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Angiosperms Helped Put the Rain in the Rainforests: The Impact of Plant Physiological Evolution on Tropical Biodiversity 1

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ANGIOSPERMS HELPED PUT THE RAIN IN THE RAINFORESTS: THE IMPACT OF PLANT PHYSIOLOGICAL EVOLUTION ON TROPICAL BIODIVERSITY[1]

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ABSTRACT

The recycling of transpired water is well known to be an important source of rainfall, particularly in the tropics, and angiosperms have transpiration capacities higher than any other plants throughout evolutionary history. Thus, the evolution and rise to ecological dominance of flowering plants are proposed to have strongly altered climate. Transpiration capacity is closely correlated with leaf vein density, and the average vein density of angiosperm leaves is four times greater than that of all other plants, living or extinct. A rapid transition to high vein densities occurred separately in three or more flowering plant lineages about 100 million years ago. Climate modeling of the impact of this physiological revolution indicates that the tropics would be hotter, drier, and more seasonal in the absence of the angiosperms, and the overall area of tropical rainforest would decline substantially. Because angiosperm diversity is influenced by rainforest area and by precipitation abundance and evenness, the high diversity of angiosperms is partially a product of a positive feedback loop with the climate modifications initiated by the angiosperms themselves. Lineage diversifications among vertebrate and invertebrate animals and nonangiospermous plants in the wake of the angiosperm radiation may be tied to the unprecedented impact of angiosperms on climate.

RESUMEN

El reciclaje de agua transpirada es bien conocida por ser una importante fuente de precipitaciones, especialmente en el trópico, y los angiospermas tienen la capacidad de transpiración más alta de la historia evolutiva. Por consiguiente, se propone que la evolución y el ascenso de angiospermas a una posición de dominancia ecológica ha alterado fuertemente el clima. La capacidad de transpiración está estrechamente relacionada con la densidad vascular de las hojas y la densidad vascular media de las hojas angiospérmicas es cuatro veces mayor que del resto de plantas, vivas o extinguidas. Hace unos 100 millones de años tuvo lugar, de forma separada, una rápida transición hacia altas densidades vasculares en tres o más linajes de angiospermas. La modelización climática del impacto de esta revolución fisiológica indica que los trópicos serían más calientes, secos, y más estacionales sin los angiospermas, con una consiguiente reducción sustancial de las áreas de selva lluviosa. La gran diversidad de angiospermas es, parcialmente, un producto de las modificaciones climáticas iniciadas por los propios angiospermas, debido a que la diversidad de angiospermas es facilitada por el área de selva lluviosa y por la abundancia y regularidad de precipitaciones. La diversificación de un número significativo de linajes entre animales vertebrados e invertebrados y plantas no angiospérmicas en pos de la radiación angiospérmica podría ser el resultado del impacto sin precedentes de los angiospermas sobre el clima.

Key words: Climate, hydraulics, leaf, precipitation, transpiration, venation.

The geographic extent of the moist tropics has varied considerably (Ziegler et al., 2003) over the approximately 380 million years since vascular plants formed the first forests (Algeo & Scheckler, 1998; Stein et al., 2007). During the Carboniferous, vast areas of tropical Euramerica were covered with wet, peat-forming forests, although they were subject to rapid contractions and expansions with replacement by more seasonally dry vegetation in association with millennial-scale glacial cycling (Montañez et al., 2007; Falcon-Lang et al., 2009). With the transition to a hothouse climatic regime during the Permian, seasonally dry conditions spread throughout the tropics to produce more savannah-like vegetation, and everwet conditions were limited to islands and narrow coastal areas of continents provided with significant maritime precipitation (Ziegler et al., 2003). Predominance of rainfall seasonality and

tropical aridity persisted through most of the Mesozoic until the expansion of high precipitation conditions beginning in the early Late Cretaceous and reaching a maximum extent in the Eocene (Parrish et al., 1982; Parrish, 1987; Upchurch & Wolfe, 1987; Vakhrameev, 1991; Morley, 2000; Beerling & Woodward, 2001; Ziegler et al., 2003; Ufnar et al., 2008).

