but longer leaf

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lifespans, such that their slower revenue (carbon uptake) rate is compensated by a longer-lasting revenue stream (Westoby et al., 2002; Wright et al., 2004). Critically, these interrelationships among leaf economic variables are not strongly affected by phylogeny (Ackerly and Reich, 1999). The leaf economics spectrum has also been linked to broader patterns and processes, including insect herbivory (Coley, 1983; Westoby et al., 2002), litter decomposition rate (Santiago, 2007; Cornwell et al., 2008), nutrient mineralization rate (Parton et al., 2007; Manzoni et al., 2008), and community assembly (Grime, 2001; Shipley et al., 2006a). The correlations that underlie the spectrum are considered causal (Reich et al., 2003; Wright et al., 2004; Shipley et al., 2006b) and thus should be broadly universal and applicable on macroevolutionary timescales.

No leaf economic trait can be measured directly from fossils. Recently, Royer et al. (2007) identified a biomechanical scaling law between petiole width (PW) and leaf mass. In brief, heavier leaves require more substantial petioles for support. The PW term is raised to the second power to better capture the two-dimensional nature of petiole cross sections and divided by leaf area (A) so that PW^2/A can be correlated directly to LMA (see Royer et al., 2007 for details about modeling the scaling relationship). Importantly for this study, LMA has been observationally linked to growth rate in many species (e.g., Poorter and Bongers, 2006; Poorter et al., 2009). Royer et al. (2007) calibrated the biomechanical relationship within extant, woody nonmonocotyledonous plants (“woody dicots”; gray circles in Fig. 1) and applied it to two Eocene floras (Republic, Washington and Bonanza, Utah). More recently, LMA was estimated for fossils spanning the Paleocene-Eocene Thermal Maximum in northern Wyoming, USA (Curran et al., 2008) and for the late Paleocene Cerrejón flora in Colombia (Wing et al., 2009). An advantage of the method is that it is based on two simple characters, petiole width and leaf area, that are measurable in many fossil leaves (see Materials and Methods and Royer et al., 2007 for further details). An alternative approach for inferring paleo-leaf economics, which we do not pursue here, relies on the correlation observed in many extant taxa between leaf vein density and transpiration (Uhl and Mosbrugger, 1999; Boyce et al., 2009).

Inferring the growth strategy of early angiosperms—Royer et al. (2007) demonstrated the considerable promise for reconstructing LMA and linked leaf economic information for fossil taxa and their associated landscapes. The method provides the opportunity to test, with fossils, previous ecophysiological interpretations of fast growth rate in early angiosperms. Here, we expand the woody dicot calibration of Royer et al. (2007) to include broad-leaved gymnosperms and herbaceous angiosperms, which allows for testing potential differences in LMA between fossil angiosperms and gymnosperms and for more rigorously estimating the LMA of putative fossil herbs. We then apply the resultant relationships to three broadly coeval sites (middle to late Albian; 110–105 Ma) that contain some of the earliest megafossil remains of angiosperms: the Winthrop Formation in north-central Washington State, the Patapsco Formation of the Potomac Group in eastern Virginia and Maryland, and the Aspen Shale in southwestern Wyoming. If reconstructed LMA for angiosperms at these sites is low (and presumably linked to short leaf lifespan, high photosynthetic rate, and rapid resource acquisition), then such a finding would support previous inferences for fast-growing plants during the Albian and increase confidence that the interpretation of a weedy lifestyle for the complete Potomac sequence (125–96 Ma) is correct.

Further, recognition of a fast growth strategy at three widely separated sites would boost confidence that fast growth was common among angiosperms at this time.

