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Dark and disturbed: a new image of early angiosperm ecology

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Abstract.—Better understanding of the functional biology of early angiosperms may clarify ecological factors surrounding their origin and early radiation. Phylogenetic studies identify *Amborella*, Nymphaeales (water lilies), Austrobaileyales, and Chloranthaceae as extant lineages that branched before the radiation of core angiosperms. Among living plants, these lineages may represent the best models for the ecology and physiology of early angiosperms. Here we combine phylogenetic reconstruction with new data on the morphology and ecophysiology of these plants to infer early angiosperm function. With few exceptions, *Amborella*, Austrobaileyales, and Chloranthaceae share ecophysiological traits associated with shady, disturbed, and wet habitats. These features include low and easily light-saturated photosynthetic rates, leaf anatomy related to the capture of understory light, small seed size, and clonal reproduction. Some Chloranthaceae, however, possess higher photosynthetic capacities and seedlings that recruit in canopy gaps and other sunny, disturbed habitats, which may have allowed Cretaceous Chloranthaceae to expand into more diverse environments. In contrast, water lilies possess ecophysiological features linked to aquatic, sunny habitats, such as absence of a vascular cambium, ventilating stems and roots, and floating leaves tuned for high photosynthetic rates in full sun. Nymphaeales may represent an early radiation into such aquatic environments. We hypothesize that the earliest angiosperms were woody plants that grew in dimly lit, disturbed forest understory habitats and/or shady streamside settings. This ecology may have restricted the diversity of pre-Aptian angiosperms and living basal lineages. The vegetative flexibility that evolved in the understory, however, may have been a key factor in their diversification in other habitats. Our inferences based on living plants are consistent with many aspects of the Early Cretaceous fossil record and can be tested with further study of the anatomy, chemistry, and sedimentological context of Early Cretaceous angiosperm fossils.

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Introduction

Flowering plants—angiosperms—today include more than 257,000 species and have dominated most terrestrial ecosystems since the Late Cretaceous (Crane 1987; Crane and Lidgard 1989; Crane et al. 1995; Wing and Boucher 1998; Lupia et al. 1999). Much discussion has focused on the ecology of the earliest angiosperms. What sorts of habitats did they occupy? How did they function? Answers remain elusive, owing in part to disparate views on the ecological starting point for flowering plant evolution (Doyle and Donoghue 1993; Sanderson and Donoghue 1994).

Previous Interpretations of Early Angiosperm Ecology.—The traditional representation of early angiosperms is that of woody magnoliids, with large bisexual flowers consisting of numerous free perianth parts, stamens, and carpels, as in extant Magnoliales and Winteraceae (e.g., Arber and Parkin 1907; Takhtajan 1969; Thorne 1976; Cronquist 1988; Gottsberger 1988). By analogy with these living taxa, the first flowering plants would be slowly growing and maturing trees or shrubs with large leaves that photosynthesized at low rates. These plants would have established in wet, low-light environments below the forest canopy (Table 1) (Bews 1927; Axelrod 1952; Takhtajan 1969; Thorne 1976; Cronquist 1988).

In contrast, others suggested that the first angiosperms were weedy, drought-tolerant shrubs

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TABLE 1. Summary of hypotheses for the ancestral ecophysiology of angiosperms. Sources for ecological details of each hypothesis are noted; ''?'' denotes that no explicit statements were made by authors regarding a particular characteristic, but traits were predicted from descriptions of ancestral habitats. ''Paleoherb'' clades include Aristolochiaceae, *Lactoris*, Piperales, monocots, *Ceratophyllum*, Nymphaeales.

	Woody magnoliid (Takhtajan 1969; Thorne 1976)	Weedy xeric shrub to riparian weed (Stebbins 1974)	Ruderal/herb (Taylor and Hickey 1992, 1996)	Aquatic origin (Sun et al. 2002)	''Dark and disturbed'' (this study)
Characters					
Modern analogs	Magnoliales, Winteraceae	Shrubby Ericaceae, Dillenaceae, and *Tasmannia* (Winteraceae)	''Paleoherb'' clades plus Chloranthaceae	? Nymphaeales, *Ceratophyllum*	*Amborella*, Chloranthaceae, Austrobaileyales
Growth habit	Large to small trees	Shrub or sub-shrub, highly branched	Rhizomatous herbs	Aquatic herb	Small tree/shrub
Seedling establishment	? Wet, shady, and stable sites	Seasonally dry, sunny	Variably wet, sunny, and disturbed habitats	? Wet, shady, and stable	Wet, shady, and disturbed habitats
Disturbance	Low	High	High, large-scale (e.g., clearings, floodplain), streamsides	? Low	High, small-scale (e.g., streamsides, steep slopes)
Seed size	? Large	? Small	Small	?	Small
Vegetative reproduction	? Low	High	High	?	High
Photosynthesis	? Low	? High or low, depending upon drought severity	High	? High to moderate	Low
Resources					
Light	Low during establishment, high later as canopy trees	High	High	High	Low
Water	High	Low	Variable, flooding with periodic drying	High, aquatic	High

that lived in open, disturbed habitats of semiarid tropical to subtropical regions (Table 1) (Stebbins 1965, 1974; Axelrod 1970). From there, other authors suggested that angiosperms moved into disturbed streamside habitats in mesic environments (Doyle and Hickey 1976; Hickey and Doyle 1977). These suggestions built on arguments that variable conditions might have favored the evolution of the reproductive and vegetative hallmarks of angiosperms, such as short generation time, the closed carpel, reduction of ovules and gametophytes, double fertilization and endosperm, and flexible seedling growth (Stebbins 1965, 1974), and on paleoecological inferences from the diversity of Early Cretaceous angiosperm pollen in the Northern Gondwana tropics, associated with indicators of aridity, and the morphology and sedimentary associations of Early Cretaceous angiosperm leaves (Brenner 1976; Doyle and Hickey 1976; Hickey and Doyle 1977). Subsequent studies, however, showed that angiosperm pollen was equally diverse in parts of Northern Gondwana that show evidence for wetter climates (Doyle et al. 1982; Brenner 1996).

A related view reconstructed the first angiosperms as fast-growing, rhizomatous, and semiherbaceous plants of sunny, unstable streamsides (Table 1). This interpretation arose from early phylogenetic analyses that rooted the angiosperms among the ''paleoherbs,'' variously including Nymphaeales, Piperaceae, Saururaceae, *Lactoris*, Aristolochiaceae, and Chloranthaceae (Donoghue and Doyle 1989; Taylor and Hickey 1992). The paleoherb hypothesis was argued to be consistent with small angiosperm seed sizes and the paucity of angiosperm wood in Early Cretaceous floras (Taylor and Hickey 1990, 1992, 1996; Doyle et al. 1994; Nixon et al. 1994; Wing and Boucher 1998; Eriksson et al. 2000). In this scenario, early angiosperms tolerated disturbance and had high leaf photosynthetic capacity and short generation times (Taylor and Hickey 1992, 1996; Wing and Boucher 1998).

Finally, the possibility that the first angiosperms were aquatic has enjoyed renewed attention with the discovery of *Archaefructus*, a remarkably complete fossil with finely dissected leaves from Barremian–Aptian lake deposits of China. *Archaefructus* was interpreted as an aquatic herb (Sun et al. 1998, 2002), and a cladistic analysis by Sun et al. (2002) placed it below the common ancestor of all living angiosperms.

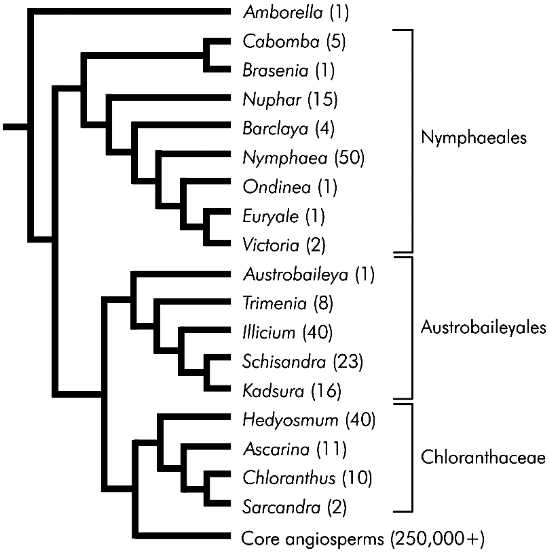

FIGURE 1. Phylogenetic systematics of basal angiosperm lineages included in this study, as identified by recent molecular phylogenetic analyses (see Doyle and Endress 2000). The number of species in each clade is denoted in parentheses (data from Smith 1976; Verdcourt 1986; Todzia 1988; Schneider and Williamson 1993; Williamson and Schneider 1993; Saunders 1998, 2000; Kong et al. 2002).

A New Perspective.—Discussions of the ancestral ecology and habitat of angiosperms have suffered from two main difficulties. First, previous hypotheses were not well constrained by robust phylogenies. However, independent molecular analyses have recently converged on similar rootings of the angiosperm tree. These studies placed *Amborella*, Nymphaeales (Cabombaceae and Nymphaeaceae, the water lilies), and Austrobaileyales (consisting of *Austrobaileya*, *Trimenia*, the star anise *Illicium*, *Kadsura*, and *Schisandra*) at the base of the angiosperm lineage (Fig. 1) (Soltis et al. 1997, 2000; Mathews and Donoghue 1999; Parkinson et al. 1999; Qiu et al. 1999; Barkman et al. 2000; Graham and Olmstead 2000; Zanis et al. 2002). Chloranthaceae, which occupied various near-basal positions in the molecular phylogenies just cited, branched immediately above this basal grade when molecular and morphological data were combined (Doyle and Endress 2000). In most studies the root was between *Amborella* and all other angiosperms, although trees in which *Amborella* plus Nymphaeales form a clade sister to the rest cannot be rejected (Barkman et al. 2000; Zanis et al. 2002). However, rooting the angiosperms near Magnoliales, Chloranthaceae, or *Ceratophyllum* can now be ruled out. Significantly, several morphological characteristics of *Amborella*, Nymphaeales, Austrobaileyales, and Chloranthaceae are known in Early Cretaceous fossil flowers, pollen, seeds, and leaves (Upchurch 1984b, 1995; Mohr and Friis 2000; Friis et al. 1997, 1999, 2000, 2001; Doyle 2001), thus supporting the view that these taxa may represent appropriate ecological models for early angiosperms.

Here *Amborella*, Austrobaileyales, Chloranthaceae, and Nymphaeales are referred to as ''basal'' lineages, as contrasted with the much larger clade nested among them that includes all remaining angiosperms (called ''core angiosperms''). The term ''basal'' is often criticized because it is sometimes misused as a synonym for ''primitive.'' In fact, basal groups can be highly autapomorphic. Also, only nodes are actually basal. While recognizing these points, we believe ''basal'' is a useful shorthand for ''a clade whose stem lineage is attached to a basal or near-basal node.'' More importantly, when several lineages branch off successively below a major clade, as is the case in angiosperms, any states that they share can be inferred to be ancestral, even if each of these lineages is autapomorphic in other characters.

A second difficulty is lack of detailed ecophysiological data for putative basal lineages with which to interpret the paleo-ecophysiology of Early Cretaceous angiosperms. Previous interpretations of early angiosperm ecology relied on structure-function relations taken from derived groups, in which the characters may have evolved convergently (Doyle and Hickey 1976; Doyle 1977, 1978; Hickey and Doyle 1977; Taylor and Hickey 1996; Wing and Boucher 1998; Eriksson et al. 2000). Although this approach may be useful, direct physiological evidence demonstrates that inferences of physiological function based on distantly related proxies can be misleading (Feild et al. 1998).

In this study we take a fresh look at the problem of early angiosperm ecology by combining an improved knowledge of phylogeny with ecophysiological observations on *Amborella*, Austrobaileyales, Chloranthaceae, and Nymphaeales, aimed at recognition of common ecophysiological patterns in these groups. We focus on traits related to growth under varying light and disturbance regimes, including comparative leaf anatomy, leaf photosynthetic performance, growth habit, seed size, and seedling establishment. The result is a new image of how the first flowering plants may have functioned and the environment they first occupied. Finally, we consider how these results relate to the Early Cretaceous fossil record.

Methods

Study Species and Field Sites

Seventy-two species of extant basal angiosperms were studied, representing *Amborella*, all water lily genera (*Barclaya*, *Brasenia*, *Cabomba*, *Euryale*, *Nuphar*, *Nymphaea*, *Ondinea*, and *Victoria*), all genera in Austrobaileyales (*Austrobaileya*, *Illicium*, *Kadsura*, *Schisandra*, *Trimenia*), and Chloranthaceae (*Ascarina*, *Chloranthus*, *Hedyosmum*, *Sarcandra*). We examined individuals in natural populations (field sites in Australia, China, Costa Rica, Fiji, French Polynesia, New Caledonia, New Zealand, Papua New Guinea, and U.S.A.; Appendix 1), a common garden, and botanical gardens. Where taxonomic sampling could not be exhaustive, species were selected to encompass the habitat range of each lineage. Fieldwork was conducted from August 1999 to October 2002.

Plants grown in the common garden (Auburn, Alabama, 32°N,85°W) were obtained from local nurseries or raised from cuttings taken from natural populations. Plants were grown for 18 months under three light environments—100%, 30%, and 5% full sunlight—before measurements were taken.

Comparative Data

Six ecological and physiological characters were obtained from the field, herbarium vouchers, and published sources. Data sources for species character-state values are given in Appendix 2. The complete character matrix for the species sampled is provided in Appendix 3.

Photosynthetic Performance: Maximum Leaf Photosynthetic Rate and Light-Saturation Point.—Chlorophyll (Chl) fluorescence emission was used to quantify leaf photosynthetic performance by determining maximum photosynthetic rate and the light intensity at which the photosynthetic system saturates (Bilger et al. 1995; Brodribb and Hill 1997; Rascher et al. 2000). We took Chl measurements of living plants in natural or garden settings with a portable pulse-amplitude modulated fluorometer (Mini-PAM, H. Walz, Effeltrich, Germany) operated using currently accepted protocols (Bilger et al. 1995; Brodribb and Hill 1997; Rascher et al. 2000). From light-response curves of Chl fluorescence emission, we calculated maximum ETR ($\mathrm{ETR_{max}}$) and the light intensity ($\mathrm{PPFD_{sat}}$) at which this flux occurred, and we used these calculations for interspecific comparisons of leaf photosynthetic performance (Appendix 4). Appendix 4 also provides a comprehensive discussion of procedures and a verification of sampling methods.

Seed Size.—Seed sizes were expressed in volume to facilitate comparison with published data on Cretaceous angiosperm seeds (Tiffney 1984; Wing and Boucher 1998; Eriksson et al. 2000). Most seeds from extant plants were collected in the field and measured directly. Some seed volumes were determined by nondestructive measurement of herbarium voucher specimens (specific sources from the University of California and Jepson herbaria are available from T. S. Feild) or from published studies (Appendix 2). For each species, the length (L) and breadth (B) of five seeds were measured with a micrometer (0.1 mm precision) and averaged. We used the approximation of Tiffney (1984), where seed thickness $(T) = 0.66$ B. To calculate seed volume (V), seeds were approximated as ellipsoids with $V = 4/3\ (ab^2)$, where $a = L/2$ and $b = (B + T)/4$ (Eriksson et al. 2000).

Seedling Habitats.—To evaluate how seedlings and small saplings (<40 cm tall, <0.5 cm stem diameter) of extant basal angiosperms were associated with habitat, eight plots (approx. 10 m × 10 m) were laid out and surveyed for seedling abundance. Plots were randomly established in a variety of habitats, including large (100 $\mathrm{m^2}$) to small (less than 20 $\mathrm{m^2}$) canopy gaps, understory, understory streamside zones, and exposed forest edges, ridgecrests, pastures, and stream banks. Species were easily identified by leaf characters. Seedling and sapling abundance was low for nearly all species studied, ranging from two to 45 plants/plot. These descriptions are limited because they rely on single-time observations and may include plants of different age.