The early diversification of angiosperms accompanied the expansion of tropical wet climates during the Cretaceous and Paleogene (Burnham & Johnson, 2004; Crepet, 2008; Feild et al., 2009). However, the exact timing of the origin of angiosperm-dominated tropical rainforests of modern aspect is debated (Upchurch & Wolfe, 1987; Morley, 2000; Burnham & Johnson, 2004; Davis et al., 2005; Wing et al., 2009). Evidence for megathermal angiosperm rainforests in the Paleocene is unambiguous at both tropical and temperate latitudes (Johnson & Ellis, 2002; Wing et al., 2009), but Cretaceous evidence is mixed. This problem persists, in part, because macrofossil records are extremely scarce in the modern tropics (Burnham & Johnson, 2004; Wing et al., 2009). Furthermore, interpretation can be ambiguous for the more frequently available evidence from microfossils, climate-sensitive sediments, geochemistry, climate modeling, and inference from living plants. However, climate-sensitive sediments and modeling support at least local persistence of environmental conditions compatible with growth of megathermal rainforests at tropical and/or temperate latitudes during the Cretaceous (Parrish et al., 1982; Barron & Washington, 1985; Parrish, 1987; Upchurch et al., 1999; Beerling & Woodward, 2001; Ziegler et al., 2003; Ufnar et al., 2008). Nonetheless, most paleobotanical macrofossil studies suggest that the establishment of angiosperm rainforests was delayed until the early Tertiary, based on the paucity of wood indicative of large angiosperm trees or of large seeds suggestive of closed-canopy environments in the Cretaceous (Tiffney, 1984; Wheeler & Baas, 1991; Wing & Boucher, 1998). This paleobotanical evidence is complicated by the leaf physiognomies of individual temperate-latitude localities suggesting warm, wet forests as early as the Cenomanian about 100 million years ago (Upchurch & Wolfe, 1987) and by recent arguments that large seed size is an advantage for germination in deep shade rather than a requirement (reviewed in Feild et al., 2004; Davis et al., 2005). Palynofloras indicate highly diverse tropical forests by the Eocene (Jaramillo et al., 2006), but palynological arguments for a Cretaceous origin of angiosperm tropical rainforests based on the first appearances of pollen from lineages that are now limited to that environment (reviewed Morley, 2000) have been questioned (reviewed in Wing et al., 2009). Molecular clock estimates for the antiquity of angiosperm lineages found in the shaded understory of modern tropical rainforests provide further support for a mid-Cretaceous origin (Davis et al., 2005), although concerns over molecular calibrations persist among paleontologists (Burnham & Johnson, 2004; Wing et al., 2009). On balance, there is no overwhelming positive evidence for angiosperm rainforests in the Cretaceous, but neither is there evidence for their complete absence. As discussed below, perhaps the strongest support for local development of warm, everwet conditions throughout the Cretaceous is that palynofloras do overwhelmingly support a tropical origin for angiosperms as a whole (Crane & Lidgard, 1989) and basal extant angiosperms are highly intolerant of drought (Sperry et al., 2007; Feild et al., 2009).

Tropical rainforests have the highest biodiversity of any ecosystem, housing more than half of all species, despite occupying less than 7% of Earth's surface (Bierregaard et al., 1992; Wilson, 1994). The niche specialization necessary for such high diversity is promoted by the high productivity of tropical rainforests, the dense stratification of their vegetation, and their coverage of a large and heterogeneous area (Grubb, 1977; Ricklefs, 1977, 2004; Leigh et al., 2004). The stability of rainforest climate then allows that potential for specialization to be reached, and specialist herbivores and pathogens further promote diversity by suppressing the emergence of dominant species (Janzen, 1970; Givnish, 1999). Alternatively, if trophically similar species are considered interchangeable and the differences between them neutral (Hubbell, 2001), then rainforest hyperdiversity would be tied more directly to their productivity and sheer abundance of individuals. The relative importance of each of these factors is widely debated, as is whether they promote tropical diversity through the creation of a cradle of high species origination rates or a museum of low extinction rates (Givnish, 1999; Hubbell, 2001; Condit et al., 2002; Leigh et al., 2004; Ricklefs, 2004; Zhou & Zhang, 2008). However, what all of these biological and ecological mechanisms share is a dependence on the underlying physical parameter of abundant and relatively aseasonal rainfall. Here, we will emphasize that, just as tropical climate has strongly influenced biotic evolution, the opposite is also true—evolution, of angiosperms in particular, has strongly influenced tropical climate.

THE EVOLUTION OF LEAF HYDRAULICS

THE SIGNIFICANCE OF LEAF VEIN DENSITY

As vascular plants absorb carbon dioxide (CO_2) from the atmosphere for photosynthesis, they lose water to the atmosphere through transpiration. If leaf

water is lost faster than it can be replaced by the vascular system, then leaf tissues desiccate. The development of a water deficit in the leaf triggers the closure of the stomatal pores through which leaf gas exchange occurs in order to limit further water loss and prevent tissue damage. Thus, photosynthetic carbon assimilation necessarily involves water loss, and a plant's ability to conduct photosynthesis is dependent on its ability to transport water to the stomata for transpirational loss (Davidoff & Hanks, 1989; Brodribb, 2009).

Replacing transpired water in leaves requires xylem to transport water efficiently from the soil to the sites of evaporation. Xylem allows mass flow of water through conduits composed of the walls of dead cells, avoiding the slower diffusion through living cells. However, leaf tissue retains a non-xylem hydraulic pathway from the ends of veins to the sites of evaporation, and this short pathway involving living tissue constitutes a major resistance to hydraulic flow. Indeed, a third or more of the total resistance from root to stem to leaf to atmosphere is concentrated in the last few centimeters of that transport pathway represented by the leaf (Sack & Holbrook, 2006; Brodribb et al., 2007). Thus, any anatomical change that decreases the transportation path length through the leaf mesophyll tissue will have a substantial impact on the hydraulic resistance of the entire plant.

The most direct way to shorten the distance between leaf xylem and stomata through the mesophyll is to increase the density of leaf veins. As a result, plants with higher leaf vein density should have higher assimilation and transpiration rates—an expectation that has been demonstrated across an ecologically and phylogenetically diverse array of vascular plants (Brodribb et al., 2007; Boyce et al., 2009; Brodribb & Feild, 2010; Fig. 1A).