MATERIALS AND METHODS

Extant calibration—To supplement the woody dicot calibration of Royer et al. (2007) ($N = 667$ species-site pairs), we weighed and photographed dried leaves from 93 species of broad-leaved gymnosperms and 58 species of herbaceous angiosperms. All leaves were nonsessile with distinct petioles. We measured leaf area (blade + petiole) and petiole width with the program ImageJ (documentation and downloads at website <http://rsbweb.nih.gov/ij/>, National Institutes of Health, Bethesda, Maryland, USA), where petiole width is measured perpendicular to the midvein in the plane of the leaf blade, at the basalmost insertion of the blade into the petiole (Royer et al., 2007). Two leaves per species were typically processed. Although all leaves were pressed while being dried, some shrinkage in petiole width may be expected, especially among herbs due to their weakly lignified tissues (Mauseth, 1988). Moreover, taphonomic processes during fossilization can lead to an inflation of petiole width (typically less than 10%) (Nilklas, 1978; Rex and Chaloner, 1983; Rex, 1986; see also Royer et al., 2007). Both of these processes would lead to an overestimation of LMA, meaning that our estimates of LMA for fossils are probably maxima. It is possible that a combination of petiole length and petiole cross-sectional shape and size may correlate more strongly with LMA than petiole width alone, but these dimensions are rarely preserved in fossils (Royer et al., 2007).

Gymnosperm material came from herbaria (National Herbarium of New South Wales, Dame Ella Campbell Herbarium, and Yale University Herbarium) with the exception of fresh *Ginkgo biloba* from the Wesleyan University campus. We made fresh collections of herbaceous angiosperms from north of Reed Gap in Wallingford, Connecticut, USA; we additionally recorded the fresh mass of these leaves (leaves weighed after being in sealed plastic bags for ~2 h). This Connecticut herb collection was supplemented with New Zealand herbs from the Allan Herbarium.

Fossil sites—Following the protocol described in the previous section, we measured the petiole widths and leaf areas for 179 fossil specimens representing 30 species-site pairs (27 angiosperm, 3 gymnosperm) from three Early Cretaceous fossil floras (Table 1). Only taxa with at least two measurable specimens and with distinct petioles were processed. Measured specimens from the Winthrop flora come primarily from quantitative census collections (Miller et al., 2006; Miller and Hickey, 2008) at the Yale Peabody Museum, the Denver Museum of Nature and Science, the National Museum of Natural History of the Smithsonian Institution, and the Burke Museum; specimens from the Patapsco come from historical collections (e.g., Clark et al., 1911; Hickey and Doyle, 1977) at the National Museum of Natural History; specimens from the Aspen Shale flora come mostly from quantitative census collections (Peppe et al., 2008) at Yale Peabody Museum.

TABLE 1. Sampling summary of fossil sites in the United States with paleolatitude and mean annual temperature (MAT). All sites are middle to late Albian in age (110–105 Ma) (see Materials and Methods for details). Taxa information is for dicotyledonous leaves only.

Flora	Location	Latitude (°N)	MAT (°C)	Taxa (N)		Specimens used (N)
				Present	Used	
Winthrop	North-central Washington	38 ^a	23.4 ^a	43 ^a	19	118
Patapsco	Eastern Virginia and Maryland	36 ^a	19.1 ^a	28 ^b	5	31
Aspen Shale	Southwestern Wyoming	50 ^c	Unknown	16 ^d	3	12

^a From Miller et al. (2006).

^b From Clark et al. (1911).

^c Based on reconstructions of Housen et al. (2003) and Torsvik et al. (2008).

^d From Peppe et al. (2008).

The Patapsco Formation of the Potomac Group, which crops out in eastern Virginia and Maryland, USA, contains sediment deposited in a large fluvial system, including stream channels, levees, crevasse splays, and meander cut-offs (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Upchurch et al., 1994). All specimens presented here come from higher energy, physically disturbed environments (channels, levees, and splays). The age of the Potomac sequence is determined biostratigraphically with pollen (Brenner, 1963; with updates from Doyle and Hickey, 1976; Hickey and Doyle, 1977; Doyle, 1992) and with plant megafossils (Doyle and Hickey, 1976; Hickey and Doyle, 1977). All localities from the Patapsco used here have been dated to Brenner's Subzone IIB (early Albian to early late Albian, 110–105 Ma; Doyle and Hickey, 1976; Hickey and Doyle, 1977).