Disturbance regime was categorized on the basis of physical attributes of the site (see below) and whether seedling establishment occurred in soil litter (undisturbed) or mineral soil (disturbed). This method of site characterization parallels that of other workers and proves useful in designating relative categories of disturbance frequency (Sakai et al. 1995; Arens 2001; Dai et al. 2002). To quantify light environment, eight measurements of diffuse PPFD were made with a hand-held light meter (Li-190; Li-COR, Lincoln, NB) above each seedling and averaged. Light availability was expressed as a percentage of average full diffuse sunlight (495 μmol photons $\mathrm{m^{-2}\ s^{-1}}$; SD 55; $n = 39$ sites) to avoid considerable heterogeneity introduced by sunflecks (Chazdon 1988). Measurements of full diffuse light were made at midday on cloudy days.

By combining light intensity data with site characteristics, three seedling habitat states were defined. *Shady, stable, and aquatic* (0) habitats have low light (<2% full diffuse sunlight) and included submerged aquatic zones with low current or wave action (e.g., muddy pond and stream bottoms rich in organic matter). *Shady, disturbed* (1) habitats have low light (<2 % full diffuse sunlight) and were recently disturbed. Examples included exposed mineral soils on steep understory slopes, margins of understory watercourses, understory trails and irrigation canals, and sites in the shade of regenerating vegetation near roadsides. *Sunny, disturbed* (2) habitats have higher light (5–100% full diffuse sunlight) and experienced recent disturbance. These sites included brighter subcanopy to open disturbed areas, such as open stream margins, cleared slopes and ravines, small canopy gaps, and exposed landslip margins.

Leaf Anatomy.—Leaf anatomy was observed in vibratome cross-sections (50 μm thick) from leaves preserved in 20% ethanol, 15% glacial acetic acid, 15% formaldehyde, and

50% water. Three leaves were taken from the same branches used for Chl *a* fluorescence measurements. Leaf sections were cleared for one hour in a solution of 50% bleach, rinsed with water, and stained with toluidine blue. Three leaf mesophyll anatomy states were defined (terminology following Esau 1977): *spongy parenchyma only* (0), consisting entirely of spherically shaped mesophyll cells; *single, weakly differentiated layer of palisade parenchyma* (1), with one tier of columnar cells organized into a distinct layer at the upper leaf surface; and *multiple layers of palisade parenchyma* (2), with two to three stacked layers of columnar cells near the upper leaf surface.

Growth Forms.—Four growth form categories were recognized. *Tree or shrub* (0) included (following Hickman 1993) woody perennials producing secondary xylem with a distinct trunk-crown architecture (trees) and woody perennials producing several trunks from the base and lacking a distinct trunk-crown system (shrubs). *Twining woody vine* (1) included woody perennials completely or partly dependent upon other plants for mechanical support and climbing with circumnutated growth. *Herbs with some secondary growth* (2) had above-ground shoots generally lacking secondary xylem, but rhizomes and bases of annual shoots developing limited secondary xylem. Finally, *herbs lacking secondary growth* (3) developed only primary xylem.

Phylogeny and Character Reconstruction

Ancestral states and patterns of character evolution were reconstructed by assembling a composite phylogenetic tree of extant basal angiosperms, including *Amborella*, Nymphaeales, Austrobaileyales, Chloranthaceae, and a placeholder for the remaining ‘‘core angiosperm’’ clade (including monocots, eudicots, Piperales, Winterales, Laurales, and Magnoliales). As the backbone, we used the single most parsimonious tree found in Doyle and Endress’s (2000) analysis of three genes (*rbcL, atpB,* 18S rDNA) plus morphology, which identified Chloranthaceae as sister to the core angiosperms. The Chloranthaceae were expanded by using a parsimony analysis of morphological data (Eklund et al. 2004), but with relationships within *Chloranthus* based on a molecular study (ITS and *trnL-F* [Kong et al. 2002]). Nymphaeales were expanded by using the single most parsimonious tree from an analysis by Les et al. (1999) of three genes (*rbcL, matK,* 18S rDNA) plus morphology. For *Illicium*, the molecular tree of Hao et al. (2000), based on ITS sequences, was used. Interspecific relations of *Schisandra* and *Kadsura* were represented by one of eight most parsimonious trees from an analysis of ITS and morphology (Hao et al. 2001). Relationships in the *Trimenia* clade have not been analyzed. For purposes of inferring discrete character evolution, we took a conservative approach and left them as an unresolved polytomy.

MacClade 4.03 (Maddison and Maddison 2001) was used to reconstruct states of discrete and continuous characters at ancestral nodes and branches. All characters were treated as unpolarized and unordered, meaning all transitions among states were equally probable. The sensitivity of ancestral state reconstructions for discrete characters to different coding schemes (binary versus multistate) and types (unordered versus ordered) was also examined. Because neither alternative coding schemes nor ordered character states affected our conclusions, we took the conservative approach of scoring characters as unordered. Coding characters for the core angiosperm clade posed problems because of lack of data; core angiosperms could only be scored for mesophyll and growth habit (following Doyle and Endress 2000).

Ancestral states for continuously varying traits (ETR_{max}, $PPFD_{sat}$, seed size) at the root of the tree were determined with two widely used methods, squared-change parsimony and linear parsimony (Maddison 1991), using MacClade. Squared-change parsimony assigns a single ancestral value to each internal node to minimize the sum of squares change over the tree. Linear parsimony reconstructs ancestral node values by minimizing total changes. Linear parsimony reconstructions were explored by using the maximum and minimum state options in MacClade. To reconstruct node values for continuous characters, we used MacClade to randomly resolve the *Trimenia* polytomy. Different random resolutions in *Trimenia* altered state values for the

TABLE 2. Ancestral-state value estimates of photosynthetic traits and seed size for basal angiosperms. Photosynthetic traits included maximum photosynthetic electron transport (ETR_{max}, μmol electrons m^{-2} s^{-1}) and light intensity at photosynthetic saturation ($PPFD_{sat}$, μmol photons m^{-2} s^{-1})]. Seed size (SS) was expressed volumetrically (mm^3). Values for the ancestral node (see Appendix 2 for data matrix and taxon sampling) were reconstructed by using the linear parsimony (LP) and squared-change parsimony (SqP) options in MacClade 4.03 (Maddison and Maddison 2001). Estimates were determined over two phylogenetic hypotheses for the branching order of these clades (taxa listed in order of divergence after the root, references noted by each hypothesis).

	Method					
	ETR_{max} [μmol m^{-2} s^{-1}]		$PPFD_{sat}$ [μmol m^{-2} s^{-1}]		SS [mm^2]	
Hypothesis	LP	SqP	LP	SqP	LP	SqP
Amborella; Nymphaeales; Austrobaileyales; Chloranthaceae (Mathews and Donoghue 1999; Qiu et al. 1999; Soltis et al. 2000)	80–87	91	466	496	2.43–3.46	10.1
(*Amborella* + Nymphaeales); Austrobaileyales; Chloranthaceae (Barkman et al. 2000; Zanis et al. 2002)	80–87	87	466	478	2.35–3.46	17.4

common ancestor of angiosperms by approximately ±10%.

Results

Patterns of Photosynthetic Evolution.—Maximum electron transport rates (ETR_{max}) ranged from 225 μmol electrons m^{-2} s^{-1} in *Nuphar polysepalum* at a saturating light intensity ($PPFD_{sat}$) of 1400 μmol photons m^{-2} s^{-1}, to 45 μmol electrons m^{-2} s^{-1} in *Ascarina solmsiana* at a $PPFD_{sat}$ of 234 μmol photons m^{-2} s^{-1} (Appendix 3). Compared with previous data (Chazdon et al. 1996; Brodribb and Hill 1997; Brodribb and Feild 2000; Brodribb et al. 2002; Franco and Lüttge 2002), ETR_{max} and $PPFD_{sat}$ values for *Amborella*, *Austrobaileya*, some Chloranthaceae (especially *Chloranthus*, *Sarcandra*) and most *Illicium* species were lower than those of most sun-adapted angiosperm and conifer species from lowland tropical rain forest, tropical cloud forests, and tropical dry forests. Instead, leaf photosynthetic properties of these taxa were in the range reported in shade-adapted taxa (40 to 115 μmol electrons m^{-2} s^{-1} ETR_{max} and 200 to 500 μmol photons m^{-2} s^{-1} $PPFD_{sat}$). ETR_{max} and $PPFD_{sat}$ for some *Ascarina* (*A. polystachya*, *A. rubricaulis*) and most *Hedyosmum* species (Chloranthaceae), some Austrobaileyales (*I. parviflorum*, *T. weinmanniifolia*, *K. coccinea*, and several *Schisandra* species, Appendix 3), and Nymphaeales overlapped the lower portion of the range reported for tropical eudicot and piperalian angiosperms and sun-adapted conifers (120 to 350 μmol electrons m^{-2} s^{-1} ETR_{max} and 700 to 1750 μmol photons m^{-2} s^{-1} $PPFD_{sat}$). Our reconstructions indicated that the common ancestor of angiosperms had ETR_{max} and $PPFD_{sat}$ values typical of a shade-adapted photosynthetic physiology (Table 2).

Patterns of Morphological Evolution.—A tree or shrub growth habit and seedlings colonizing shady, disturbed habitats were reconstructed as ancestral in angiosperms (Fig. 2). Character-state reconstructions under parsimony also suggested that the common ancestor of angiosperms possessed leaves with spongy parenchyma only (Fig. 2) (see Doyle and Endress 2000).

The most recent common ancestor of Nymphaeales, in contrast, was herbaceous, with leaves having multiple layers of palisade tissue, and seedling recruitment in shady, stable aquatic habitats (Fig. 2). Eight origins of seedling colonization in sunny, disturbed habitats were recognized across the composite tree. Five independent origins of a single, weakly differentiated palisade layer were found among basal angiosperms: three within clades originally with spongy mesophyll and two in Nymphaeales from ancestors with multiple palisade layers (Fig. 2). Other changes in growth form include three to four origins of twining woody vines in Austrobaileyales, and one or two origins of herbs with some secondary growth in *Chloranthus* (Fig. 2). Ancestral seed size, expressed as volume, was small under the linear parsimony method (approx. 2–3 mm^2) and relatively small (10–17 mm^2 de-

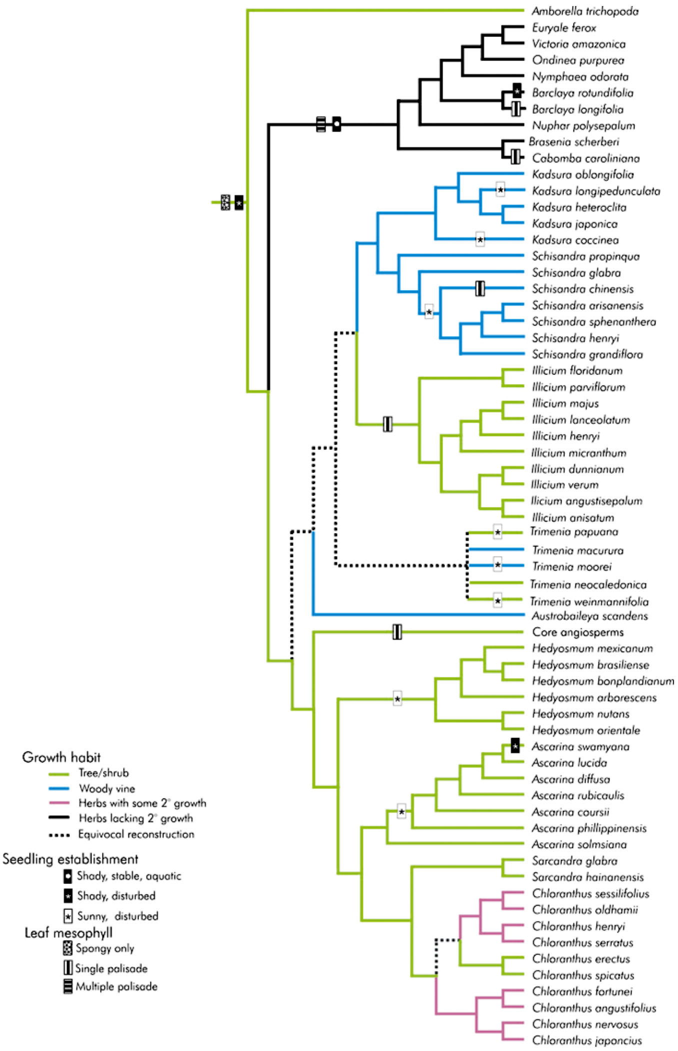

FIGURE 2. Phylogenetic mapping of growth habit, leaf mesophyll anatomy, and habitat of seedling establishment in extant basal angiosperms. The composite phylogenetic tree was assembled as described in ''Materials and Methods.''

pending on the phylogenetic hypothesis; Table 2) under squared-change parsimony.

Discussion

The Dark and Disturbed Pattern

Mapping ecophysiological characters onto the phylogeny of extant basal angiosperms suggests that their common ancestor was a tree or shrub that established in disturbed habitats under low light (Fig. 2). In contrast, the herbaceous habit, higher leaf photosynthetic rates and light-saturation points, palisade mesophyll tissue, and seedling recruitment in more brightly lit, disturbed habitats were derived in separate lineages. This interpretation of the ancestral ecology is novel in combining two habitat characteristics that have not been previously associated: understory shade and disturbance. Earlier hypotheses reconstructed the earliest angiosperms as shade-tolerant but slow-growing residents of stable understory habitats, or weedy, shade-intolerant colonizers of open disturbed habitats (Table 1). Blanc (1986: p. 110) suggested that angiosperms were originally understory shrubs, like some Chloranthaceae, but he did not emphasize the role of disturbance. Below we consider how inferred ancestral ecophysiological characters relate to shady and disturbed habitats. We also discuss preliminary results on basal angiosperm water-use physiology that indicate early angiosperms were adapted to wet habitats.

Ancestral Characters Related to Shade.—A leaf cross-section dominated by spongy parenchyma was ancestral in angiosperms (Fig. 2). The spheroid cellular shapes making up spongy parenchyma create numerous light-reflecting air-water interfaces that produce more light-scattering than palisade tissue. Increased scattering consequently lengthens the path of light through the leaf, increasing the likelihood that photons will be harvested for carbon gain—an important trait in light-limited forest understories (Vogelmann et al. 1996; Smith et al. 1997). The reconstructed ancestral photosynthetic physiology (maximum photosynthetic electron transport rate and light-saturation point) was typical of shade-adapted tropical understory plants (Table 1, Appendix 3) (Bilger et al. 1995; Chazdon et al. 1996; Brodribb and Hill 1997; Brodribb and Feild 2000; Brodribb et al. 2002; Franco and Lüttge 2002). Low leaf photosynthetic capacity offers an advantage in shady understory habitats because such leaves are less costly to build and maintain (Givnish 1979, 1988; Chazdon et al. 1996). Low photosynthetic capacity, however, can constrain a plant's ability to exploit high-light open habitats because of greater risk of photoinhibition (Demmig-Adams et al. 1995; Smith et al. 1997).