In addition to the functional significance of leaf vein density, there is a practical application for the study of physiological evolution. Vein density is readily measurable from many leaf compression fossils, thereby allowing assessment of physiological traits that would otherwise be unavailable from fossil organisms. For example, assuming that fossil cycads had low assimilation rates to match the slow growth of extant cycads would be dangerous because the modern taxa have been marginalized by the ecological expansion of angiosperms. Hence, extinct cycads may have had a greater diversity of ecologies, growth habits, and growth rates (Wing & Sues, 1992). However, all leaf vein density measurements in fossil cycads have been equally as low as the extant forms, thereby providing a functional basis for the interpretation of low primary productivity throughout their evolutionary history (Boyce, 2008).

EVOLUTION OF LEAF VEIN DENSITY

Paleozoic origins and later history of nonangiosperms

Laminate leaves are common among euphyllophyte vascular plants, but are not all homologous (Galtier, 1981; Kenrick & Crane, 1997; Tomescu, 2008; Boyce, 2010). Leaf laminae evolved independently at least four times within the seed plants, archaeopterid progymnosperms, ferns, and horsetail-related sphenophylls, although the number could be significantly higher given the possibility of separate origins in ophioglossoid, marattioid, and leptosporangiate ferns and in minor fossil groups of enigmatic affinities, like the Noeggerathiales (Boyce & Knoll, 2002). Despite multiple origins, the densities of veins in early leaves are nearly uniform across these groups (Fig. 1B). The vein density of the first Devonian and Carboniferous leaf fossils averages between 2 and 3 mm mm^{-2} and rarely ranges beyond 1–4 mm mm^{-2} (leaf vein density is measured as the length of vein [mm] per area of leaf [mm²] [Boyce et al., 2009]).

The leaf vein density of nonangiosperms has remained extremely consistent, with the mean value for any time interval never reaching higher than the 2.8 mm mm^{-2} of the Pennsylvanian or lower than the 1.8 mm mm^{-2} of the modern world (Fig. 2). This uniformity is in itself remarkable given the extreme variations in climate regime, paleogeography, and atmospheric composition over the same time period. Finer phylogenetic and stratigraphic sampling is needed, but there are no obvious vein density changes to match the multiple transitions between icehouse and hothouse climates through earth history (Fig. 2), as might be expected from the presence of both high and low vein densities in a variety of modern climate regimes. The lack of a relationship between vein density and atmospheric CO_2 concentration (Uhl & Mosbrugger, 1999; Fig. 2) is more perplexing. CO_2 concentrations strongly influence assimilation rates, and a greater sensitivity to vein density variation has been predicted for low CO_2 regimes because of a greater dependence of photosynthetic rate on stomatal conductance (Brodribb & Feild, 2010). A CO_2 driver has been suggested for some vein density fluctuations at a fine stratigraphic scale (Retallack, 2005), but average vein density among nonangiosperms has remained remarkably flat through longer time scales even as CO_2 concentrations have fluctuated over an order of magnitude and stomatal densities have responded with fluctuations over almost three orders of magnitude (Fig. 2).

Angiosperms

Averaging near 2 mm mm^{-2} and almost never reaching above 6 mm mm^{-2}, the uniformity of vein
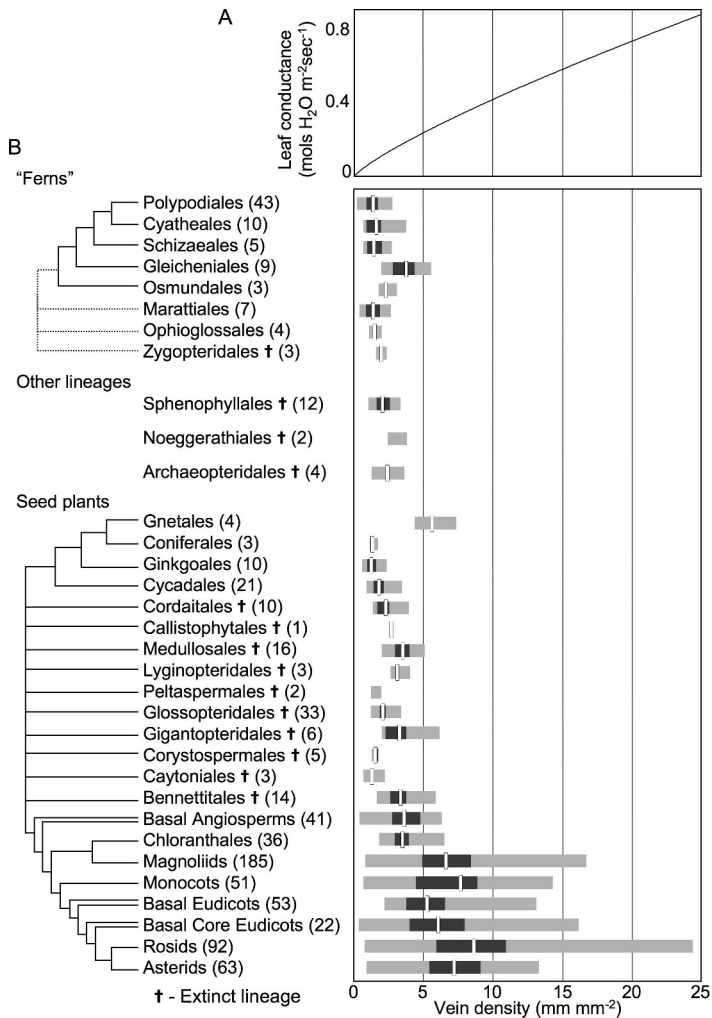
Figure 1. Leaf vein density and transpiration. —A. Empirically derived relationship between leaf vein density and maximum conductance of leaves to water vapor, which is equivalent to transpiration under standard atmospheric conditions (Boyce et al., 2009). —B. Distribution of leaf vein densities among seed plants, one or more independent evolutions among ferns, and in two or three additional independent lineages (affinities of the Noeggerathiales are equivocal). Bars represent full maximum to minimum ranges. Mean vein density (white line) and median 50% of values (darker shading) indicated where sampling was sufficient, with the parenthetical numbers for each lineage indicating the number of taxa sampled). Vein density values compiled from Boyce et al. (2009) and Brodribb and Feild (2010) with some supplementation (Retallack, 2005; McKown & Dengler, 2009).