The Winthrop Formation, in north-central Washington State, USA, contains a sequence of fossiliferous crevasse splay deposits and finer-grained, rooted, incipient paleosols (Miller et al., 2006; Miller and Hickey, 2008). Biostratigraphically, the Winthrop flora correlates most closely with Subzone IIB of the Potomac. Ammonites from the underlying Harts Pass Formation constrain the maximum age to middle Albian (~109 Ma), while the minimum age is constrained by a U/Pb-zircon age from a cross-cutting dike (97.5 Ma) and by the occurrence of *Vitiphyllum*, *Nelumbites*, *Rogersia*, *Menispermities*, and a high diversity of *Sapindopsis* species (>99.6 Ma) (Miller et al., 2006; Miller and Hickey, 2008).

The final flora comes from the upper part of the Aspen Shale in southwestern Wyoming, USA (Brown, 1933; Peppe et al., 2008). The fossiliferous beds are interpreted as a sequence of incipient paleosols and ashfall deposits in a paludal setting. Biostratigraphic correlation places the Aspen Shale flora in Subzone IIB of the Potomac Group and more broadly to the middle to late Albian based on comparisons with other western United States floras (Peppe et al., 2008).

Statistics—We used the ordinary least squares regression and standardized major axis modules in the program SMATR (v. 2; documentation and download at website <http://www.bio.mq.edu.au/ecology/SMATR/>) (Warton et al., 2006) to generate predictive transfer functions for LMA and to test for slope and intercept differences between regression lines, respectively; see Warton et al. (2006) for a discussion of the applicability of both regression approaches. The 95% prediction intervals for individual (fossil) predictions of LMA, which include a sensitivity to sample size, follow Sokal and Rohlf (1995); coefficients for calculating prediction intervals of woody dicots and broad-leaved gymnosperms are provided in Royer et al. (2007) and Appendix S1 with the online version of this article, respectively.

RESULTS

The proportional scaling between area-normalized petiole width (PW^2/A) and LMA is significant within both broad-leaved gymnosperms and herbaceous angiosperms (Fig. 1; see online Appendix S2 for species data). For broad-leaved gymnosperms, the slope of the relationship is similar to woody dicots (P -value for common slope = 0.25) but the y -intercept is shifted toward higher LMA values ($P = 0.003$ for shift in elevation). For herbaceous angiosperms, the slope is significantly flatter ($P = 0.03$) and LMA values at a given PW^2/A are substantially lower than for woody dicots.

Application of the scaling laws to angiosperms in the Winthrop, Patapsco, and Aspen Shale floras reveals universally low LMA: values range from 50.7–97.5 g/m^2 in the Winthrop, 75.0–94.0 g/m^2 in the Patapsco, and 60.2–124.5 g/m^2 in the Aspen Shale (filled circles in Fig. 2B; see online Appendix S3 for species data). These estimates assume that all taxa are woody, but some taxa may be herbaceous (see introduction). For these putative herbs, their estimated LMA decreases by ~55% due to the different scaling relationship between herbaceous angiosperms and woody dicots (black triangles in Fig. 2B).

The Winthrop flora also contains three well-preserved gymnosperm taxa that are appropriate for LMA analysis (nonsessile leaves with distinct petioles). The LMA for these taxa are considerably higher than their companion angiosperms, ranging