Ancestral Characters Related to Disturbance.—Our data suggest that early angiosperms recruited in disturbed habitats. Generally, the disturbed sites colonized by seedlings of *Amborella*, most Austrobaileyales, and Chloranthaceae were small (2–20 m^2). Examples included limbfall gaps, understory stream banks, and steep mineral soil patches exposed by erosion or the activity of large animals (Appendix 3). Excepting water lilies, basal angiosperm seedlings established on unstable substrates prone to shifting, such as brittle clay, stony sand and shaly soils, and sites between or in moss mat crevices on rotting logs. Traits that permit recruitment on disturbed sites and allow plants to survive root and shoot damage are essential for survival in these habitats (Greig 1993; Bond and Midgely 2001, 2003).

One such trait is small seed size. The inferred common ancestor of angiosperms produced small seeds (Tables 1, 2) and probably small embryos (Doyle and Endress 2000; Forbis et al. 2002). Although large seeds are viewed as advantageous in shady environments because abundant carbon reserves are needed to establish in low light (Salisbury 1942; Harper et al. 1970; Grime 1979; Leishman et al. 2000; but see Kelly 1995), recent work demonstrates that small seeds (volumes less than ca. 10 mm^3) can also be viable in shady, disturbed habitats, such as steep understory slopes, exposed mineral soil washouts, and stream banks—exactly the habitats where most extant basal angiosperms occur, as opposed to undisturbed forest floor microsites choked with litter (Lusk 1995; Grubb 1998; Lusk and Kelly 2003). Despite limited carbon reserves, small seeds establish in these habitats because they are more readily lodged in small litter-free microsites than larger seeds (Lusk and Kelly 2003).

The diversity of vegetative regeneration modes found in basal angiosperms also increases tolerance of disturbance (Table 3). *Amborella*, Austrobaileyales, and Chloranthaceae sprout abundantly from the base of adult (flowering) and juvenile (nonflowering) plants. Their seedlings become highly ramified, passing through a creeping establishment phase consisting of a decumbent lignotuber with several basal sprouts (Table 3) (Blanc 1986). Austrobaileyales and Chloranthaceae, in addition, display layering of debris-pinned shoots, rhizomes, and ability of snapped shoots to reroot and establish in the humid forest understory or near creeks (Table 3). Extensive clonal growth, resulting in shoot redundancy and high meristem dispersion across the forest floor, makes basal angiosperms diffuse and resilient targets for limbfalls, trampling, and herbivore damage. These kinds of disturbance are those most typical of the forest understory (Greig 1993; Sakai et al. 1995; Canham et al. 1999; Gavin and Peart 1999; Bond and Midgely 2001, 2003). Our results support the conjecture of Wells (1969)

TABLE 3. Modes of clonal growth and regeneration among basal angiosperms. Definitions for vegetative modes were modified from Greig 1993. Basal sprouting refers to the production of stem suckers, whereby new trunks arise from the base of the original plant from basal buds in plants that have flowered (adults) or not (juveniles). Creeping seedlings refers to a pattern of rhizomatous seedling development that is monocot-like, characterized by a decumbent (''creeping'') lignotuber, from which several ascending shoots emerged. Layering was defined as the production of adventitious roots when trunks or branches become pinned to the ground and then new stems grow upward. Shoot fragmentation was defined as the ability of snapped-off pieces of stems to re-root and eventually form a new plant. Rhizomes and stolons are underground or above-ground stems that give rise to closely spaced, interconnected shoot systems. Observations are based on observations of field-grown plants or from literature sources (Blanc 1986; Schneider and Williamson 1993; Williamson and Schneider 1993; Barrat-Segretain 1996). *n* is the total number of species observed; see Appendix 1 for the species studied. ''Common'' means that all or more than 75% of species were observed regenerating in a particular way, whereas ''infrequent'' refers to between 30% and 74% of species, and ''rare'' to fewer than 29% of species. The presence (''yes'') and absence (''no'') for particular mode was used for lineages containing one or two species.

Taxon	*n*	Basal sprouting Adult/Juvenile	Creeping seedlings	Layering	Recruitment by fragments	Rhizomes or stolons
Amborella	1	yes	yes	no	no	no
Nymphaeales	7	common	no	infrequent	common	infrequent
Austrobaileyales						
Austrobaileya	1	yes	yes	yes	no	yes
Illicium	14	common	common	common	rare	rare
Kadsura and *Schisandra*	15	common	common	common	rare	common
Trimenia	4	common	common	infrequent	infrequent	infrequent
Chloranthaceae						
Ascarina	8	common	common	infrequent	common	rare
Chloranthus	6	common	common	infrequent	no	common
Hedyosmum	6	common	common	infrequent	common	rare
Sarcandra	2	yes/yes	yes	yes	no	yes

that sprouting is an ancestral trait of angiosperms.

Ancestral Characters Related to Moist Conditions.—Preliminary data on basal angiosperms suggest that early angiosperms were adapted to high water availability. *Amborella*, Austrobaileyales, and Chloranthaceae are largely restricted to tropical and subtropical habitats, predominantly nonseasonal montane cloud forests, with high rainfall (3000 to 10,000 mm yr^{-1}) and mist (Todzia 1988; Feild et al. 2000, 2003a; Feild unpublished data 2002). Species from drier temperate regions (>1700–2200 mm) occur in wet microsites, such as perennial understory water courses and springs (Stone 1968; Kwit et al. 1998; Luo and Li 1999; Feild unpublished data 2002). Consistent with a preference for wet habitats, the physiologies of most basal angiosperms are tuned to low evaporative demand. Terrestrial basal angiosperm leaves possess low stomatal densities (45–115, $\bar{x} = 65$ stomata mm^{-2}, SD = 4, $n = 75$ taxa) as well as low instantaneous (Feild et al. 2003a) and integrated leaf water-use efficiencies (the ratio of carbon gain to transpirational water loss), as inferred from leaf stable carbon isotopic composition (Farquhar et al. 1982; Feild unpublished data 2002). *Amborella* and *Austrobaileya* stems possess lower ability to transport water compared with most tropical eudicots (Feild et al. 2000, 2001, 2003a; Feild unpublished data 2002). Consistent with xylem hydraulic measurements, vascular features characteristic of moisture-loving plants pervade woods of *Amborella*, Austrobaileyales, and Chloranthaceae, including vesselless xylem with scalariform pitting (*Amborella*) and wood with short, angular vessels (4–120 mm long in stems 2–5 mm in diameter) dominated by scalariform pits with incompletely hydrolyzed pit membranes (Carlquist 1975, 1984; Carlquist and Schneider 2002; Feild unpublished data 2002). More detailed exploration of these lines of evidence would be desirable.

Exceptions to the Dark and Disturbed Pattern

Water Lilies.—The aquatic habit of Nymphaeales contrasts with that reconstructed for the common ancestor of extant angiosperms (Fig. 2). Inferred specializations for freshwater aquatic zones include herbaceousness (Fig. 2) and evolution of aerenchymatous gas-exchange canals, running from leaf to root, which allow downward oxygen transport into anaerobic muddy soils and upward flow of toxic methane (Sculthorpe 1967; Dacey 1980). Some water lily leaves also show modifications for underwater photosynthesis, such as finely dissected shape (*Cabomba*) and lack of cuticle, stomata, and/or intercellular air-spaces (Sculthorpe 1967). Consequently, only floating ''lily pad'' and emergent leaves of Nymphaeales are potentially comparable to leaves of terrestrial basal angiosperms. Even in these leaves, large functional differences, related to the occupation of brightly lit open-water habitats, were found. For example, water lilies evolved considerably higher leaf photosynthetic rates and light-saturation points (except *Cabomba*; Appendix 3), as well as multiple-layered palisade mesophyll tissue (Fig. 2) and leaves with dense stomata (up to 500 mm^{-2} [Schneider and Williamson 1993]). According to the most parsimonious distribution of ancestral states, water lily ecophysiology bears weakly on that of the first angiosperms because aquatic habitats appear to be derived.

If Nymphaeales are so specialized, one may ask if the ecology of the other basal lines might be equally unlike that of the first angiosperms. However, in light of current phylogenies, the alternative that the features related to dark and disturbed habitats arose independently in *Amborella*, Austrobaileyales, and Chloranthaceae is less parsimonious than the view that they were retained from the first angiosperms. It is interesting to note, however, that one extant water lily, *Barclaya rotundifolia*, may have reinvaded wet, shady, disturbed forest understory habitats (Fig. 2) (Schneider and Carlquist 1995).

Interestingly, there is fossil evidence for early angiosperm aquatics. Friis et al. (2001) compared a Barremian–Aptian flower from Portugal with Nymphaeales, but in the absence of vegetative parts, there is no direct evidence it was aquatic. More clearly aquatic plants, resembling Nymphaeales in having palmately veined leaves attached to a short axis, are known from the Aptian–Albian of Brazil (Mohr and Friis 2000). Another early aquatic is *Archaefructus* (Sun et al. 1998, 2002), from the Barremian–Aptian of China, with a herbaceous habit and finely dissected, feathery leaves. A cladistic analysis placed *Archaefructus* below all extant angiosperms, raising the possibility that the aquatic habit is ancestral (Sun et al. 2002). Examination of the data set, however, indicated that it is equally parsimonious to place *Archaefructus* within extant angiosperms, as an extinct member of Nymphaeales, and it might also be a less reduced relative of *Ceratophyllum* or an extinct basal eudicot lineage (Friis et al. 2003). Even if *Archaefructus* is basal, the ancestral habit would still be equivocal, because the woody plant *Amborella* is at the next node. Furthermore, the hypothesis that aquatic herbs were ancestral must deal with the observation that *Amborella* and other basal angiosperms (except Nymphaeales) develop normal secondary vascular tissue, as in other seed plants, which would have to reoriginate in essentially the ancestral form, lacking any of the anomalies usually associated with secondary woodiness.

Chloranthaceae.—Our analyses also suggest that some Chloranthaceae may have been among the first terrestrial lineages to ''break out'' of the dark and disturbed environment. Unlike *Amborella* and most Austrobaileyales, *Ascarina* and *Hedyosmum* independently evolved seedling recruitment in wet, disturbed, and higher-light habitats, such as cloud forest land slips, large forest light-gaps, and roadsides (Fig. 2) (Todzia 1988; Martin and Ogden 2002). The ecophysiological traits underlying expansion into these zones require further study. However, greater ecological flexibility in Chloranthaceae is not linked to herbaceousness. Herbs with limited secondary xylem appear to be derived (once or twice) within *Chloranthus*, and these herbaceous groups occur in shady, disturbed habitats (Fig. 2) (Luo and Li 1999). *Hedyosmum orientale*, which occurs in sunny, disturbed habitats and has been described as herbaceous (Verdcourt 1986; Todzia 1988), is a possible exception. Recent results, however, showed that *H. orientale*'s growth habit and stem vasculature are different from those of *Chloranthus* herbs; plants reach 3.5 m in height and produce woody, canelike shoots with up to 3 cm of secondary xylem (Feild unpublished data 2002).

Consistent with greater ecological amplitude, the fossil record indicates that Chloranthaceae were the first conspicuous and widespread extant angiosperm lineage (although their abundance may be overestimated by high pollen production for wind pollination [Endress 1987]). Fossil pollen types comparable to *Ascarina* and *Hedyosmum*, named ''*Clavatipollenites*'' and *Asteropollis* respectively, were abundant in Early Cretaceous lowland sediments worldwide (Archangelsky and Gamerro 1967; Playford 1971; Volkheimer and Salas 1975; Brenner 1996; Walker and Walker 1984; Burger 1990, 1993; Archangelsky and Taylor 1993; Dettmann 1994; Hughes 1994; Eklund et al. 2004). ''*Clavatipollenites*'' is not necessarily related to *Ascarina*, as it represents the ancestral pollen type for the family, but *Asteropollis* has been associated with *Hedyosmum*-like fruits (Friis et al. 1997, 2000; Eklund et al. 2004). Many Early Cretaceous leaf fossils, also found worldwide, show chloranthaceous features, including chloranthoid teeth, cuticular striations, and stomata with variable subsidiary cell arrangement (Upchurch 1984b, 1995; Pons 1984; Romero and Archangelsky 1986; Upchurch and Dilcher 1990; Cantrill and Nichols 1996; Kong 2001). These foliar features, however, also occur in *Amborella* and Austrobaileyales and may be plesiomorphic in angiosperms (Upchurch 1984b; Doyle and Endress 2000; Doyle 2001; Feild et al. 2003b).

Fossil Evidence Bearing on the Hypothesis

Although reconstructing ancestral traits on the basis of extant phylogeny is a powerful tool, it is desirable to test hypotheses thus generated with evidence from the fossil record. In the following section, we critically examine existing fossil data bearing on each component of the dark and disturbed hypothesis, and suggest ways in which morphological and sedimentological observations might be used, in combination, to diagnose ephemeral, shady, and wet habitats (Wing and DiMichele 1992; Arens 1997; Davies-Vollum and Wing 1998; Behrensmeyer et al. 2000). Many modern basal angiosperms grow on erosional substrates that are unlikely to be preserved in the sedimentological record (Behrensmeyer et al. 2000). However, stream margins and channels—two disturbed habitats—are common terrestrial depositional settings (Wing and DiMichele 1992).

Much discussion of early angiosperm ecology was based on the Potomac Group (Aptian–Albian) of eastern North America (e.g., Fontaine 1989; Berry 1911; Brenner 1963; Doyle 1969; Wolfe et al. 1975; Doyle and Hickey 1976; Hickey and Doyle 1977; Upchurch 1984a, b; Crane 1987; Crane et al. 1993, 1994). Doyle and Hickey (1976; Hickey and Doyle 1977) argued that the morphology and sedimentary facies associations of Potomac leaves indirectly supported Stebbins's (1965, 1974) view that the first angiosperms were disturbance-tolerant species of semiarid tropical environments, as opposed to woody plants of stable forests. Later, Taylor and Hickey (1990, 1996) suggested that the record in the Potomac Group and elsewhere supported a herbaceous origin. However, most aspects of the Potomac record are equally or more consistent with the dark and disturbed hypothesis.

Fossil Evidence for Light Habitat.—Light environment can be discerned from a variety of leaf morphological features. Low-light environments are believed to favor larger leaves (Givnish 1988), although correlations across species for light habitat and leaf size are inconsistent (Niinemets and Kalevi 1994; Ackerly and Donoghue 1998). At the anatomical scale, spongy mesophyll is more strongly correlated with low-light conditions (Smith et al. 1997; Kott and Britton 1985; Arens 1997). Some cuticle features, such as stomata only on the leaf undersurface, large stomata, and low stomatal density, also appear linked to shady habitats (Givnish 1988; Smith et al. 1997).

Doyle and Hickey (1976; Hickey and Doyle 1977) argued that many lower Potomac angiosperms were low shrubs of sunny stream-margin habitats, judging from their small leaf size, poor petiole differentiation, and disorganized leaf venation (plus sedimentary evidence discussed below). Because some of these have chloranthoid features (Upchurch 1984a), it would not be surprising if they grew in open habitats. However, there are indications that other angiosperms were in the forest understory. At two lower Potomac localities, Fredericksburg and Fish Hut above Dutch Gap, both no longer extant, large angiosperm leaves called *Ficophyllum* occur at low abundance in rich assemblages of ferns, conifers, and cycadophytes (Fontaine 1889; Berry 1911; Hickey and Doyle 1977; Doyle personal observations on material at the Smithsonian Institution, 1971). On the basis of this association, Doyle and Hickey (1976; Hickey and Doyle 1977) concluded that these plants lived in the shady forest understory. They suggested that the understory was one of the first new habitats occupied by early angiosperms, but it could equally well represent the ancestral habitat. There is stronger evidence for occupation of open habitats in the upper Potomac (Albian), where platanoid leaves are often dominant in stream-margin sediments (Hickey and Doyle 1977; Crane et al. 1993).