density among nonangiosperms across 380 million years and multiple leaf originations would suggest a single hydraulic optimum for leaf construction upon which all early lineages converged and to which all later generations adhered. Such a conclusion would be reasonable based on all plant life as recent as the Early Cretaceous, but since then angiosperms have established a mean above 8 mm mm^{-2} and have reached densities higher than 24 mm mm^{-2} (Boyce et al., 2009).

High vein density is not a characteristic of the angiosperms as a whole (Fig. 1B). Lineages at the base of extant angiosperm phylogeny, including *Amborella* Baill., Nymphaeales, Austrobaileyales, and the common ancestor of the Chloranthales, magnoliids, and eudicots, possess vein densities that can be moderately high (4–5 mm mm^{-2}), but within the range of ferns and nonangiospermous seed plants (Boyce et al., 2009; Brodribb & Feild, 2010). High vein densities greater than 9 mm mm^{-2} appear to have been achieved by some derived magnoliids (e.g., *Actinodaphne* Nees at 15.2 mm mm^{-2}), monocots (e.g., *Hyparrhenia* Andersson ex E. Fourn. at 11.3 mm mm^{-2}), and eudicots (e.g., species of *Populus* L.
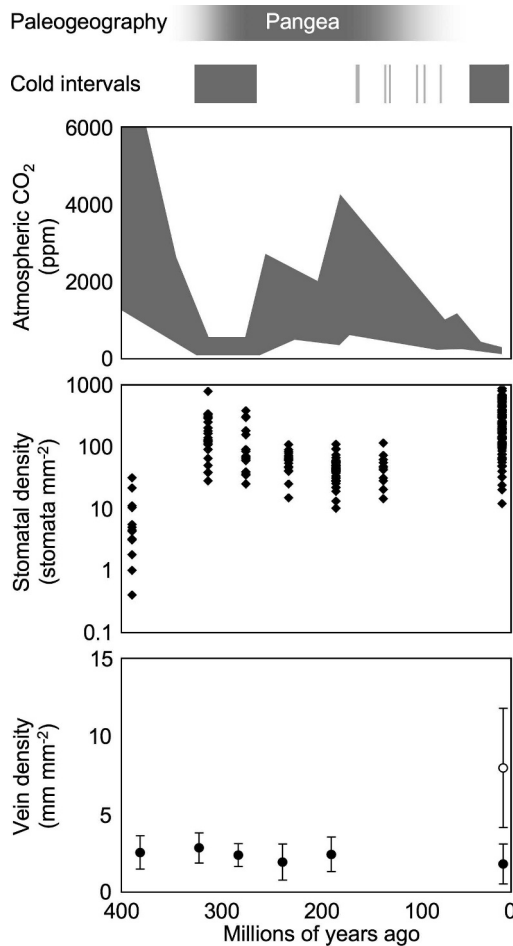
Figure 2. Mean leaf vein density through time among nonangiosperms (closed circles) and angiosperms (open circle) along with stomatal densities and extrinsic factors that could potentially influence leaf evolution and hydraulics, including paleogeography (Scotese, 2004), cold intervals (Royer et al., 2004), and the range of potential atmospheric CO_2 concentrations through time (Berner & Kothavala, 2001). Stomatal densities were compiled from the literature (Harms & Leisman, 1961; Pant & Verma, 1963; Ludlow & Wolf, 1975; Reihman & Schabilion, 1978; Batenburg, 1981; Tanner & Kapos, 1982; Sugden, 1985; Pigg, 1990; Rolleri et al., 1991; Knapp, 1993; Pigg & Taylor, 1993; McElwain & Chaloner, 1995; Arens, 1997; Beerling & Woodward, 1997; Edwards et al., 1998; McElwain et al., 1999; Chen et al., 2001; Liu & Yao, 2002; Hesselbo et al., 2003; Yao & Liu, 2004; Krings et al., 2005).

ranging from 9.0 to 23.3 mm mm^{-2}) independently (Boyce et al., 2009; Brodribb & Feild, 2010). These evolutionary transitions to high vein densities appear to have occurred around 100 million years ago (Brodribb & Feild, 2010), coinciding with the explosive radiation of the rosids (Wang et al., 2009), which possess many of the highest vein densities. Even among derived eudicots, angiosperm evolution

represents an increase in the upper bound of leaf vein densities, not a wholesale departure from low values (Fig. 1B). However, low values in the range of 1–3 mm mm^{-2} are found among derived angiosperms only in thick-leaved, drought-adapted succulents (e.g., *Crassula* L. at 0.4 mm mm^{-2} or *Phalaenopsis* Blume at 0.7 mm mm^{-2}; Noblin et al., 2008), presenting a radically different morphology than the thin-leaved ferns for which such values are also common.