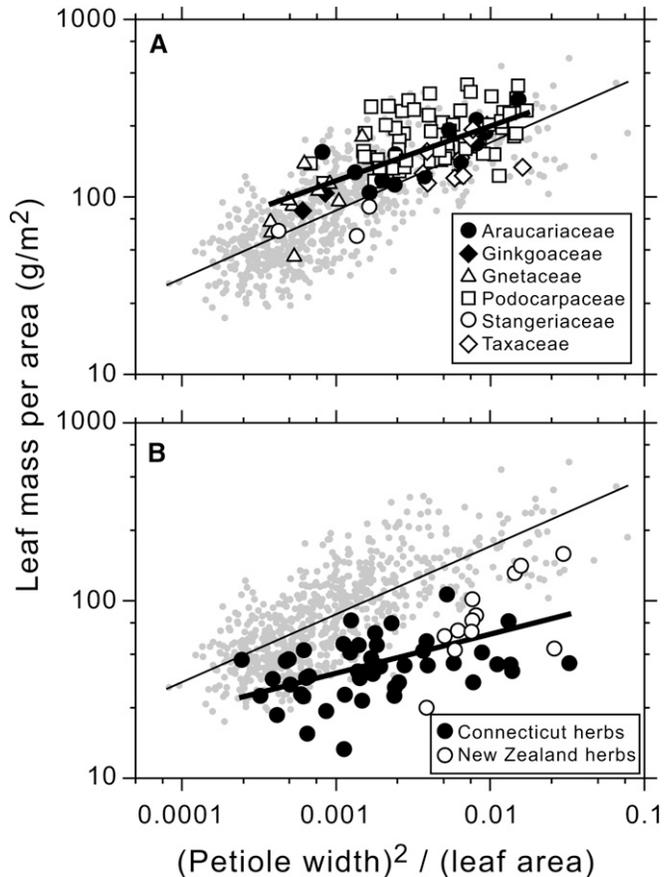


Fig. 1. Power-law scaling in extant vegetation between area-normalized petiole width (PW^2/A) and leaf dry mass per area (LMA). Gray symbols and thin regression line in both panels correspond to the woody dicot compilation of Royer et al. (2007) ($\log[LMA] = 0.3820 \times \log[PW^2/A] + 3.070$; $N = 667$ species-site pairs, $r^2 = 0.55$, $F_{1,666} = 825$, $P < 0.0001$). (A) Broad-leaved gymnosperms ($\log[LMA] = 0.3076 \times \log[PW^2/A] + 3.015$; $N = 93$ species, $r^2 = 0.44$, $F_{1,93} = 72.4$, $P < 0.0001$). The two data points for Ginkgoaceae (*Ginkgo biloba*) correspond to leaves from short and long shoots. (B) Herbaceous angiosperms ($\log[LMA] = 0.2204 \times \log[PW^2/A] + 2.245$; $N = 58$ species, $r^2 = 0.32$, $F_{1,57} = 19.45$, $P < 0.0001$).

from 243–326 g/m^2 (open circles in Fig. 2B). Another difference is that gymnosperms are found mostly on stable paleosol sites, while angiosperms (and ferns) dominate on more highly disturbed crevasse splay deposits.

DISCUSSION

Biomechanical scaling in herbs and gymnosperms—The scaling relationships between area-normalized petiole width (PW^2/A) and LMA in herbaceous angiosperms and broad-leaved gymnosperms are each different than the scaling in woody dicots reported by Royer et al. (2007) (Fig. 1). Across the range of calibrated PW^2/A , LMA is on average 43–75% lower for herbs than for woody dicots at a given PW^2/A (Fig. 1B). One reason for this disparity may be differences in leaf water content. The mean water content (by mass) in our freshly collected herbs was 82.8%, which compares favorably to other published values (82.2%, $N = 579$ species; Vile et al., 2005). Woody dicots, in contrast, have distinctly lower water contents