Because leaf size correlates inconsistently with light habitat, future work will need to focus on anatomical features of Early Cretaceous angiosperm leaves. Internal anatomy, however, is only rarely preserved in fossil leaves, although it is known from permineralized and fusainized (charcoalified) material (e.g., Alvin 1974; Schabilion and Reihman 1985) and from compressions in fine-grained, clay-rich sediments (Chandrasekharam 1972; Gandolfo et al. 2001). Leaf cuticle is more commonly preserved but must be interpreted with care. For example, stomatal density and size may also respond to atmospheric CO_2 concentrations (Van de Water et al. 1994; McElwain and Chaloner 1996; Beerling and Royer 2002). To control for this effect, these characters should be considered relative to a broad range of other taxa from the same stratigraphic horizon. No studies of Potomac Group leaves have yet specifically focused on ecomorphological correlates with light environment. Upchurch (1984b), however, noted that the stomata of many lower Potomac angiosperms were around 30 μm wide, which is large compared with most extant, tropical sun-adapted angiosperms (Bongers and Popma 1990).

Fossil Evidence for Disturbance.—Some morphological features can point toward tolerance of disturbance, the most easily quantified being small seed size (discussed above; Harper et al. 1970; Grubb 1998; Lusk and Kelly 2003). In addition, evidence for vigorous vegetative reproduction (Bond and Midgely 2001, 2003), such as rhizomes with abundant sprouting, could indicate adaptation to disturbance. Although it is unusual to find plant fossils complete enough to reveal growth form, such extraordinary fossils are known (e.g., Mohr and Friis 2000; Sun et al. 2002).

Existing seed size data from Barremian–Aptian angiosperm floras (Wing and Boucher 1998; Eriksson et al. 2000) are comparable to those in living basal angiosperms (Tables 1, 2). Consequently, the extant data imply that the small size of these fossils does not rule out a woody habit or low-light, closed forest habitats, as some have argued (Taylor and Hickey 1996; Eriksson et al. 2000). Instead, small seed size may reflect a generalized adaptation to disturbance (Grubb 1998; Lusk and Kelly 2003).

Previous arguments that early angiosperms were adapted to disturbance focused on the association of lower Potomac leaves with coarse-grained sediments deposited in or near active channels (Doyle and Hickey 1976; Hickey and Doyle 1977; Crane 1987). At the Fredericksburg locality, plant fossils occurred in a lens of fine sand in a sand and gravel sequence (Fontaine 1889), suggesting rapid filling of an abandoned channel in a braided stream system. The matrix from Fish Hut above Dutch Gap is darker, organic-rich clay containing significant sand and mica (Doyle personal observations, 1971), suggesting a crevasse splay, where sand was deposited on the floodplain after a levee break. Similar deposits occur at Dutch Gap Canal, ca. 1.5 km downstream (Upchurch and Doyle 1981). At Drewrys Bluff, angiosperm leaves occur in sands (Doyle and Hickey 1976) and a thin clay lens, apparently representing a channel fill (Upchurch 1984a; Crane and Upchurch 1987).

Crevasse-splay deposits such as those at Dutch Gap potentially offer ‘‘snapshots’’ of understory microsites on the vegetated floodplain. If autochthonous preservation can be demonstrated (e.g., Calder et al. 1996), such deposits may allow cryptic disturbed understory microsites to be identified in the fossil record. Future work should focus on more detailed sedimentological analyses of early angiosperm floras, combining bed form observations with grain size distributions and mineralogy. This may allow for more confident distinction of ephemeral substrates from more stable habitats

(Wing and DiMichele 1992; Davies-Vollum and Wing 1998; Davies-Vollum 1999; Behrensmeyer et al. 2000; Royer et al. 2003).

Fossil Evidence for Wet Conditions.—Leaf and cuticle characters can often discriminate between wet and dry habitats (Wing and DiMichele 1992; Wolfe 1993; Wilf et al. 1998). For instance, leaf size correlates well with moisture regime (Givnish 1979; Wilf et al. 1998), although influences of whole-plant branching pattern as well as flower and fruit placement can occasionally override this relation (Bond and Midgely 1988; Ackerly and Donoghue 1998). Thick cuticles, sunken stomata, and stomata protected by vestibules, papillae, or trichomes are generally indicative of dry conditions (Wing and DiMichele 1992; Upchurch 1995). In some cases, however, these features may reflect high herbivory, low nutrient conditions, and extremely high rainfall (e.g., cloud forests [Feild et al. 1998, 2003a; see also Wing and DiMichele 1992]).

Doyle and Hickey (1976; Hickey and Doyle 1977) argued that the Potomac record supported a semiarid origin of the angiosperms (Stebbins 1974). However, this was based not on evidence of aridity in the Potomac area, but rather on the supposition that the disturbed stream margins where the plants were preserved were the habitats most likely to be occupied by ''weedy'' immigrants from dry areas. Both leaf floras and paleoclimatic models imply that the Potomac Group climate was moist and subtropical (Upchurch and Wolfe 1987; Beerling and Woodward 2001). The angiosperms range from small leaves with chloranthoid teeth to larger leaves of the *Ficophyllum* type. Most of the taxa studied anatomically have thin cuticles and stomata in the plane of the leaf surface, except *Eucalyptophyllum*, which has a thicker cuticle and sunken stomata (Upchurch 1984a,b), traits likely related to broadly mesic conditions (Wing and DiMichele 1992; Feild et al. 1998). Similarities between these cuticles and those of modern basal angiosperms (Upchurch 1984a,b) also suggest that they were ecologically comparable.

Several authors took the diversity of early angiosperm pollen in Northern Gondwana, coupled with dominance of xeromorphic Cheirolepidiaceae and Gnetales, rarity of fern spores, and salt deposits, as support for a semiarid origin (Brenner 1976; Doyle et al. 1977; Hickey and Doyle 1977). However, angiosperms were as or more diverse in northern South America and the Middle East, where there are fewer Cheirolepidiaceae, more ferns, and coal deposits, indicating a wetter climate (Doyle et al. 1982; Schrank 1983, 1990; Brenner 1996). Climate models also predict higher rainfall in these areas (Parrish 1987; Beerling and Woodward 2001). Barremian-Aptian angiosperm leaves from Colombia (Pons 1984) are smaller than *Ficophyllum*, but they overlap lower Potomac angiosperm leaves in size and other features (unfortunately, no cuticle was preserved). The Colombian flora is dominated by matoniaceous ferns (*Weichselia*), with some cycadophytes and broad-leaved conifers (Pons 1984); this flora represents the wet extreme in Northern Gondwana. Together these observations indicate that early angiosperms occurred in both wet and dry tropical areas, and it would be premature to assume they originated in one environment rather than the other.

Interpretations of whole-plant water balance derived from cuticular anatomy of ancient plants would be strengthened by independent estimates of leaf gas-exchange performance. Stable carbon isotopic composition ($\delta^{13}C$, the ratio of $^{13}CO_2$ to $^{12}CO_2$) is the most promising proxy for leaf water-use efficiency (Farquhar et al. 1982; Condon et al. 1993). Using well-understood relationships from modern angiosperms, it should be possible to apply $\delta^{13}C$ measurements of fossil cuticles to infer relative leaf water-use efficiency of early angiosperms within a fossil assemblage. Although the absolute $\delta^{13}C$ value of an individual fossil can be influenced by a variety of factors, including ecology, the isotopic composition of atmospheric CO_2, and taphonomy (Arens et al. 2000; Arens and Jahren 2000, 2002; Beerling and Royer 2002), sampling a range of taxa within an assemblage may allow seriation of plants along a gradient of water-use efficiency. For example, Nguyen Tu et al. (1999) used $\delta^{13}C$ of fossil cuticles to infer leaf water-use efficiency of angiosperms, conifers, cycads, and ginkgoes and ordinate them along a salinity gradient.

Implications for the Early Evolution of Angiosperms

The dark and disturbed hypothesis provides a new perspective on the selective environment in which early angiosperms evolved. Stebbins (1965, 1974) hypothesized that the distinctive features of angiosperms arose under seasonally dry climates and unstable habitats, where rapid reproduction and high vegetative flexibility were favored. This view has been variously modified by other authors (Axelrod 1970; Doyle and Hickey 1976; Hickey and Doyle 1977; Doyle 1978; Doyle and Donoghue 1986, 1993; Crane et al. 1995; Taylor and Hickey 1996). Our analysis raises another possibility: Key angiosperm traits (e.g., vessels, reticulate leaf venation, and the carpel) may be linked to low light and high moisture availability, coupled with frequent disturbance.

Current phylogenies imply that vessels were absent in the first angiosperms (*Amborella* is vesselless, and Nymphaeales are vesselless or have cells intermediate between tracheids and vessel elements [Schneider et al. 1995; Feild et al. 2000]). Vessels, however, probably appeared early in angiosperm evolution, as Austrobaileyales and Chloranthaceae are vessel-bearing (Doyle and Endress 2000; Carlquist and Schneider 2002). Previous interpretations of vessel origin in angiosperms emphasized increased hydraulic efficiency and rapid transpiration in open, tropical environments (Doyle et al. 1982; Doyle and Donoghue 1986). In contrast, we propose that vessels confer disturbance tolerance in shady understory habitats, where evaporative demand is low. By providing a more open path for water moving through the stem, vessels allow a given amount of leaf area to be supported at lower shoot construction cost, as found especially in basal angiosperm understory lianas (Brodribb and Feild 2000; Feild et al. 2000, 2003a; Sperry 2003). This interpretation is bolstered by vessel structure in basal taxa such as Austrobaileyales and some Chloranthaceae, which lack features maximizing hydraulic conductivity, such as simple perforation plates (some *Schisandra* species are an exception [Carlquist 1999]) and completely open pit membranes (Carlquist and Schneider 2002). Thus, the initial selection pressures for vessels may have been increased vegetative growth efficiency under carbon-limited (shady), humid conditions, rather than water stress in dry climates or under high transpiration load in full sun.

Reticulate leaf venation may also provide physiological advantages in forest understories (Givnish 1979; Roth-Nebelsick et al. 2001). By increasing within-leaf hydraulic redundancy and structural support, reticulate venation may have facilitated the evolution of larger photosynthetic surfaces capable of more efficient use of understory sunflecks.

Envisioning early angiosperms in a humid climate also has implications for the origin of the carpel. Carpels in *Amborella*, Nymphaeales, Austrobaileyales, and Chloranthaceae are urnlike (ascidiate) and not sealed by postgenital (cellular) fusion (Endress 2001). Instead, they are ''plugged'' to varying degrees by mucilage-like pectin and arabinogalactan secretions (Bernhardt et al. 2003; T. L. Sage unpublished data 2003 for *Amborella* and *Illicium*). Although these extracellular polysaccharides are strongly hydrophilic, water stored in them is easily liberated at low xylem tensions (Morse 1990). Thus, this mode of carpel closure may offer little protection from drought. Furthermore, such carpels would have promoted outbreeding or acted as effective shields against fungal invasion and/or insect damage (Stebbins 1974; Doyle and Donoghue 1986) only under conditions of locally high humidity (e.g., forest understories, cloud forests, or aquatic habitats). Interestingly, many of the oldest known fossil angiosperm flowers appear to have ascidiate carpels (Friis et al. 1999, 2000; Doyle 2001).

Selective Pressures and Diversification.—The low species richness and ecophysiological variation of extant basal lineages (Fig. 1), combined with the rarity of angiosperm fossils before the Barremian–Aptian, suggest that the traits promoting angiosperm diversification arose after the origin of the crown group (i.e., the common ancestor of all extant taxa; Doyle and Donoghue 1993; Sanderson and Donoghue 1994; Magallón and Sanderson 2001). Instead of being the key to diversification, the dark and disturbed lifestyle may have been a way for angiosperms to gain a root-hold in well-established Mesozoic plant communities.

Greater architectural flexibility and dispersion of meristems may have offered early angiosperms a crucial advantage in disturbed understory habitats. For instance, rhizomatous growth and lianoid habits, with heavy reliance on vegetative propagation (Table 3), increase the discovery and exploitation of ephemeral, resource-rich patches in the forest understory (Cook 1983). Multistemmed growth, characterized by large ''bud banks'' for shoot iteration following damage, also allows long-term persistence in disturbed habitats (Greig 1993; Bond and Midgely 2001, 2003). With evolution of vessels, carbon costs for shoot and root reiteration may have decreased (see above). In contrast, the squat, unbranched, sparsely leaved forms of many Bennettitales (e.g., *Cycadeoidea*; Crane 1985) and cycads were probably less able to use patchy understory resources and may have been at greater risk of fatal damage from limbfall disturbance. Extant understory cycads (e.g., *Zamia*) recover slowly from limbfall-induced shoot damage because they have a limited capacity to resprout and add new leaves slowly (Clark and Clark 1988; Clark et al. 1992). In their reliance on vegetative growth, early angiosperms may have been more like ferns than other seed plants. Flexible growth and varied regeneration modes (vegetative as well as sexual) may have been particularly advantageous in understories disturbed by dinosaurs, a significant agent in Mesozoic forests (Bakker 1978; Wing and Tiffney 1987; Barrett and Willis 2001).

If the dark and disturbed ecology did not promote diversity, later innovations may have been responsible for spurring angiosperm radiation into a wide range of new habitats. As angiosperms broke out of the understory, we suggest that vessels and reticulate leaf venation were co-opted for new adaptive roles. Modifications of vessels (e.g., longer functional length and simple perforation plates joining vessel elements) increased hydraulic conductivity. This vascular system, coupled with increasing vein density, could support the higher transpiration rates required to dissipate heat in sunny environments and enable the evolution of higher photosynthetic rate. Thus, the exaptation of vessels for sunnier and/or drier landscapes may be more closely linked to the explosive diversification of angiosperms in the Albian and Late Cretaceous. In turn, these new habitats would have exposed angiosperms to many new pressures for changes in pollination and dispersal mode (cf. Doyle et al. 2003).

Pre-Cretaceous Angiosperm History.—Our hypothesis also bears on one of the most vexing questions in paleobotany: Where was the angiosperm line before the Cretaceous? Axelrod (1952, 1970) argued that crown-group angiosperms originated and diversified cryptically before the Cretaceous. This scenario, however, is unlikely given the primitive character suites of Early Cretaceous angiosperms and their morphological diversification through the period (Doyle 1969, 1977, 1978, 2001; Doyle and Hickey 1976; Doyle and Donoghue 1993; Crane et al. 1995). If crown-group angiosperms existed earlier, they must have been rare and plesiomorphic. In this case, features essential for angiosperm diversification arose after the origin of the crown group, unless some extrinsic factor suppressed diversification of the clade (Doyle and Donoghue 1993). The dark and disturbed hypothesis provides a plausible scenario: Low-diversity basal groups were initially restricted to dark, wet, and disturbed forest understories where population sizes were low. Later, Chloranthaceae and core angiosperms evolved greater sun-tolerance and diversified both phylogenetically and in habitat preference.

Significantly, everwet tropical climates were rare in the Triassic and Jurassic. Both sedimentological evidence and climate models suggest that atmospheric circulation in tropical latitudes was strongly monsoonal (Parrish et al. 1982; Ziegler et al. 1987; Barron et al. 1994; Rees et al. 2000; Beerling and Woodward 2001). In the Early Cretaceous tropics, paleobotanical and sedimentary evidence and climate models indicate that mesic climates were restricted to northern South America, the Middle East, and Southeast Asia (Parrish 1987; Doyle et al. 1982; Barron et al. 1994; Doyle 1999; Rees et al. 2000; Beerling and Woodward 2001). If wet tropical habitats were rare, it becomes more plausible that pre-Cretaceous angiosperms, or their immediate precursors, escaped detection. However, unlike the upland theory of Axelrod (1952, 1970) or the semiarid theory of Stebbins (1965, 1974), the dark and disturbed hypothesis is testable by study of known and yet-to-be-discovered fossil floras of appropriate age.