IMPACT OF ANGIOSPERMS ON CLIMATE

The contribution of re-evaporated moisture, also termed "recycling," is important in feeding precipitation in forested regions (Salati et al., 1979; Eltahir & Bras, 1996). Recycled water moistens the atmospheric boundary layer—typically from the surface to a height of 1 km—and can decrease atmospheric stability (Fu et al., 1999), causing convective rainfall. Soil moisture status, which is a primary determinant of evapotranspiration rates in water-stressed terrestrial environments, has been studied as a possible indicator for forecasting precipitation. Summer precipitation has been shown to be sensitive to late spring to early summer soil moisture content from studies using a unique network of soil moisture measurements in Illinois, U.S.A. (Findell & Eltahir, 1997; D'Odorico & Porporato, 2004). Precipitation increases have also been observed in response to the increased evapotranspiration associated with crop irrigation (Stidd, 1975).

The changes in plant physiology heralded by greatly increased leaf vein density suggest that the radiation of angiosperms was accompanied by more than a doubling of photosynthetic capacity (Brodribb & Feild, 2010) and approximately a fourfold increase in transpirational capacity (Boyce et al., 2009) on a leaf area basis. The impact of these changes on the global carbon and hydrologic cycles is likely to have been profound. Because the recycling of rainfall through evapotranspiration can be an important contributor to precipitation, any increase in transpiration capacities that accompanied angiosperm evolution should strongly influence climate, particularly in the tropics and during the growing season at higher latitudes. Of course, the Intertropical Convergence Zone will always have produced a tropical belt of at least seasonally high precipitation, orographic rainfall can be significant on the windward side of mountain ranges, and proximity to large bodies of water can also feed precipitation. However, transpiration represents an important addition to these physical processes.

Because direct quantification of recycling requires the difficult task of distinguishing different water sources (Salati et al., 1979), climate models have long

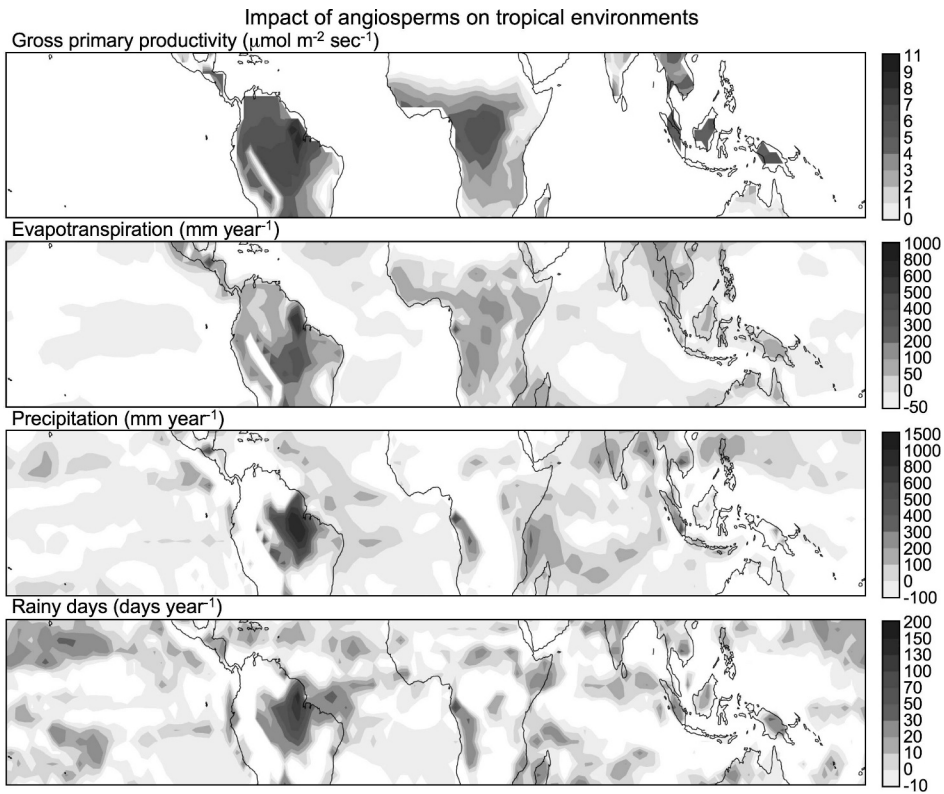Impact of angiosperms on tropical environments

Figure 3.   Climate modeling of the differences in a world with angiosperms relative to a world without them (Boyce & Lee, 2010; Lee & Boyce, in press). Absence of angiosperms was simulated by a 75% reduction in transpiration rates. All other factors were held as fixed at modern values, including sea surface temperatures, geography, and vegetative biomass. A rainy day is defined as one with at least 3 mm of precipitation.

been used to estimate the influence of land evapotranspiration on precipitation. These studies show that recycling is greater during the growing season (e.g., Koster et al., 1986; Lee, 2005) and that the observed precipitation response to soil moisture is indeed related to the atmospheric response to the added evapotranspiration (Findell & Eltahir, 2003). Regions where precipitation is dependent on soil-moisture status coincide with areas with a large recycling ratio (Koster et al., 2004; Dirmeyer et al., 2009). How important the evolution of angiosperm transpiration capacities might have been can be similarly constrained with climate modeling.