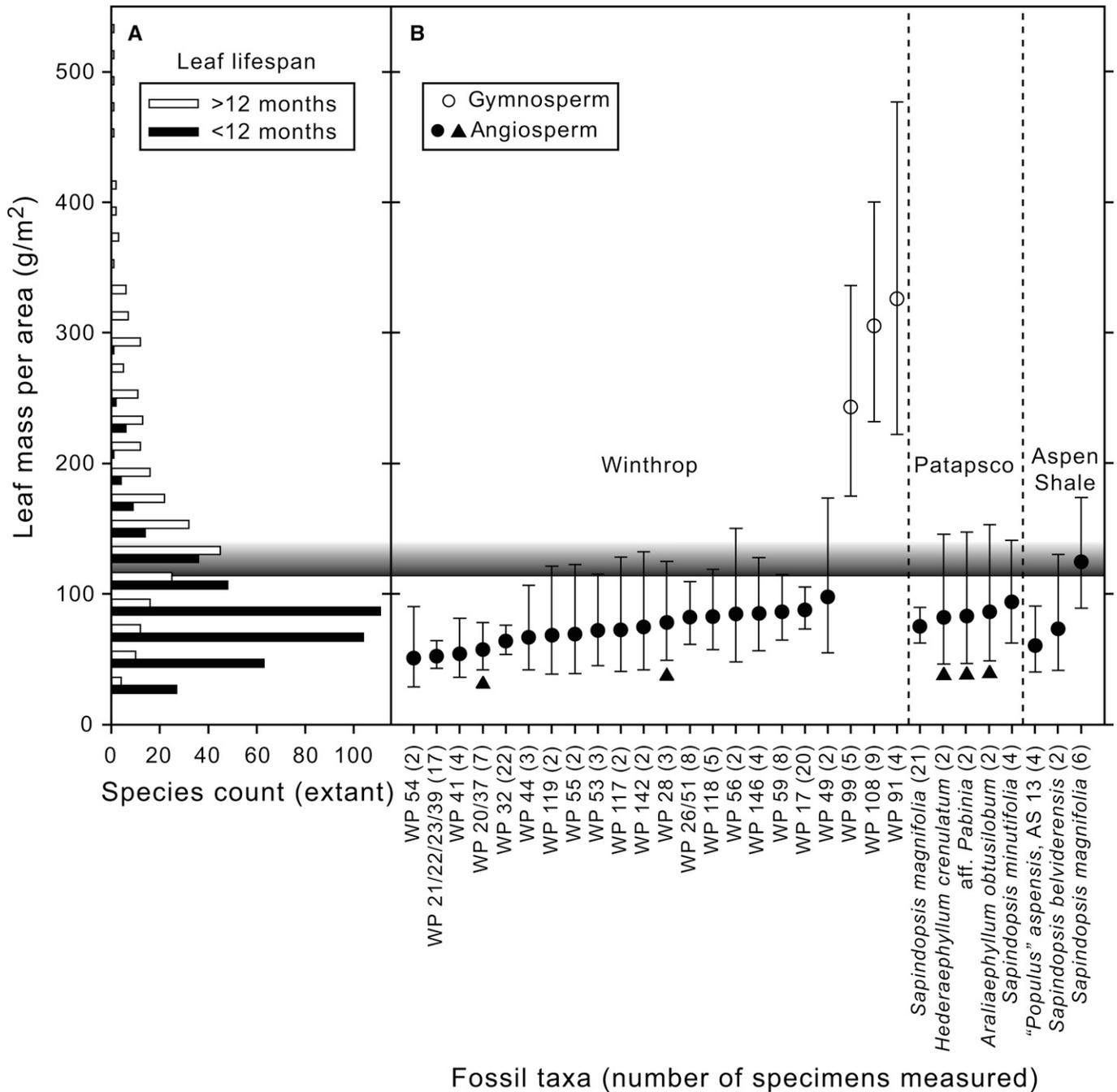


Fig. 2. Estimated leaf dry mass per area (LMA) for three Early Cretaceous floras and comparison to extant vegetation. (A) Relationship between LMA and leaf lifespan for 678 extant species of gymnosperms, angiosperms (woody and herbaceous), and ferns (data from Wright et al., 2004). The LMA bin size is $20 \text{ g}/\text{m}^2$. The LMA threshold that best differentiates leaves with a lifespan of $>12 \text{ mo}$ (evergreen) from $<12 \text{ mo}$ (mostly deciduous within woody taxa) is marked with a gray bar ($129 \text{ g}/\text{m}^2$). (B) Estimated LMA for species in the Winthrop, Potomac, and Aspen Shale floras. Taxon-appropriate regressions were used (gymnosperm and woody dicot; circles; see Fig. 1A); for putative herbs, LMA estimates from the herb-specific regression (Fig. 1B) are included (triangles). Errors are 95% prediction intervals. Taxonomy follows Miller (2007) for the Winthrop, Doyle and Hickey (1976) and Hickey and Doyle (1977) for the Potomac, and Peppe et al. (2008) for the Aspen Shale.