Conclusion

Cogent arguments on the forces driving angiosperm origin and diversification depend on an accurate picture of early angiosperm ecology. To develop such a picture, we mapped ecophysiological data from extant basal angiosperms onto their phylogeny to reconstruct the ecology of their common ancestors. This analysis yielded an ecological hypothesis of the first angiosperms that is subtly, but importantly, different from previous ideas: Angiosperms may have first occupied shaded, disturbed, and possibly wet understory habitats.

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Literature Cited

Ackerly, D. D., and M. J. Donoghue. 1998. Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). American Naturalist 152:767–791.

Alvin, K. L. 1974. Leaf anatomy of *Weichselia* based on fusainized material. Palaeontology 17:587–598.

Arber, E. A. N., and J. Parkin. 1907. On the origin of angiosperms. Journal of the Linnean Society (Botany) 38:29–80.

Archangelsky, S., and J. C. Gamerro. 1967. Spore and pollen types of the Lower Cretaceous in Patagonia (Argentina). Review of Palaeobotany and Palynology 1:211–217.

Archangelsky, S., and T. N. Taylor. 1993. The ultrastructure of in situ *Clavatipollenites* pollen from the Early Cretaceous of Patagonia. American Journal of Botany 80:879–885.

Arens, N. C. 1997. Responses of leaf anatomy to light environment in the tree fern *Cyathea caracasana* (Cyatheaceae) and its application to some ancient seed ferns. Palaios 12:84–94.

———. 2001. Variation in performance of the tree fern *Cyathea caracasana* (Cyatheaceae) across the successional mosaic of an Andean cloud forest. American Journal of Botany 88:545–551.

Arens, N. C., and A. H. Jahren. 2000. Carbon isotope excursion in atmospheric CO_2 at the Cretaceous-Tertiary boundary: evidence from terrestrial sediments. Palaios 15:314–322.

———. 2002. Chemostratigraphic correlation of four fossil-bearing sections in southwestern North Dakota. Geological Society of America Special Paper 361:75–93.

Arens, N. C., A. H. Jahren, and R. Amundson. 2000. Can C_3 plants faithfully record the carbon isotopic composition of atmospheric carbon dioxide? Paleobiology 26:137–164.

Axelrod, D. I. 1952. A theory of angiosperm evolution. Evolution 6:29–60.

———. 1970. Mesozoic paleogeography and early angiosperm history. Botanical Review 36:277–319.

Bakker, R. T. 1978. Dinosaur feeding behaviour and the origin of flowering plants. Nature 274:661–663.

Barkman, T. J., G. Chenery, J. R. McNeal, J. Lyons-Weiler, W. J. Ellisens, G. Moore, A. D. Wolfe, and C. W. de Pamphilis. 2000. Independent and combined analyses of sequences from all three genomic compartments converge on the root of flowering plant phylogeny. Proceedings of the National Academy of Sciences USA 97:13166–13171.

Barrat-Segretain, M.-H. 1996. Germination and colonization dynamics of *Nuphar lutea* (L.) Sm. in a former river channel. Aquatic Botany 55:31–38.

Barrett, P. M, and K. J. Willis. 2001. Did dinosaurs invent flowers? Dinosaur-angiosperm coevolution revisited. Biological Reviews 76:411–447.

Barron, E. J., P. J. Fawcett, D. Pollard, and S. L. Thompson. 1994. Model simulations of Cretaceous climates: the role of geography and carbon dioxide. Pp. 99–108 *in* J. R. L. Allen, B. J. Hoskins, B. W. Sellwood, R. A. Spicer, and P. J. Valdes, eds. Palaeoclimates and their modelling: with special reference to the Mesozoic Era. Chapman and Hall, London.

Beerling, D. J., and D. L. Royer. 2002. Fossil plants as indicators of the Phanerozoic global carbon cycle. Annual Review of Earth and Planetary Sciences 30:527–556.

Beerling, D. J., and F. I. Woodward. 2001. Vegetation and the terrestrial carbon cycle: modelling the first 400 million years. Cambridge University Press, Cambridge.

Behrensmeyer, A. K., S. M. Kidwell, and R. A. Gastaldo. 2000. Taphonomy and paleobiology. Paleobiology 26:103–147.

Bernhardt, P., T. L. Sage, P. Weston, H. Azuma, M. Lam, L. B. Thien, and J. Bruhl. 2003. The pollination of *Trimenia moorei* (Trimeniaceae): floral volatiles, insect/wind pollen vectors, and stigmatic self-incompatibility in a basal angiosperm. Annals of Botany 92:445–458.

Berry, E. W. 1911. Systematic paleontology, Lower Cretaceous, Pteridophyta-Dicotyledonae. Pp. 214–508 *in* W. B. Clark, ed. Maryland Geological Survey, Lower Cretaceous. Johns Hopkins University Press, Baltimore.

Bews, J. W. 1927. Studies in the ecological evolution of angiosperms. New Phytologist 26:1–21.

Bilger, W., U. Schreiber, and M. Bock. 1995. Determinants of the quantum efficiency of photosystem II and nonphotochemical quenching of chlorophyll fluorescence in the field. Oecologia 102:425–432.

Björkman, O., and B. Demmig. 1987. Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170:489–504.

Blanc, P. 1986. Edification d'arbres par croissance d'établissement de type monocotylédonien: l'exemple de *Chloranthaceae*. Pp. 101–123 *in* Colloque international sur l'arbre 1986. Naturalia Monspeliensia, numéro hors série, Montpellier.

Bond, W. J., and J. J. Midgely. 1988. Allometry and sexual differences in leaf size. American Naturalist 131:901–910.

———. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution 16:45–51.

———. 2003. The evolutionary ecology of sprouting. International Journal of Plant Sciences 164(Suppl.):S103–S114.

Bongers, F., and J. Popma. 1990. Leaf characteristics of the tropical rain forest flora of Los Tuxtlas, Mexico. Botanical Gazette 151:354–365.

Brenner, G. J. 1963. The spores and pollen of the Potomac Group of Maryland. Maryland Department of Geology, Mines and Water Resources Bulletin 27:1–215.

———. 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. Pp. 23–47 *in* C. B. Beck, ed. Origin and early evolution of angiosperms. Columbia University Press, New York.

———. 1996. Evidence for the earliest stage of angiosperm pollen evolution: a paleoequatorial section from Israel. Pp. 91–115 *in* D. W. Taylor and L. J. Hickey, eds. Flowering plant origin, evolution and phylogeny. Chapman and Hall, New York.

Brodribb, T. J., and T. S. Feild. 2000. Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. Plant, Cell and Environment 23:1381–1388.

Brodribb, T., and R. S. Hill. 1997. Light response characteristics of a morphologically diverse group of southern hemisphere conifers as measured by chlorophyll fluorescence. Oecologia 110:10–17.

Brodribb, T. J., N. M. Holbrook, and M. V. Gutierrez. 2002. Hydraulic and photosynthetic coordination in seasonally dry tropical forest. Plant, Cell and Environment 25:1435–1444.

Burger, D. 1990. Early Cretaceous angiosperms from Queensland, Australia. Review of Palaeobotany and Palynology 65: 153–163.

———. 1993. Early and middle Cretaceous angiosperm pollen grains from Australia. Review of Palaeobotany and Palynology 78:183–234.

Calder, J. H., M. R. Gibling, C. F. Eble, A. C. Scott, and D. J. MacNeil. 1996. The Westphalian D fossil lepidodendrid forest at Table Head, Sydney Basin, Nova Scotia: sedimentology, paleoecology and floral response to changing edaphic conditions. International Journal of Coal Geology 31:277–313.

Canham, C. D., R. K. Kobe, E. F. Latty, and R. L. Chazdon. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia 121:1–11.

Cantrill, D. J., and G. J. Nichols. 1996. Taxonomy and paleoecology of Early Cretaceous (Late Albian) angiosperm leaves from Alexander Island, Antarctica. Review of Palaeobotany and Palynology 92:1–28.

Carlquist, S. 1975. Ecological strategies of xylem evolution. University of California Press, Berkeley.

———. 1984. Wood anatomy of Trimeniaceae. Plant Systematics and Evolution 144:103–118.

———. 1987. Presence of vessels in wood of *Sarcandra* (Chloranthaceae): comments on vessel origin in angiosperms. American Journal of Botany 74:1765–1771.

———. 1992a. Wood anatomy and stem of *Chloranthus*; summary of wood anatomy of Chloranthaceae, with comments on relationships, vessellessness, and the origin of monocotyledons. International Association of Wood Anatomists Bulletin 13:3–16.

———. 1992b. Wood anatomy of *Hedyosmum* (Chloranthaceae) and the tracheid-vessel element transition. Aliso 13:447–462.

———. 1999. Wood and bark anatomy of Schisandraceae: implications for phylogeny, habit, and vessel evolution. Aliso 18: 45–55.

Carlquist, S., and E. L. Schneider. 2002. The tracheid-vessel element transition in angiosperms involves multiple independent features: cladistic consequences. American Journal of Botany 89:185–195.

Chandrasekharam, A. 1972. Spongy mesophyll remains in fossil leaf compressions. Science 177:354–356.

Chazdon, R. L. 1988. Sunflecks and their importance to forest understory plants. Advances in Ecological Research 18:1–63.

Chazdon, R. L., R. W. Pearcy, D. W. Lee, and N. Fetcher. 1996. Photosynthetic responses of tropical forest plants to contrasting light environments. Pp. 5–55 *in* S. S. Mulkey, R. L. Chazdon, and A. P. Smith, eds. Tropical forest plant ecophysiology. Chapman and Hall, London.

Clark, D. B., and D. A. Clark. 1988. Leaf production and the cost of reproduction in the neotropical rain forest cycad, *Zamia skinneri*. Journal of Ecology 76:1153–1163.

Clark, D. B., D. A. Clark, and M. H. Grayum. 1992. Leaf demography of a neotropical rain forest cycad, *Zamia skinneri* (Zamiaceae). American Journal of Botany 79:28–33.

Condon, A. G., R. A. Richards, and G. D. Farquhar. 1993. Relationships between carbon isotopic discrimination, water use efficiency, and transpiration efficiency for dryland wheat. Australian Journal of Agricultural Research 44:1693–1711.

Cook, R. E. 1983. Clonal plant populations. American Scientist 71:244–253.

Crane, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. Annals of the Missouri Botanical Garden 72:716–793.

———. 1987. Vegetational consequences of the angiosperm diversification. Pp. 107–144 *in* E. M. Friis, W. G. Chaloner, and P. R. Crane, eds. The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge.

Crane, P. R., and S. Lidgard. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. Science 246:675–678.

Crane, P. R., and G. R. Upchurch. 1987. *Drewria potomacensis* gen. et sp. nov., an Early Cretaceous member of Gnetales from the Potomac Group of Virginia. American Journal of Botany 74: 1722–1736.

Crane, P. R., K. R. Pedersen, E. M. Friis, and A. N. Drinnan. 1993. Early Cretaceous (early to middle Albian) platanoid inflorescences associated with *Sapindopsis* leaves from the Potomac Group of eastern North America. Systematic Botany 18:328–344.

Crane, P. R., E. M. Friis, and K. R. Pedersen. 1994. Paleobotanical evidence on the early radiation of magnoliid angiosperms. Plant Systematics and Evolution 8(Suppl.):51–72.

———. 1995. The origin and early diversification of angiosperms. Nature 374:27–33.

Cronquist, A. 1988. The evolution and classification of flowering plants, 2d ed. New York Botanical Garden, New York.

Dacey, J. W. H. 1980. Internal winds in water lilies: an adaptation for life in anaerobic sediments. Science 210:1017–1019.

Dai, N., S. Kenji, and A. Sakai. 2002. Seedling establishment of deciduous trees in various topographic positions. Journal of Vegetation Science 13:35–44.

Davies-Vollum, K. S. 1999. The formation of beds underlying carbonaceous shales in aquic paleosols: examples from the Bighorn Basin of Wyoming. International Journal of Coal Geology 41:239–255.

Davies-Vollum, K. S., and S. L. Wing. 1998. Sedimentological, taphonomic, and climatic aspects of Eocene swamp deposits (Willwood Formation, Bighorn Basin, Wyoming). Palaios 13: 28–40.

Demmig-Adams, B., W. W. Adams, B. Logan, and A. Verhoeven. 1995. Xanthophyll cycle dependent energy dissipation and flexible photosystem II efficiency in plants acclimated to light stress. Australian Journal of Plant Physiology 22:249–260.

Dettmann, M. E. 1994. Cretaceous vegetation: the microfossil record. Pp. 143–188 *in* R. S. Hill, ed. History of the Australian vegetation. Cambridge University Press, Cambridge.

Donoghue, M. J., and J. A. Doyle. 1989. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. Pp. 14–45 *in* P. R. Crane and S. Blackmore, eds. Evolution, systematics, and fossil history of the Hamamelidae, Vol. 1. Clarendon, Oxford.

Doyle, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic Coastal Plain and its evolutionary significance. Journal of the Arnold Arboretum 50:1–35.

———. 1977. Patterns of evolution in early angiosperms. Pp. 501–546 *in* A. Hallam, ed. Patterns of evolution. Elsevier, Amsterdam.

———. 1978. Origin of angiosperms. Annual Review of Ecology and Systematics 9:365–392.

———. 1999. The rise of angiosperms as seen in the African Cretaceous pollen record. *In* K. Heine, ed. Palaeoecology of Africa 26:3–29.

———. 2001. Significance of molecular phylogenetic analyses for paleobotanical investigations on the origin of angiosperms. Palaeobotanist 50:167–188.

Doyle, J. A., and M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. Botanical Review 52:321–431.

———. 1993. Phylogenies and angiosperm diversification. Paleobiology 19:141–167.

Doyle, J. A. and P. K. Endress. 2000. Morphological phylogenetic analysis of basal angiosperms: comparison and combination with molecular data. International Journal of Plant Sciences 161(Suppl.):S121–S153.

Doyle, J. A., and L. J. Hickey. 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. Pp. 139–206 *in* C. B. Beck, ed. Origin and early evolution of angiosperms. Columbia University Press, New York.

Doyle, J. A., P. Biens, A. Doerenkamp, and S. Jardiné. 1977. Angiosperm pollen from the pre-Albian Cretaceous of Equatorial Africa. Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine 1:451–473.

Doyle, J. A., S. Jardiné, and A. Doerenkamp. 1982. *Afropollis*, a new genus of early angiosperm pollen, with notes on the Cretaceous palynostratigraphy and paleoenvironments of Northern Gondwana. Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine 6:39–117.

Doyle, J. A., M. J. Donoghue, and E. A. Zimmer. 1994. Integration of morphological and ribosomal RNA data on the origin of angiosperms. Annals of the Missouri Botanical Garden 81: 419–450.

Doyle, J. A., H. Eklund, and P. S. Herendeen. 2003. Floral evolution in Chloranthaceae: implications of a phylogenetic analysis of morphological characters. International Journal of Plant Sciences 164(Suppl.):S365–S382.

Edwards, G. E., and N. R. Baker. 1993. Can assimilation in maize leaves be predicted accurately from chlorophyll fluorescence analysis? Photosynthesis Research 37:89–102.

Eklund, H., J. A. Doyle, and P. S. Herendeen. 2004. Morphological phylogenetic analysis of living and fossil Chloranthaceae. International Journal of Plant Sciences (in press).

Endress, P. K. 1987. The Chloranthaceae: reproductive structures and phylogenetic position. Botanische Jahrbücher für Systematik 109:153–226.