CASE STUDY OF THE MODERN WORLD

Although any influence of angiosperms on climate would have been first felt in the Cretaceous, modern climate is far better understood and provides the best system to try to isolate and study the effect of elevated angiosperm transpiration. In climate simulations coupling atmospheric and land models, biomass was held constant and the only change imposed on the

modern system was a drop of maximum transpiration rate by a factor of four (Boyce & Lee, 2010; Lee & Boyce, in press). In these simulations, the impact of angiosperm transpiration is large and widespread (Boyce & Lee, 2010; Fig. 3). The most dramatic effects are seen in the tropics, which are drier, hotter, and more seasonal in the absence of angiosperms. Although higher-latitude precipitation effects are dwarfed by the tropics in absolute terms, they can still be proportionally large (Boyce & Lee, 2010).

The influence of transpiration on climate is largest in South America (Boyce & Lee, 2010; Lee & Boyce, in press) where the projected loss in annual rainfall in the absence of angiosperms can be greater than 1500 mm per year. This decline involves both less precipitation every month of the year and greater seasonality, with the dry season extending 80 days longer over the eastern Amazon Basin. This is significant given the high sensitivity of rainforest trees and lianas to drought (van Nieuwstadt & Sheil, 2005; Nepstad et al., 2007; Phillips et al., 2009), with the greatest effects of transpiration seen in the transition periods between dry and wet seasons.

Together, these effects result in a reduction to one fifth in total everwet rainforest area without angiosperm transpiration, as defined as areas with 240 wet days or more per year (Boyce & Lee, 2010). Because evaporation entails the transfer of large amounts of energy from sensible to latent heat (Lee et al., 2005), angiosperm transpiration also exerts a strong cooling effect with temperatures seasonally up to 5°C warmer in their absence.

The lesser impact on precipitation seen in Southeast Asia and Malesia and in Africa (Fig. 3) highlights that elevated transpiration is an addition to a system that is still largely governed by physical parameters. Proximity to the sea ensures that precipitation remains abundant throughout much of Southeast Asia and Malesia regardless of transpiration rates. Conversely, unusually high topography keeps Africa drier and more seasonal and confines rainforest development to the west (Ziegler et al., 2003). These effects are all dependent on orogeny and continental configurations that are in constant flux—the East African Plateau, for example, did not exist 10 million years ago (Partridge, 1997). Thus, the larger influence of transpiration on climate exhibited in South America may well have been more widespread in the geologic past, including other areas of the tropics and perhaps extratropical latitudes during the warmer periods of the Cretaceous and Paleogene.

ANGIOSPERMS AND DEEP-TIME CLIMATE

How many leaves?

Vegetative biomass and leaf area were held constant in the above climate modeling in order to isolate the impact of changes in transpiration rate. Over the geological record, changes in transpiration rate per unit leaf area conceivably could be offset by changes in total leaf area. Such a possibility must be treated with particular caution because the leaf area index (LAI; total leaf surface area divided by the land surface area) can never be measured directly from fossils, and some living conifers can have an LAI three to four times that of typical angiosperms. However, several lines of evidence indicate that the compensation of increasing transpiration rates by decreasing leaf area is unlikely. First, conifer LAI also can be quite low and extremely high LAI values are found primarily in the Pinaceae (Oren et al., 2001; DeLucia et al., 2003; Fetene & Beck, 2004; Teske & Thistle, 2004), but the Pinaceae have never been an important element in the lowland tropics (Brenner, 1976; Rees et al., 2000; Brodribb & Feild, 2008). Second, the LAI of other plants aside from angiosperms and conifers is often quite low: the LAI of

Ginkgo L. is below the angiosperm average, and tree ferns, which are representative of a rosette architecture common in the geological past with groups such as cycads, medullosans, and Bennettitales, can approach LAI values as low as 1 (Harrington et al., 2001). Third, plants with high LAI values are found in open, often semi-arid environments because they require high levels of light, i.e., high LAI individuals tend to be found in low LAI landscapes. Given the high leaf area and deep shading already present in tropical rainforests (Clark et al., 2008), simply quadrupling the number of nonangiospermous leaves does not seem like a compelling mechanism to offset increased angiosperm transpiration rates. Thus, LAI values may have been somewhat higher or lower in a pre-angiosperm world, but they are unlikely to have been dramatically higher. Finally, because biomass is dependent on precipitation, a negative feedback loop can be expected in a world without angiosperms whereby the lack of elevated angiosperm transpiration rates results in less precipitation, which results in less biomass, which results in even less transpiration and precipitation. As a result, the overall impact of angiosperm transpiration may actually be larger than indicated by changes in vein density alone.