(63.0%, $N = 410$ species; Cornelissen et al., 1996; Niinemets, 2001; Vile et al., 2005). Because petioles are designed to support fresh leaf mass, not just dry leaf mass, this consistent difference in water content may lead to offsets when PW^2/A is plotted against leaf dry mass per area (LMA); we plot against leaf dry mass per area, not leaf fresh mass per area, because the

former is much more informative about leaf economics (Wright et al., 2004). However, even when the average offset in water content is accounted for (30.3%), LMA is still 25–66% lower on average for the adjusted herbs than for woody dicots at a given PW^2/A (online Appendix S4). Thus, differences in water content are just one factor that contributes to the different

PW²/A–LMA scaling in Fig. 1B. Another likely contributing factor is the weakly lignified stems and petioles of herbs (Mauseth, 1988), which require herbs to build thicker petioles relative to woody taxa for leaves of equivalent mass.

For broad-leaved gymnosperms, LMA is on average somewhat higher (19–58%) than for woody dicots at a given PW²/A (Fig. 1A). In contrast to the herbs, this offset cannot be explained by large differences in water content (gymnosperms: 68.9%, $N = 8$ species; Cornelissen et al., 1996; Niinemets et al., 2002; woody dicots: 63.0%, see previous paragraph). However, most gymnosperm petioles are at least as lignified as woody dicots (Mauseth, 1988); this increased strength provides a functional explanation for why gymnosperm leaves are heavier per unit petiole width than woody dicots.

Ecophysiology of early angiosperms—The low reconstructed LMA for angiosperms in the Winthrop, Patapsco, and Aspen Shale floras (Fig. 2B) is most consistent with a strategy that prioritizes rapid resource acquisition. If any of the taxa were herbaceous, then estimated LMA would be even lower (Fig. 2B). We surmise that these early angiosperms were fast growers with a high photosynthetic rate and short leaf lifespan (see introduction). Wright et al. (2004) observed a strong relationship in extant vegetation between LMA and leaf lifespan, where an LMA of 129 g/m² corresponded to an average leaf lifespan of 12 mo (Fig. 2A). If we assume a similar relationship in the past, then all of our angiosperm taxa had leaf lifespans shorter than 12 mo. In contrast, gymnosperms, with their high estimated LMA (Fig. 2B), were pursuing a fundamentally different, slow-return economic strategy (although our data are limited; $N = 3$ species).

While low LMA is linked to fast growth rates in many species (e.g., Poorter and Bongers, 2006; Poorter et al., 2009), the relationships within the leaf economics spectrum are noisy. For example, the r^2 of the log-log relationship between LMA and leaf lifespan is 0.42 ($N = 678$ species–site pairs; Wright et al., 2004). A number of factors contribute to the noise; for example, leaves from shade-tolerant plants typically have a lower LMA than shade-intolerant plants with the same leaf lifespan (Poorter et al., 2009). Thus, we cannot be certain that all of our fossil species had leaf lifespans <12 mo and a fast-return growth strategy. But, because the low LMA syndrome is ubiquitous among all the fossil angiosperms, we consider our data best support the presence of a weedy growth strategy in some, and probably most, of these plants.

The suite of angiosperm LMA values in the Winthrop flora, our largest collection ($N = 19$ species), best matches extant riparian vegetation (Fig. 3). This is perhaps unsurprising considering the Winthrop's depositional environment is interpreted as riparian (Miller et al., 2006; Miller and Hickey, 2008) (see also Materials and Methods), but as discussed earlier it is risky to assume a priori that a relationship between “fast-return” species and streamside environments held in the past. At minimum, the analysis of LMA provides an opportunity to directly test such assumptions. Because climate affects LMA (Wright et al., 2005; Poorter et al., 2009), the most appropriate riparian comparison to the Winthrop, which is interpreted as warm (mean annual temperature [MAT] = 23.4°C) (Miller et al., 2006) and mesic (e.g., see climate model simulations and compilation of climatically sensitive sediments in Beerling and Woodward, 2001), is Big Hammock Wildlife Management Area, a warm-temperate, mesic site in south Georgia (Fig. 3C; MAT = 19.0°C; mean annual precipitation = 120 cm). The LMA suite in the nearby non-