———. 2001. The flowers in extant basal angiosperms and inferences on ancestral flowers. International Journal of Plant Sciences 162:1111–1140.

Eriksson, O., E. M. Friis, and P. R. Crane. 2000. Seed size, fruit size, and dispersal systems in angiosperms from the Early Cretaceous to the Late Tertiary. American Naturalist 156:47–58.

Esau, K. 1977. Anatomy of seed plants. Wiley, New York.

Farquhar, G. D., M. H. O'Leary, and J. A. Berry. 1982. On the relationship between carbon isotopic discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology 9:121–137.

Feild, T. S., M. A. Zwieniecki, M. J. Donoghue, and N. M. Holbrook. 1998. Stomatal plugs of *Drimys winteri* (Winteraceae) protect leaves from mist but not drought. Proceedings of the National Academy of Sciences USA 95:14256–14259.

Feild, T. S., T. Brodribb, T. Jaffré, and N. M. Holbrook. 2001. Responses of leaf anatomy, photosynthetic light-use, and xylem hydraulics to light in the basal angiosperm *Amborella trichopoda* (Amborellaceae). International Journal of Plant Sciences 162:999–1008.

Feild, T. S., M. A. Zwieniecki, T. Brodribb, T. Jaffré, M. J. Donoghue, and N. M. Holbrook. 2000. Structure and function of tracheary elements in *Amborella trichopoda*. International Journal of Plant Sciences 161:705–712.

Feild, T. S., P. J. Franks, and T. L. Sage. 2003a. The shade-adapted ecophysiology of *Austrobaileya scandens*. International Journal of Plant Sciences 164:313–324.

Feild, T. S., N. C. Arens, and T. E. Dawson. 2003b. The ancestral ecology of flowering plants: emerging perspectives from extant basal lineages. International Journal of Plant Sciences 164(Suppl.):S129–S142.

Fontaine, W. M. 1889. The Potomac or Younger Mesozoic flora. U.S. Geological Survey Monograph 15.

Forbis, T. A., S. K. Floyd, and A. de Queiroz. 2002. The evolution of embryo size in angiosperms and other seed plants: implications for the evolution of seed dormancy. Evolution 56: 2112–2125.

Franco, A. C., and U. Lüttge. 2002. Midday depression in savanna trees: coordinated adjustments in photochemical efficiency, photorespiration, CO_2 assimilation, and water-use efficiency. Oecologia 131:356–365.

Friis, E. M., P. R. Crane, and K. R. Pedersen. 1997. Fossil history of magnoliid angiosperms. Pp. 121–156 *in* K. Iwatsuki and P. R. Raven, eds. Evolution and diversification of land plants. Springer, Tokyo.

Friis, E. M., K. R. Pedersen, and P. R. Crane. 1999. Early angiosperm diversification: the diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous floras from Portugal. Annals of the Missouri Botanical Garden 86:259–296.

———. 2000. Reproductive structure and organization of basal angiosperms from the Early Cretaceous (Barremian or Aptian) of western Portugal. International Journal of Plant Sciences 161(Suppl.):S169–S182.

———. 2001. Fossil evidence of water lilies (Nymphaeales) in the Early Cretaceous. Nature 410:357–360.

Friis, E. M., J. A. Doyle, P. K. Endress, and Q. Leng. 2003. *Archaefructus*: angiosperm precursor or specialized early angiosperm? Trends in Plant Science 8:369–373.

Gandolfo, M. A., K. C. Nixon, and W. L. Crepet. 2001. Turonian Pinaceae of the Raritan Formation, New Jersey. Plant Systematics and Evolution 226:187–203.

Gavin, D. G., and D. R. Peart. 1999. Vegetative life history of a dominant rain forest canopy tree. Biotropica 31:288–294.

Genty, B., J.-M. Briantais, and N. R. Baker. 1989. The relationship between the quantum yield of photosynthetic electron transport rate and quenching of chlorophyll fluorescence. Biochimica Biophysica Acta 990:87–92.

Givnish, T. J. 1979. On the adaptive significance of leaf form. Pp. 375–407 *in* O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven, eds. Topics in plant population biology. Columbia University Press, New York.

———. 1988. Adaptation to sun and shade: a whole-plant perspective. Australian Journal of Plant Physiology 15:63–92.

Gottsberger, G. 1988. The reproductive biology of primitive angiosperms. Taxon 37:630–643.

Graham, S. W., and R. G. Olmstead. 2000. Utility of 17 chloroplast genes for inferring the phylogeny of the basal angiosperms. American Journal of Botany 87:1712–1730.

Greig, N. 1993. Regeneration mode in neotropical *Piper*: habitat and species comparisons. Ecology 74:2125–2135.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, Chichester, U.K.

Grubb, P. J. 1998. Seeds and fruits of tropical rainforest plants: interpretation of the range in seed size, degree of defense, and flesh/seed quotients. Pp. 1–24 *in* D. M. Newbery, H. H. T. Prins, and N. D. Brown, eds. Dynamics of tropical communities. Blackwell Scientific, Oxford.

Hao, G., R. M. K. Saunders, and M.-L. Chye. 2000. A phylogenetic analysis of the Illiciaceae based on sequences of internal transcribed spacers (ITS) of nuclear ribosomal DNA. Plant Systematics and Evolution 223:81–90.

Hao, G., M.-L. Chye, and R. M. K. Saunders. 2001. A phylogenetic analysis of the Schisandraceae based on morphology and nuclear ribosomal ITS sequences. Botanical Journal of the Linnean Society 135:401–411.

Harper, J. L., P. H. Lovell, and K. G. Moore. 1970. The shapes and sizes of seeds. Annual Review of Ecology and Systematics 1:327–356.

Hickey, L. J., and J. A. Doyle. 1977. Early Cretaceous fossil evidence for angiosperm evolution. Botanical Review 43:1–104.

Hickman, J. C. 1993. The Jepson manual of higher plants of California. University of California Press, Berkeley.

Hughes, N. F. 1994. The enigma of angiosperm origins. Cambridge University Press, Cambridge.

Kelly, C. K. 1995. Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. Oecologia 102:377–388.

Kong, H.-Z. 2001. Comparative morphology of leaf epidermis in the Chloranthaceae. Botanical Journal of the Linnean Society 136:281–296.

Kong, H.-Z., Z.-D. Chen, and A.-M. Lu. 2002. Phylogeny of *Chloranthus* (Chloranthaceae) based on nuclear ribosomal ITS and plastid *trnL-F* sequence data. American Journal of Botany 89:940–946.

Kott, L. S., and D. M. Britton. 1985. Role of morphological characteristics of leaves and the sporangial region in the taxonomy of *Isoetes* in northeastern North America. American Fern Journal 75:44–55.

Krause, G. H., and E. Weis. 1991. Chlorophyll fluorescence and photosynthesis: the basics. Annual Review of Plant Physiology and Plant Molecular Biology 42:313–349.

Kwit, C., M. W. Swartz, W. J. Platt, and J. P. Geaghen. 1998. The distribution of tree species in steepheads of the Apalachicola River Bluffs, Florida. Journal of the Torrey Botanical Society 125:309–318.

Leishman, M. R., I. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. Pp. 31–57 *in* M. Fenner, ed. Seeds: the ecology of regeneration in plant communities. CABI Publishing, Wallingford, U.K.

Les, D. H., E. L. Schneider, D. J. Padgett, P. S. Solis, D. E. Soltis, and M. Zanis. 1999. Phylogeny, classification, and floral evolution of water lilies (Nymphaeaceae: Nymphaeales): a synthesis of non-molecular, *rbcL, matK,* and 18S rDNA data. Systematic Botany 24:28–46.

Luo, Y.-B., and Z.-Y. Li. 1999. Pollination ecology of *Chloranthus serratus* (Thunb.) Roem. et Schult. and *Ch. fortunei* (A. Gray) Solms-Laub. (Chloranthaceae). Annals of Botany 83:489–499.

Lupia, R., S. Lidgard, and P. R. Crane. 1999. Comparing palynological abundance and diversity: implications for biotic replacement during the Cretaceous angiosperm radiation. Paleobiology 25:305–340.

Lusk, C. K. 1995. Seed size, establishment sites, and species coexistence in a Chilean rainforest. Journal of Vegetation Science 6:249–256.

Lusk, C. K., and C. K. Kelly. 2003. Interspecific variation in seed size and safe sites in a temperate rain forest. New Phytologist 158:535–541.

Maddison, W. P. 1991. Squared-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. Systematic Zoology 40:305–314.

Maddison, W. P., and D. R. Maddison. 2001. MacClade 4: analysis of phylogeny and character evolution, Version 4.03. Sinauer, Sunderland, Mass.

Magallón, S., and M. J. Sanderson. 2001. Absolute diversification rates in angiosperm clades. Evolution 55:1762–1780.

Martin, T. J., and J. Ogden. 2002. The seed ecology of *Ascarina lucida*: a rare New Zealand tree adapted to disturbance. New Zealand Journal of Botany 40:397–404.

Mathews, S., and M. J. Donoghue. 1999. The root of angiosperm phylogeny inferred from duplicate phytochrome genes. Science 286:947–950.

McElwain, J. C., and W. G. Chaloner. 1996. The fossil cuticle as a skeletal record of environment change. Palaios 11:376–388.

Metcalfe, C. R. 1987. Anatomy of the dicotyledons, 2d ed., Vol. III. Magnoliales, Illiciales, and Laurales (*sensu* Armen Takhtajan). Clarendon, Oxford.

Mohr, B. A. R., and E. M. Friis. 2000. Early angiosperms from the Lower Cretaceous Crato Formation (Brazil), a preliminary report. International Journal of Plant Sciences 161(Suppl.): S155–S167.

Morse, S. R. 1990. Water balance in *Hemizonia luzulifolia*: the role of extracellular polysaccharides. Plant, Cell and Environment 13:39–48.

Nguyen Tu, T. T., H. Bocherens, A. Mariotti, F. Baudin, D. Pons, J. Broutin, S. Derenne, and C. Largeau. 1999. Ecological distribution of Cenomanian terrestrial plants based on $^{13}C/^{12}C$ ratios. Palaeogeography, Palaeoclimatology, Palaeoecology 145:79–93.

Niinemets, U., and K. Kalevi. 1994. Leaf weight per area and leaf size of 85 Estonian woody species in relation to shade tolerance and light availability. Forest Ecology and Management 70:1–10.

Niklas, K. J. 1997. The evolutionary biology of plants. University of Chicago Press, Chicago.

Nixon, K. C., W. L. Crepet, D. Stevenson, and E. M. Friis. 1994. A reevaluation of seed plant phylogeny. Annals of the Missouri Botanical Garden 81:484–533.

Parkinson, C. L., K. L. Adams, and J. D. Palmer. 1999. Multigene analyses identify the three earliest lineages of extant flowering plants. Current Biology 9:1485–1488.

Parrish, J. T. 1987. Global palaeogeography and palaeoclimate of the Late Cretaceous and Early Tertiary. Pp. 51–73 *in* E. M. Friis, W. G. Chaloner, and P. R. Crane, eds. The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge.

Parrish, J. T., A. M. Ziegler, and C. R. Scotese. 1982. Rainfall patterns and the distribution of coals and evaporites in the Mesozoic and Cenozoic. Palaeogeography Palaeoclimatology Palaeoecology 40:67–101.

Pearcy, R. W. 1990. Sunflecks and photosynthesis in plant canopies. Annual Review of Plant Physiology and Plant Molecular Biology 41:421–453.

Philipson, W. R. 1986. Trimeniaceae. Flora Malesiana Series I 10: 327–333.

Playford, G. 1971. Palynology of Lower Cretaceous (Swan River) strata of Saskatchewan and Manitoba. Palaeontology 14:533–565.

Pons, D. 1984. Le Mésozoïque de Colombie: macroflores et microflores. Editions du CNRS, Paris.

Qiu, Y.-L., J. Lee, F. Bernasconi-Quadroni, D. E. Soltis, P. S. Soltis, M. Zanis, E. A. Zimmer, Z. Chen, V. Savolainen, and M. W. Chase. 1999. The earliest angiosperms: evidence from mitochondrial, plastid and nuclear genomes. Nature 402:404–407.

Rascher, U., M. Liebig, and U. Lüttge. 2000. Evaluation of instant light-response curves of chlorophyll fluorescence parameters obtained with a portable chlorophyll fluorometer on site in the field. Plant, Cell and Environment 23:1397–1405.

Rees, P. M., A. M. Ziegler, and P. J. Valdes. 2000. Jurassic phytogeography and climates: new data and model comparisons. Pp. 297–318 *in* B. T. Huber, K. G. MacLeod, and S. L. Wing, eds. Warm climates in earth history. Cambridge University Press, Cambridge.

Roberts, M. L., and R. R. Haynes. 1983. Ballistic seed dispersal in *Illicium* (Illiciaceae). Plant Systematics and Evolution 143:227–232.

Rodenburg, W. F. 1971. A revision of the genus *Trimenia* (Trimeniaceae). Blumea 19:3–15.

Romero, E. J., and S. Archangelsky. 1986. Early Cretaceous angiosperm leaves from southern South America. Science 234:1580–1582.

Roth-Nebelsick, A., D. Uhl, V. Mosbrugger, and H. Kerp. 2001. Evolution and function of leaf venation architecture: a review. Annals of Botany 87:553–566.

Royer, D. L., L. J. Hickey, and S. L. Wing. 2003. Ecological conservatism in the ‘‘living fossil’’ *Ginkgo*. Paleobiology 29:84–104.

Sakai, A., T. Ohsawa, and M. Ohsawa. 1995. Adaptive significance of sprouting of *Euptelea polyandra*, a deciduous tree growing on steep slopes with shallow soil. Journal of Plant Research 108:377–386.

Salisbury, E. J. 1942. The reproductive capacity of plants: studies in quantitative biology. G. Bell, London.

Sanderson, M. J., and M. J. Donoghue. 1994. Shifts in diversification rate with the origin of angiosperms. Science 264:1590–1593.

Saunders, R. M. K. 1998. Monograph of *Kadsura* (Schisandraceae). Systematic Botany Monographs 54:1–106.

———. 2000. Monograph of *Schisandra* (Schisandraceae). Systematic Botany Monographs 58:1–146.

Schabilion, J. T., and M. A. Reihman. 1985. Anatomy of petrified *Neuropteris scheuchzeri* pinnules from the Middle Pennsylvanian of Iowa: a paleoecological interpretation. Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère, Compte Rendu, 5:3–12.

Schneider, E. L., and S. Carlquist. 1995. Vessels in the roots of *Barclaya rotundifolia* (Nymphaeaceae). American Journal of Botany 82:1343–1349.

Schneider, E. L., and P. S. Williamson. 1993. Nymphaeaceae. Pp. 486–493 *in* K. Kubitzki, ed. The families and genera of vascular plants. Springer, New York.

Schneider, E. L., S. Carlquist, K. Beamer, and A. Kohn. 1995. Vessels in Nymphaeaceae: *Nuphar*, *Nymphaea*, and *Ondinea*. International Journal of Plant Sciences 156:857–862.

Schrank, E. 1983. Scanning electron and light microscopic investigations of angiosperm pollen from the Lower Cretaceous of Egypt. Pollen et Spores 25:213–242.

———. 1990. Palynology of the clastic Cretaceous sediments between Dongola and Wadi Muqaddam, northern Sudan. Berliner Geowissenschaftliche Abhandlungen, Reihe A 120:149–167.

Sculthorpe, C. D. 1967. The biology of aquatic vascular plants. Arnold, London.

Smith, A. C. 1947. The families Illiciaceae and Schisandraceae. Sargentia 7:1–224.