Angiosperm radiation and rainforests

If tropical rainforest angiosperms are both dependent on and partially responsible for the high rainfall of their environment, then how could modern angiosperm lowland tropical rainforests have become established? A possible solution lies with the long entertained (Axelrod, 1959), but since discarded (Doyle & Hickey, 1976), possibility that angiosperms originated in tropical cloud forest sites in coastal uplands (Feild et al., 2009). Early-diverging clades encompassing the first five or six major nodes of angiosperm phylogeny are extremely drought-intolerant and are characterized by a profound loss of xylem water transport ability at very modest water potentials (Sperry et al., 2007; Feild et al., 2009). These lineages are today largely confined either to low insolation, upland tropical cloud forests with high and daily precipitation or to freshwater aquatic zones (Feild & Arens, 2007). The high rainfall expected for orographic reasons on the windward side of mountain belts close to oceans during the Early Cretaceous continuation of Pangea fragmentation could have allowed for the initial viability of higher vein density and transpiration rates among early, drought-intolerant angiosperms. The potential for positive feedback between increasing vein density and rainfall then could have permitted a gradual expansion of angiosperms into environments that were increasingly

distant from maritime and orographic precipitation sources as transpiration-fed hydrological cycles were established.

Early Cenozoic warmth

At their Eocene apogee, warm high precipitation forests blanketed the tropics and extended past the subtropic desert belts well into the temperate zone (Morley, 2000). Although this expansion clearly related to the unusually warm conditions of the time period, previous warm periods in earth history resulted in the spread of conditions that were at least seasonally dry (Ziegler et al., 2003). Direct comparisons between the later and earlier hothouse climates of the Early Cenozoic versus the Permian and Triassic are difficult because the extreme size of the supercontinent Pangea promoted seasonality and aridity in its interior. However, Pangea fragmentation had already begun in the Early Cretaceous, and high sea levels also resulted in epeiric seas that would have further disrupted continental aridity (Ziegler et al., 2003; Ufnar et al., 2008). The widespread development of moist megathermal forests in the Early Cenozoic and their comparative lack in the Cretaceous may be attributable to the intervening spread of the climate-modifying potential of angiosperm ecological dominance. Simulations of the absence of angiosperms indicate a 50% reduction in precipitation in modern eastern North America (Boyce & Lee, 2010), and this impact would be considerably greater in warmer climates that would allow high transpiration in the temperate latitudes to continue through a year-round growing season (J.-E. Lee, unpublished).

Environmental perturbations

With angiosperm dominance, tropical forests are cooler, wetter, and less seasonal. As with modern tropical deforestation (Shukla et al., 1990; Eltahir & Bras, 1996; Laurance & Williamson, 2001), disruption of this strong environmental buffering provided by angiosperm ecosystems by destructive environmental events in the geologic past may have brought increased risks of amplified environmental response (Boyce & Lee, 2010). For example, the Cretaceous/Tertiary bolide impact is thought to have produced a variety of climate effects, including global heating from the initial impact shockwave, global cooling from the blocking of sunlight by aerosols and dust injected into the upper atmosphere, followed by further global warming from the release of gravitational energy as heat as the enormous quantity of fine particulates settled from the atmosphere (O'Keefe & Ahrens, 1989;

Gupta et al., 2001; Beerling et al., 2002; Schulte et al., 2010). In addition to these relatively immediate effects, the destruction of angiosperm tree canopies wherever their dominance had been already established in the Cretaceous would have resulted in heating and drying unique to those terrestrial environments because of the loss of angiosperm transpiration. If these climate changes slowed the reestablishment of angiosperm forests, this effect would have lasted at least decades to centuries, although such short timescales are difficult to resolve directly from the fossil record. The loss of forest canopies during earlier events that caused widespread disruption of terrestrial ecosystems but predated the angiosperms, such as the end-Permian (Looy et al., 1999) or Triassic/Jurassic extinctions (McElwain et al., 2009), would have resulted in much smaller climate effects because of the smaller transpiration capacities of the plants involved.

As a more complicated example, the Paleocene/Eocene Thermal Maximum (PETM) was a rapid global warming event lasting approximately 50,000 years in which sea temperatures increased by 5°C. Warming was triggered by the injection of greenhouse gases into the atmosphere from widely debated sources perhaps including the disassociation of methane hydrates from continental slope sediments (Katz et al., 1999; Zachos et al., 2003, 2005; Panchuk et al., 2008). In response, terrestrial plant populations migrated 1000 km or more to higher latitudes (Wing et al., 2005; Smith et al., 2007). Immediately before the PETM, angiosperm transpiration would have kept many terrestrial environments cooler than otherwise would be expected from oceanic forcing alone. If PETM-induced plant migrations involved wholesale destruction of forest canopies, then terrestrial temperature changes would have involved both the gain of abiotic heating from atmospheric changes and the loss of biotic cooling from transpiration. This cooling is seasonally as large as 5°C in the modern angiosperm-dominated world during the dry months when transpiration has the largest climatic effect (Boyce & Lee, 2010). Thus, the magnitude of temperature increases on land could have been significantly larger than in the oceans because the terrestrial temperature increases expected from the marine record would have been reached from a transpirationally depressed pre-PETM baseline temperature. However, if the PETM onset was slow enough to allow species migrations within a continuously existing canopy, then terrestrial temperature increases would be no more than expected from the marine record. Ocean temperatures as high as those of the PETM were also reached several million years later during the Eocene Thermal Optimum, but were reached gradually rather than as a discrete event,

giving ample time for gradual plant migrations in continuously existing forests. Thus, comparing terrestrial climate indicators from the PETM and later Eocene could constrain the rapidity of PETM onset and the extent of initial environmental degradation.