riparian Little Pee Dee State Park differs from the Winthrop in that it contains an important subcomponent of high LMA angiosperm species (Fig. 3D). Thus, the commonly observed association today between angiosperms with a fast-return growth strategy and riparian habitats (e.g., Fig. 3B, C) (Grime, 2001) appears very long-lived.

Similar to the Potomac (see introduction), angiosperms and gymnosperms in the Winthrop occupied different subenvironments on the floodplain: fast-return angiosperms dominate in the higher energy, crevasse splays while slow-return gymnosperms are more common in the paleosols, which are interpreted as low energy, distal floodplain deposits. Ferns are the only other plant group that commonly coexists with these early angiosperms. Early angiosperms were likely competing directly with ferns (Hickey and Doyle, 1977; Lidgard and Crane, 1990; Peppe et al., 2008), which today both share the capacity for rapid reproduction (Gifford and Foster, 1988; Mauseth, 1988) and vegetative growth (Brodribb et al., 2005; Boyce et al., 2009). This competition model (Hickey and Doyle, 1977; Bond, 1989; Lidgard and Crane, 1990; Taylor and Hickey, 1996) argues that the capacity for rapid growth was integral to the “tool-kit” of early angiosperms, which when coupled with their rapid flower-to-seed time gave them competitive superiority in physically disturbed, nutrient-rich environments. Our quantitative data support this model.

Our study provides ecological information about a single time interval (middle to late Albian; 110–105 Ma) some 30 Myr after the first unambiguous evidence for angiosperms (Brenner, 1996). At least four taxa in our data set are from basal families (noneudicots), including Chloranthaceae and Monimiaceae (Miller, 2007; Peppe et al., 2008), suggesting that a fast-return strategy predates the middle Albian. Angiosperm leaf fossils from the Potomac extend back to the early Aptian (~125 Ma), but unfortunately they are not appropriate for LMA estimation (clear and distinct petioles, reconstructable leaf area) owing to their flimsy construction (Hickey and Doyle, 1977). The riparian depositional environment (Doyle and Hickey, 1976; Hickey and Doyle, 1977) of these older fossils, however, argues for the presence of a fast growth strategy. Further, the cheap construction of these leaves implies a low LMA and a weedy lifestyle. The only other angiosperm megafossils from this early interval are likely aquatic in habit, including unambiguous Nymphaeales (water lilies) (Friis et al., 2001) from the Early Albian (112–109 Ma; Heimhofer et al., 2007) and *Archaeofructus*, a genus of aquatic herbs from the late Berremian/early Aptian (~125 Ma) (Sun et al., 2002; Zhou et al., 2003).

What was the ecology of the earliest angiosperms? The megafossil record best supports a weedy or aquatic origin; moreover, most phylogenetic reconstructions (Qiu et al., 1999; Doyle and Endress, 2000; Moore et al., 2007; Saarela et al., 2007) contain families near the angiosperm root that are also consistent with these two origin hypotheses (Chloranthaceae for the weedy origin; Nymphaeales for the aquatic origin) (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Friis et al., 2001). These oldest fossils are ~10 Myr younger than the first evidence for angiosperm pollen, but they still place serious constraints on the range of possible habitats in which angiosperms evolved. In the case of the weedy origin hypothesis, though, *Amborella*, Nymphaeales, and Austrobaileales form a clade basal to Chloranthaceae in most recent molecular phylogenies (Qiu et al., 1999; Moore et al., 2007). Ecophysiological observations of the remnant, extant representatives of this basal clade (excluding Nymphaeales) suggest that the earliest angiosperms