———. 1976. Studies of Pacific Island plants, XXXIII. The genus *Ascarina* (Chloranthaceae) in the southern Pacific. Journal of the Arnold Arboretum 57:405–425.

Smith, W. K., T. C. Vogelmann, E. H. DeLucia, D. T. Bell, and K.

A. Shepherd. 1997. Leaf form and photosynthesis. Bioscience 47:785–793.

Smits, A. J. M., R. van Ruremonde, and G. van der Velde. 1990. Germination requirements and seed banks of some nymphaeid macrophytes: *Nymphaea alba* L., *Nuphar lutea* (L.) Sm., and *Nymphoides peltata* (Gmel.) O. Kuntze. Freshwater Biology 24:315–326.

Soltis, D. E., P. S. Soltis, D. L. Nickrent, L. A. Johnson, W. J. Hahn, S. B. Hoot, J. A. Sweere, R. K. Kuzoff, K. A. Kron, M. W. Chase, S. M. Swensen, E. A. Zimmer, S.-M. Chaw, L. J. Gillespie, W. J. Kress, and K. J. Sytsma. 1997. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. Annals of the Missouri Botanical Garden 84:1–49.

Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, K. C. Nixon, and J. S. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL,* and *atpB* sequences. Botanical Journal of the Linnean Society 133:381–461.

Sperry, J. S. 2003. Evolution of water transport and xylem structure. International Journal of Plant Sciences 164(Suppl.):S115–S127.

Stebbins, G. L. 1965. The probable growth habit of the earliest flowering plants. Annals of the Missouri Botanical Garden 52:457–468.

———. 1974. Flowering plants: evolution above the species level. Harvard University Press, Cambridge.

Stone, D. E. 1968. Cytological and morphological notes on the southeastern endemic *Schisandra glabra* (Schisandraceae). Journal of the Elisha Mitchell Scientific Society 84:351–356.

Sun, G., D. L. Dilcher, S. Zheng, and Z. Zhou. 1998. In search of the first flower: a Jurassic angiosperm, *Archaefructus*, from northeast China. Science 182:1692–1695.

Sun, G., Q. Ji, D. L. Dilcher, S. Zheng, K. C. Nixon, and X. Wang. 2002. Archaefructaceae, a new basal angiosperm family. Science 296:899–904.

Swamy, B. G. L., and I. W. Bailey. 1950. *Sarcandra*, a vesselless genus of the Chloranthaceae. Journal of the Arnold Arboretum 31:117–129.

Takhtajan, A. L. 1969. Flowering plants: origin and dispersal. Smithsonian Institution Press, Washington, D.C.

Taylor, D. W., and L. J. Hickey. 1990. An Aptian plant with attached leaves and flowers: implications for angiosperm origin. Science 247:702–704.

———. 1992. Phylogenetic evidence for the herbaceous origin of angiosperms. Plant Systematics and Evolution 180:137–156.

———. 1996. Evidence for and implications of an herbaceous origin for angiosperms. Pp. 232–266 *in* D. W. Taylor and L. J. Hickey, eds. Flowering plant origin, evolution, and phylogeny. Chapman and Hall, New York.

Thien, L. B., D. A. White, and L. Y. Yatsu. 1983. The reproductive biology of a relict: *Illicium floridanum* Ellis. American Journal of Botany 70:719–727.

Thorne, R. F. 1976. A phylogenetic classification of the Angiospermae. Evolutionary Biology 9:35–106.

Tiffney, B. H. 1984. Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. Annals of the Missouri Botanical Garden 71:551–576.

Todzia, C. A. 1988. Chloranthaceae: *Hedyosmum*. Flora Neotropica Monograph 48:1–139.

Upchurch, G. R. 1984a. Cuticular anatomy of angiosperm leaves from the Lower Cretaceous Potomac Group. I. Zone I leaves. American Journal of Botany 71:192–202.

———. 1984b. Cuticle evolution in Early Cretaceous angiosperms from the Potomac Group of Virginia and Maryland. Annals of the Missouri Botanical Garden 71:522–550.

———. 1995. Dispersed angiosperm cuticles: their history, preparation, and application to the rise of angiosperms in Cretaceous and Paleocene coals, southern western interior of North America. International Journal of Coal Geology 28:161–227.

Upchurch, G. R., and D. L. Dilcher. 1990. Cenomanian angiosperm leaf megafossils, Dakota Formation, Rose Creek locality, Jefferson County, southeastern Nebraska. U.S. Geological Survey Bulletin 1915:1–55.

Upchurch, G. R., and J. A. Doyle. 1981. Paleoecology of the conifers *Frenelopsis* and *Pseudofrenelopsis* (Cheirolepidiaceae) from the Cretaceous Potomac Group of Maryland and Virginia. Pp. 167–202 *in* R. C. Romans, ed. Geobotany II. Plenum, New York.

Upchurch, G. R., and J. A. Wolfe. 1987. Mid-Cretaceous to Early Tertiary vegetation and climate: evidence from fossil leaves and woods. Pp. 75–105 *in* E. M. Friis, W. G. Chaloner, and P. R. Crane, eds. The origins of angiosperms and their biological consequences. Cambridge University Press, Cambridge.

Van de Water, P. K., S. W. Leavitt, and J. L. Betancourt. 1994. Trends in stomatal density and $^{13}C/^{12}C$ ratios of *Pinus flexilis* needles during last glacial-interglacial cycle. Science 264:239–243.

Verdcourt, B. 1986. Chloranthaceae. Flora Malesiana Series I 10:123–144.

Vogelmann, T. C., J. N. Nishio, and W. K. Smith. 1996. Leaves and light capture: light propagation and gradients of carbon fixation within leaves. Trends in Plant Science 1:65–70.

Volkheimer, W., and A. Salas. 1975. Die älteste Angiospermen-Palynoflora Argentiniens von der Typuslokalität der unterkretazischen Huitrín-Folge des Neuquén-Beckens. Mikrofloristische Assoziation und biostratigraphische Bedeutung. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 1975:424–436.

Walker, J. W., and A. G. Walker. 1984. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. Annals of the Missouri Botanical Garden 71: 464–521.

Wells, P. V. 1969. The relation between mode of reproduction and extent of species in woody genera of the California chaparral. Evolution 23:264–267.

Wilf, P., S. L. Wing, D. R. Greenwood, and C. L. Greenwood. 1998. Using fossil leaves as paleoprecipitation indicators: an Eocene example. Geology 26:203–206.

Williamson, P. S., and E. L. Schneider. 1993. Cabombaceae. Pp. 157–161 *in* K. Kubitzki, ed. The families and genera of vascular plants. Springer, New York.

Williamson, P. S., E. Schneider, and L. Malins. 1989. Tuber and leaf structure of *Ondinea purpurea* Den Hartog (Nymphaeaceae). Western Australian Naturalist 18:52–61.

Wing, S. L., and L. D. Boucher. 1998. Ecological aspects of the Cretaceous flowering plant radiation. Annual Review of Earth and Planetary Sciences 26:379–421.

Wing, S. L., and W. A. DiMichele. 1992. Ecological characterization of plants. Pp. 140–180 *in* A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing, eds. Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals. University of Chicago Press, Chicago.

Wing, S. L., and B. H. Tiffney. 1987. The reciprocal interaction of angiosperm evolution and tetrapod herbivory. Review of Palaeobotany and Palynology 50:179–210.

Wolfe, J. A. 1993. A method of obtaining climatic parameters from leaf assemblages. U.S. Geological Survey Bulletin 2040: 1–71.

Wolfe, J. A., J. A. Doyle, and V. M. Page. 1975. The bases of angiosperm phylogeny: paleobotany. Annals of the Missouri Botanical Garden 62:801–824.

Zanis, M. J., D. E. Soltis, P. S. Solits, S. Mathews, and M. J. Donoghue. 2002. The root of the angiosperms revisited. Proceedings of the National Academy of Sciences USA 99:6848–6853.

Ziegler, A. M., A. L. Raymond, T. C. Gierlowski, M. A. Howell, D. B. Rowley, and A. L. Lottes. 1987. Coal, climate, and terrestrial productivity: the present and Early Cretaceous compared. Pp. 25–49 *in* A. C. Scott, ed. Coal and coal-bearing strata: recent advances. Geological Society, London.

Appendix 1

Study Sites and Species Included in the Study

Amborellales

1. *Amborella*, *A. trichopoda* Baillon., just below the summit of Massif Aoupinié, 800–1000 m, Province Nord, New Caledonia, second population on Plateau de Dogny, 650–750 m, Province Sud, New Caledonia.

Austrobaileyales

1. *Austrobaileya*, *A. scandens* C. T. White, at the base of Mt. Bartle Frere, 650 m, Queensland, Australia.

2. *Kadsura*, *K. coccinea* (Lemaire) A. C. Smith, west of Sok Kwu Wan, Lamma Island, Hong Kong, second population at the home of Mr. Liu Shu-Zhian, riverside, Xinning Co., Hunan, China; *K. heteroclita* (Roxburgh) Craib, 1100 m, Luohangdong, Ziyunshan, Forestry Park, Xinning Co. Hunan, China; *K. japonica* (L.) Dunal, collected in South Korea, grown in a common garden, Berkeley, California, U.S.A.; *K. longipenduculata* Finet & Gagnepain, 1100 m, Luohangdong, Ziyunshan, Forestry Park, Xinning Co. Hunan, China; *K. oblongifolia* Merrill, 1000 m, Mt. Dialoushan, Hainan Dao, China.

3. *Illicium*, *I. angustisepalum* A. C. Smith, Sunset Peak, 460 m, Lantau Island, Hong Kong; *I. anisatum* L., collected from Japan, grown in a common garden, Lee Co., Auburn, Alabama, U.S.A.; *I. dunnianum* Tutch. Wu Kau Tang, New Territories, Hong Kong, *I. floridanum* Ellis, Highway 169, toward Phenix City, Lee Co., Alabama, U.S.A., second population located along Apalachicola River, near Bristol, Liberty Co., Florida, U.S.A.; *I. henryi* Diels, collected from China, grown in a common garden, Lee Co., Auburn, Alabama, U.S.A.; *I. lanceolatum* A. C. Smith, Fanshuijian, Shuhuanshan, Xinning Co., Hunan, China, a second population at 750 m, Bajiaozhai, Nangshan, Xinning Co., Hunan, China; *I. majus* Hook.f. & Thoms., 850 m, Luohandong, Ziyushan, Forestry Park, Xinning Co., Hunan, China; *I. mexicanum* A. C. Smith, collected from Veracruz, Mexico, grown in a common garden, Lee Co., Auburn, Alabama, U.S.A.; *I. micranthum* Dunn, Ma On Shan 450 m, Hong Kong; Lizhishan Village, Xinning Co., Hunan, China; two km down from home of Mr. Liu Shu-Zhian, riverside, Xinning Co., Hunan, China; *I. oligodandrum* Merril & Chun (1100 m, ridge top forest, Mt. Dialoushan, Hainan Dao, China; *I. parviflorum* Michx. Ex Vent., Alexander Springs, Lake Co., near Ocala, Florida, U.S.A.; *I. simonsii* Maxim, collected from Sichuan, China, grown in the UC Botanic Garden, Berkeley, California, U.S.A.; *I. ternstroemioides*, A. C. Smith, 1100 m, ridge-top forest, Mt. Dialoushan, Hainan Dao, China.

4. *Schisandra*, *S. arisanensis* subspecies *viridis* (A. C. Smith) R. M. K. Saunders, Lizhishan Village, Xinning Co., Hunan, China; *S. bicolor* W.-C. Cheng 1200 m, Luohangdong, Ziyunshan, Forestry Park, Xinning Co. Hunan, China; *S. chinensis* (Turcz.) Baill. collected from South Korea, grown in a common garden, Berkeley, California, U.S.A.; *S. glabra* (Brickell) Rehder Crowley's Ridge, Three Rivers State Park, Whynne, Arkansas; property of Mr. Dan S. Miller, Tallahassee, Florida; plants of both populations collected and grown in a common garden, Lee Co. Auburn, Alabama, U.S.A.; *S. grandiflora* (Wallich) Hooker f. & Thomson collected in China, grown in a common garden, Berkeley, California, U.S.A.; *S. henryi* Clarke Luohangdong, Ziyunshan, Forestry Park, Xinning Co. Hunan, China; *S. lancifolia* (Rehder & E. H. Wilson) A. C. Smith collected in China, grown in a common garden, Berkeley, California, U.S.A.; *S. propinqua* (Wallich) Baillon grown in a common garden, Berkeley, California, U.S.A.; *S. repanda* (Siebold & Zuccarini) Radlkofer collected in Japan, grown in a common garden, Berkeley, California, U.S.A.; *S. sphenanthera* Rehder & E. H. Wilson 800 m, Sazijiang, Ziyunshan Forestry Farm, Xinning Co., Hunan, China.

5. *Trimenia*, *T. moorei* (Oliv. in Bth.) Philipson Stockyard Creek, near Armidale, New South Wales, Australia; *T. neocaledonica* Baker below the summit of Massif Aoupinié, near village of Goapin, Province Sud, New Caledonia; *T. papuana*, 2300 m, Mt. Gumi, Morobe Province, Papua New Guinea; *T. weinmanniifolia* Seeman summit of Des Vouex Peak, 990 m, Bouma village, Taveuni, Fiji.

Chloranthaceae

1. *Ascarina*, *A. lucida* Hook.f., Saltwater Forest, 25 m, near Hokitika, New Zealand; *A. phillipensis*, 2200 m, Kuper Range, Morobe Province, Papua New Guinea; *A. polystachya* J. R. & Forester, Mt. Marau, 780 m, Tahiti, French Polynesia; *A. rubricaulis* Solms-Laub., Mt. Dzumac, 990 m, Province Sud, New Caledonia; *A. solmsiana* Schlechter, below the summit of Mt. Dzumac, 980 m, Province Sud, New Caledonia; *A. swamyana* A. C. Smith, below Des Vouex Peak, 1000 m, Bouma Village, Tavenui, Fiji.

2. *Chloranthus*, *C. fortunei* 350 m, Sankoudu, Shuichaoyuan, Jinshizhen, Xinning Co., Hunan, China; *C. henryi* 1100 m, Luohandong, Ziyushan, Forestry Park, Xinning Co., Hunan, China; *C. japonicus* Siebold collected in China, raised in a common garden at UC Berkeley, California, U.S.A.; *C. serratus* Roem & Schlt. 90 m, New Territories, Hong Kong; 450 m, Sankoudu, Shuichaoyuan, Jinshizhen, Xinning Co., China; *C. spicatus* Pei native to China, greenhouse cultivated, UC Berkeley, California, U.S.A.; *C. sessilifolius* Pei 700–800 m, Fanshuijianm Shunhungshan, Forestry Park, Xinning Co., Hunan, China.

3. *Hedyosmum*, *H. bonplandianum* Humboldt, Bonpland & Kunth 1450 m, Estacion Cacao, Volcan Cacao, Guancaste, Costa Rica; *H. costaricense* Burger 1300 m, Río Grande de Orosí, Cartago, Costa Rica; *H. goudotianum* var. *goudotianum* Solms-Laubach 2500 m, 7 mi. W of Ojo del Agua, Cerro de la Muerte, Cordillera de Talamanca, Cartago, Costa Rica; *H. orientale* Merrill & Chun 1150 m, Mt. Dialoushan, Hainan Dao, China; *H. mexicanum* Cordemoy 2500 m, along the Pan American Highway, Cordillera de Talamanca, Cartago, Costa Rica.