ECOLOGY AND EVOLUTION IN AN ANGIOSPERM-DOMINATED WORLD

TROPICAL DIVERSITY

While temperature increases can be a positive stimulus for diversity in colder climates, the greatest correlates of plant diversity within the tropics are overall precipitation abundance and the evenness of precipitation as measured by the annual number of wet days (Kreft & Jetz, 2007). Beyond the precipitation at any one spot, the size of contiguous rainforest area has also been considered an important additional factor (Reed & Fleagle, 1995; Leigh et al., 2004; Jaramillo et al., 2006). Because these factors promoting biodiversity—precipitation abundance, evenness, and rainforest area—are all fostered by angiosperm transpiration, angiosperm diversity is largely a result of the ecosystem modifications initiated by the angiosperms themselves.

When viewed in this climatic context, the evolution of angiosperm leaf physiology stands out as an intriguing key innovation for their success. Other angiosperm characteristics, such as their co-evolution with insects, reproductive barriers that promote outcrossing, and shortened generation times, may have revolutionized intrinsic plant biology, but the increased transpiration capacity that angiosperm venation represents likely initiated a series of positive feedbacks at the ecosystem level that re-engineered climate in a way that increasingly favored angiosperm productivity as the angiosperms transitioned from a species-rich but ecologically secondary group (Wing et al., 1993) to their current overwhelming dominance.

The fostering of diversity initiated by the angiosperms has not been limited to the angiosperms. The growing list of lineages that diversified closely following the angiosperm radiation includes ferns, bryophytes, ants, bees, beetles, mammals, and amphibians (Farrell, 1998; Wilf et al., 2000; Schneider et al., 2004; Moreau et al., 2006; Bininda-Emonds et al., 2007; Roelants et al., 2007; Wilson et al., 2007; Wahlberg et al., 2009; Wang et al., 2009). Explanations for how angiosperm evolution might have driven the evolutionary patterns in other lineages often rely on generalized evocations of increased ecological complexity (e.g., Schneider et al., 2004; Schuettpelz & Pryer, 2009), but the impact of angiosperms on climate is consistent with a concrete mechanism driven by the rainfall increases initiated by flowering plants. Ferns and other plants have passively benefited from the increased precipitation that accompanied angiosperm diversification, while animal radiations have been in response to the increased productivity and diversity of the vegetation that flourished in the new climate regimes that the angiosperms helped engender.

The impact of angiosperm evolution on tropical environments may be recorded in the changing ecological opportunities available in tropical forests through geologic time. Epiphytes lack contact with soil water and are dependent on reliably frequent precipitation for survival. Warm, high precipitation environments have existed throughout the history of vascular plants, but epiphytes have not. A Carboniferous fern interpreted as an epiphyte (Rothwell, 1991) suggests epiphytism has long been a possibility if conditions are suitable, yet other fossil examples are lacking before the evolution of angiosperms 200 million years later. In contrast, vines and lianas, which can make use of groundwater, have been abundant in non-arid environments throughout the fossil record (Krings et al., 2005; DiMichele et al., 2006; Burnham, 2009). True epiphytes radiated in parallel in the ferns, lycopods, bryophytes, and angiosperms (Wikstrom & Kenrick, 1997; Givnish et al., 2007; Heinrichs et al., 2007; Schuettpelz & Pryer, 2009; Silvera et al., 2009) only after the evolution of angiosperm forests, suggesting epiphytism was a less viable strategy before the buffering of precipitation regularity by angiosperms.

BIOGEOCHEMICAL CYCLING

The environmental impact of angiosperms may extend beyond climate to modifying the exchange of important elements between soil, ocean, and atmosphere. First, the expansion of environments with abundant rainfall has shifted checks to tropical productivity in many areas from water limitation to nutrient limitation. We posit that the efficiency of nutrient scavenging strategies by rainforest vegetation in order to maintain high productivity on low fertility soils has likely evolved since the propagation of angiosperm-modified tropical environments. Finally, the chemical weathering of silicate minerals is a principal sink for the drawdown of CO_2 from the atmosphere (Berner, 1999), and the deeper weathering of tropical sediments with angiosperm enhancement of the hydrologic cycle may have contributed (along with other biological and geological factors) to the steady decline of global atmospheric CO_2 concentrations since the Cretaceous.

Conclusions

The first order limitation on photosynthesis in low latitude regions is the availability of water to accommodate the evaporative demands of high solar energy influx. The unique capacity of angiosperms to transpire water has changed precipitation patterns and led to the spread of high rainfall environments, particularly in the tropics. This angiosperm flood has raised the diversity of other organismal groups, including both the consumers dependent on the angiosperm bounty and other producers that have benefited from angiosperm-driven increases in precipitation. Discussions of the hyperdiversity of angiosperms often center on how their floral and pollination biology have allowed them to more finely subdivide biotic productivity into a greater number of species (Doyle & Hickey, 1976). Such mechanisms are surely important, but we argue angiosperms have also increased the amount of productivity available for such subdivision through their propagation of high rainfall environments.

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