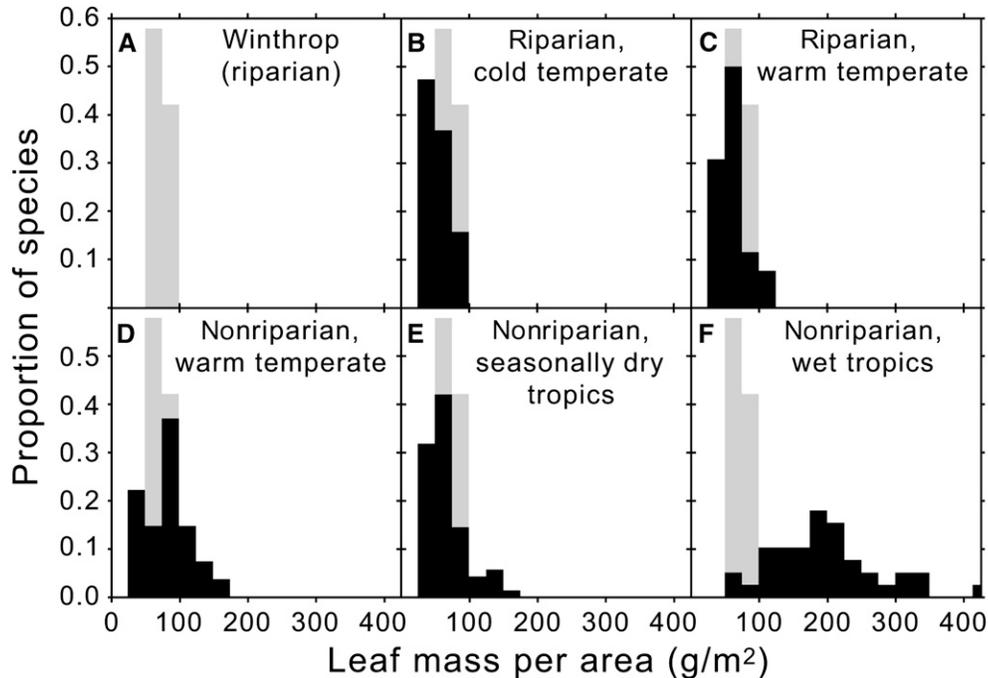


Fig. 3. Comparison of the estimated LMA distribution from the Winthrop fossil flora with extant sites. (A) Winthrop (replicated in all panels) (mean annual temperature [MAT] = 23.4°C), (B) Connecticut River near Middletown, Connecticut (online Appendix S5) (MAT = 10.1°C; mean annual precipitation [MAP] = 121 cm), (C) Big Hammock Wildlife Refuge Area, Georgia (Royer et al., 2005) (MAT = 19.0°C; MAP = 120 cm), (D) Little Pee Dee State Park, South Carolina (Royer et al., 2005) (MAT = 17.0°C; MAP = 122 cm), (E) Barro Colorado Island, Republic of Panama (Royer et al., 2005) (MAT = 26.5°C; MAP = 262 cm), (F) Buena Vista, Puerto Rico (online Appendix S5) (MAT = 22.1°C; MAP = 249 cm). For the Winthrop, only angiosperms are included and the woody dicot regression (thin line in Fig. 1) is used for estimating LMA (i.e., filled circles in Fig. 2B). The extant sites are composed of exclusively woody dicots. The LMA bin size is 25 g/m².

were slow-growing, understory evergreen shrubs and small trees in dimly lit, evermoist, physically disturbed montane forests (Feild et al., 2004, 2009). However, the use of extant taxa as analogs to the past require robust phylogenies and no modifications over time in the measured traits (Stebbins, 1974; Doyle and Hickey, 1976; Feild and Arens, 2005, 2007). Unfortunately, the ecology of the earliest angiosperms remains uncertain. A substantial challenge for resolving this debate is the recovery of megafossils from the first 10 Myr of the angiosperm record. With such fossil leaves in hand, the analysis of LMA from petiolar dimensions, perhaps in conjunction with vein density measurements (Boyce et al., 2009), could yield powerful and complementary insights.

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