4. *Sarcandra*, *S. glabra* (Thunb.) Nakai Victoria Peak 350 m, Hong Kong; 450 m, Ma On Shan, Hong Kong; Sunset Peak, 640 m, Lantau Island, Hong Kong; plants collected from Japan, raised in a common-garden at UC Berkeley, California, U.S.A.; *S. hainanensis* (Pei) Swamy & Bailey 1000 m, Mt. Dialoushan, Hainan Dao, China.

Nymphaeales

1. *Brasenia*, *Brasenia schreberi* J. Gmelin Lake Audrain, Dorado Co., California, U.S.A.

2. *Cabomba*, *C. caroliniana* Gray, collected from Texas, grown in an experimental aquarium, Berkeley, California, U.S.A.

3. *Nuphar*, *Nuphar lutea* (L.) Sibth. & Sm. subsp. *polysepala* (Engelm.) E. Beal Lily Pad Lake, Marin Co., California, U.S.A.

4. *Nymphaea*, *N. odorata* Aiton Tom Pond, Harvard Forest, Petersham, Massachusetts, U.S.A.

Appendix 2

Data Sources Used for Phylogenetic Character-State Reconstruction

Character	Sources
Seeds	*Hedyosmum* Todzia (1988); *Illicium* Roberts and Haynes (1983); *Kadsura* Saunders (1998); *Schisandra* Saunders (2000)
Seedling habitats	*Chloranthus* Luo and Li (1999); *Ondinea* Williamson et al. 1989; *Nuphar* Smits et al. (1990); Barrat-Segretain (1996); *Trimenia* Philipson (1986)
Leaf anatomy	*Amborella* Metcalfe (1987); *Ascarina* Metcalfe (1987), Todzia (1988); *Austrobaileya* Feild et al. (2003a); *Barclaya* E. L. Schneider personal communication 2002; *Brasenia* and *Cabomba* Williamson and Schneider (1993); *Chloranthus* and *Hedyosmum* Todzia (1988); *Euryale*, *Nuphar*, *Nymphaea*, and *Ondinea* Sculthorpe (1967), Williamson et al. (1989), Schneider and Williamson (1993); *Sarcandra* Swamy and Bailey (1950); *Trimenia* Rodenburg (1971)
Growth forms	*Amborella* Feild et al. (2001); *Ascarina* Smith (1976), Blanc (1986), Verdcourt (1986); *Austrobaileya* Feild et al. (2003a); *Barclaya* Schneider and Carlquist (1995); *Brasenia* and *Cabomba* Williamson and Schneider (1993); *Chloranthus* Verdcourt (1986), Carlquist (1992a), Luo and Li (1999), Kong et al. (2002); *Hedyosmum* Todzia (1988), Carlquist (1992b); *Illicium* Smith (1947), Roberts and Haynes (1983), Thien et al. (1983); *Kadsura* Smith (1947), Saunders (1998); *Euryale*, *Nuphar*, *Nymphaea*, *Ondinea*, and *Victoria* Williamson et al. (1989), Schneider and Williamson (1993), Williamson and Schneider (1993), Les et al. (1999); *Sarcandra* Swamy and Bailey (1950), Verdcourt (1986), Carlquist (1987); *Schisandra* Smith (1947), Stone (1968), Saunders (2000); *Trimenia* Rodenburg (1971), Philipson (1986)

Appendix 3

Characters and character states (discrete characters all unordered) used in phylogenetic character reconstruction analyses: 1. *Maximum leaf photosynthetic rate* (ETR_{max}, μmol electrons m^{-2} s^{-1}); 2. *Light-saturation point* ($PPFD_{sat}$, μmol m^{-2} s^{-1}); 3. *Seed size* (SV, mm^3); 4. *Leaf mesophyll* (0) spongy parenchyma only, (1) single-layered palisade parenchyma, (2) multiple-layered palisade parenchyma; 5. *Seedling establishment habitat* (0) shady, stable, and aquatic, (1) shady, disturbed, (2) sunny, disturbed; 6. *Growth habit* (0) tree or shrub, (1) twining woody vine, (2) herbs with some secondary growth, (3) herbs lacking secondary growth. * denotes that the phylogenetic position is uncertain.

	Character					
Species	1 ETR_{max}	2 $PPFD_{sat}$	3 SV	4 Mesophyll	5 Seeding habitat	6 Growth habit
Amborella trichopoda	87 ± 11	466 ± 48	3.46	0	1	0
Ascarina coursii	?	?	?	0	2	0
Ascarina diffusa	?	?	?	0	2	0
Ascarina lucida	92 ± 23	598 ± 86	0.33	0	2	0
Ascarina rubricaulis	133 ± 24	670 ± 57	0.26	0	2	0
Ascarina philippinensis	?	?	0.99	0	1	0
*Ascarina polystachya**	144 ± 13	535 ± 29	0.24	0	2	0
Ascarina solmsiana	45 ± 4	234 ± 9	0.65	0	1	0
Ascarina swamyana	77 ± 8	320 ± 15	0.95	0	1	0
Austrobaileya scandens	48 ± 8	290 ± 5	73.20	0	1	1
Barclaya longifolia	?	?	?	1	0	3
Barclaya rotundifolia	?	?	?	2	1	3
Brasenia schreberi	135 ± 8	585 ± 13	2.51	2	0	3
Cabomba caroliniana	50 ± 5	400 ± 10	1.03	1	0	3
Chloranthus angustifolius	?	?	?	0	1	2
Chloranthus erectus	?	?	2.00	0	1	0
Chloranthus fortunei	72 ± 13	389 ± 14	0.88	0	1	2
Chloranthus henryi	46 ± 1	347 ± 2	1.22	0	1	2
Chloranthus japonicus	66 ± 12	374 ± 5	1.52	0	1	2
Chloranthus nervosus	?	?	?	0	1	2
Chloranthus oldhamii	?	?	?	0	1	2
Chloranthus serratus	54 ± 7	309 ± 59	0.76	0	1	2
Chloranthus spicatus	48 ± 8	395 ± 34	2.01	0	1	0
Chloranthus sessilifolius	49 ± 5	284 ± 10	1.94	0	1	2
‘‘Core Angiosperms’’	?	?	?	1	?	?
Euryale ferox	?	?	63.14	2	0	3
Hedyosmum arborescens	?	?	?	0	2	0
Hedyosmum bonplandianum	150 ± 22	600 ± 12	1.68	0	2	0
Hedyosmum brasiliense	?	?	1.02	0	2	0

Appendix 3. Continued.

*Hedyosmum costaricense**	102 ± 16	500 ± 14	?	0	2	0
*Hedyosmum goudotianum**	141 ± 11	570 ± 15	?	0	2	0
*Hedyosmum mexicanum**	134 ± 9	550 ± 14	0.84	0	2	0
Hedyosmum nutans	?	?	0.56	0	2	0
Hedyosmum orientale	80 ± 9	490 ± 12	?	0	2	0
Illicium angustisepalum	72 ± 7	405 ± 21	?	1	1	0
Illicium anisatum	79 ± 9	337 ± 25	12.19	1	1	0
Illicium dunnianum	100 ± 10	495 ± 10	?	1	1	0
Illicium floridanum	101 ± 6	501 ± 19	5.94	1	1	0
Illicium henryi	115 ± 16	526 ± 21	4.01	1	1	0
Illicium lanceolatum	99 ± 16	490 ± 12	?	1	1	0
Illicium majus	68 ± 15	358 ± 20	?	1	1	0
*Illicium mexicanum**	100 ± 10	495 ± 12	?	1	1	0
Illicium verum	110 ± 8	488 ± 13	7.88	1	1	0
Kadsura coccinea	121 ± 9	608 ± 53	64.58	0	2	1
Kadsura heteroclita	59 ± 1	303 ± 37	8.91	1	1	1
Kadsura japonica	77 ± 11	400 ± 35	4.24	1	?	1
Illicium micranthum	67 ± 10	409 ± 17	?	1	1	0
*Illicium oligodandrum**	77 ± 9	393 ± 15	?	1	1	0
Illicium parviflorum	125 ± 11	525 ± 13	7.84	1	1	0
*Illicium simonsii**	87 ± 11	460 ± 15	?	1	1	0
*Illicium ternstroemioides**	100 ± 9	450 ± 28	?	1	1	0
Kadsura longipedunculata	53 ± 27	389 ± 44	2.82	1	2	1
Kadsura oblongifolia	45 ± 8	290 ± 48	2.84	0	1	1
Nuphar lutea ssp. *polysepala*	225 ± 15	1400 ± 20	2.02	2	0	3
Nymphaea odorata	78 ± 5	425 ± 34	5.61	2	0	3
Ondinea purpurea	?	?	0.71	2	0	3
Sarcandra glabra	40 ± 5	200 ± 4	1.11	0	1	0
Sarcandra hainanensis	46 ± 8	282 ± 21	1.12	0	1	0
Schisandra arisanensis	111 ± 14	575 ± 53	5.75	?	2	1
*Schisandra bicolor**	61 ± 2	325 ± 5	6.42	?	0	1
Schisandra chinensis	115 ± 13	525 ± 28	6.63	1	2	1
Schisandra glabra	69 ± 8	325 ± 33	6.57	0	1	1
Schisandra grandiflora	90 ± 11	477 ± 8	4.41	0	2	1
Schisandra henryi	106 ± 13	536 ± 61	2.47	1	2	1
*Schisandra lancifolia**	105 ± 11	520 ± 22	18.65	?	2	1
Schisandra propinqua	89 ± 11	480 ± 8	4.50	0	1	1
*Schisandra repanda**	56 ± 11	320 ± 8	12.06	?	2	1
Schisandra sphenanthera	110 ± 26	560 ± 103	4.92	1	2	1
*Trimenia macurura**	?	?	?	0	1	1
*Trimenia moorei**	87 ± 11	500 ± 48	1.52	0	2	1
*Trimenia neocaledonica**	78 ± 12	470 ± 25	5.47	0	1	0
*Trimenia papuana**	?	?	4.13	0	2	0
*Trimenia weinmanniifolia**	113 ± 11	510 ± 48	1.42	0	2	0
Victoria amazonica	?	?	?	2	0	3

Appendix 4

Field Analysis of Photosynthetic Performance Using Chlorophyll Fluorescence Emission

We chose this measure of photosynthesis because many field sites were exceedingly wet and remote, making standard leaf gas-exchange flux measurements impossible. Maximum leaf photosynthetic rate and the point at which photosynthesis reaches light saturation were calculated from chlorophyll (Chl) *a* fluorescence data. These calculations exploit the positive relationship between PS II efficiency and increasing photosynthetic photon flux density (PPFD, μmol photons $m^{-2}\,s^{-1}$), termed a ''rapid light response curve'' (Bilger et al. 1995; Rascher et al. 2000). Chl *a* fluorescence provides information on the rate at which light energy is transferred to photosystem (PS) II, a portion of the biochemical mechanism by which plants generate the reducing power (NADPH) needed to reduce carbon dioxide in the photosynthetic dark reactions (Krause and Weis 1991). PS II efficiency (ϕ_{PSII}) expresses the number of active PS II reaction centers and the efficiency with which these centers transduce light to chemical energy (Genty et al. 1989). ϕ_{PSII} was calculated as:

$$\phi_{PSII} = (F_m{}' - F)/F_m{}' \tag{1}$$

F is the steady-state fluorescence emission of the leaf while photosynthesizing, and $F_m{}'$ is the maximum light-adapted fluorescence of the leaf when a saturating pulse (duration = 0.8 s, intensity = 4500 μmol $m^{-2}\,s^{-1}$) is superimposed on the prevailing light to momentarily close all active PS II reaction centers (Genty et al. 1989).

ϕ_{PSII} was determined at eight light intensities, from 2% to 100% full sunlight (i.e., 20–2000 μmol $m^{-2}\,s^{-1}$), taking measurements from lowest to highest light intensity. The leaf was illuminated at each intensity until *F* values were stable at least 15 s, which required 30–90 s, and a saturating pulse was then applied. Although ϕ_{PSII} light response measurements under short illumination times are likely to be quasi–steady state, Rascher et al. (2000) demonstrated when leaves are fully photosynthetically induced, rapid light response curves are identical those produced by longer illumination times. This result was confirmed for greenhouse-raised plants of *Austrobaileya scandens*, *Chloranthus spicatus*, *Illicium floridanum*, *Illicium henryi*, *Illicium parviflorum*, *Kadsura japonica*, *Sarcandra glabra*, and *Schisandra lancifolia* (Feild unpublished data 2001). Consequently, care was taken that leaves in the field were exposed to morning light for at least one to two hours to allow full induction of photosynthesis and stomatal opening (Pearcy 1990). Measurements were made between 1030 and 1230 h to avoid time-dependent effects on photosynthetic performance (Rascher et al. 2000). Mean leaf temperatures averaged 21°C (± 2°C).

Estimates of ϕ_{PSII} were used for calculating the apparent rate of photosynthetic electron transport (ETR). ETR expresses the relative rate at which electrons move through PS II, and is generally close to the rate at which $NADP^+$ is reduced and made available for carbon fixation (Edwards and Baker 1993; Bilger et al. 1995; Brodribb and Hill 1997). ETR (μmol electrons $m^{-2}\,s^{-1}$) was calculated as:

$$\mathrm{ETR} = (\phi_{PSII}) \times (\mathrm{PPFD}) \times (0.5) \times \alpha \qquad (2)$$

ϕ_{PSII} is calculated in equation (1). Photosynthetic photon flux density (PPFD) is the incident light intensity (μmol $m^{-2}\,s^{-1}$) and α is percent leaf light absorbance. The constant 0.5 accounts for the fact that absorbed light is evenly distributed between PSII and PSI. Measurements of PPFD (in the waveband from 380 to 710 nm) were made near the leaf surface by the microquantum sensor of the Mini-PAM, calibrated against a Li-190 light sensor (Li-COR, Lincoln, Nebraska). PPFD values were corrected for the 2 mm difference between the distance of the photodiode and leaf plane as described by Rascher et al. (2000). The internal halogen lamp of the Mini-PAM provided light, which was directed to the leaf via a fiber optic bundle. The average value of $\alpha = 0.84$ for green leaves (Björkman and Demmig 1987) was used here. This value is a good approximation because all leaves measured were healthy and of similar color. Note, however, that ETR values will not be precise because leaf absorbance differences between species were not measured. Polynomial regression was used to fit the light response data from each species, and saturating PPFD (PPFD_{sat}) and maximum ETR (at PPFD_{sat}) were read from these curves as described by Brodribb and Hill (1997). PPFD_{sat} was taken as the light intensity at the peak of the ETR versus PPFD response curve.

Some sampled species occurred in a variety of light environments. For example, *Hedyosmum bonplandianum* (Chloranthaceae) occurred in open habitats on cloud forest land slips (about 30–50% full sun, defined as ~2000 μmol photons $m^{-2}\,s^{-1}$ [Chazdon et al. 1996]) under persistent cloud cover, semi-shaded forest light-gaps (10–25% full sun), and in forest understory sites (<2% full sun). For such species, five replicate light curves were taken from five individuals from each of the three light environments. Curves were averaged within each environment. The average curve yielding the greatest mean values of ETR_{max} and PPFD_{sat} was then used for interspecific comparisons. For water lilies, photosynthetic measurements were restricted to species with floating leaves (e.g., *Brasenia*, *Cabomba*, *Nuphar*, *Nymphaea*) because leaf photosynthetic performance in submersed and aerial environments is not commensurate (Niklas 1997). Light environment for each species was characterized with local measurements of PPFD taken with a photodiode-based meter (Li-190, Li-COR) held horizontally above leaves of the same branches sampled for anatomical and physiological studies. Measurements were taken from 1000 and 1230 h on representative clear periods and cloudy days. Leaves from branches with maximum photosynthetic capacity were used for assessment of anatomical/morphological leaf characters.