

Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution

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The flowering plants that dominate modern vegetation possess leaf gas exchange potentials that far exceed those of all other living or extinct plants. The great divide in maximal ability to exchange CO₂ for water between leaves of nonangiosperms and angiosperms forms the mechanistic foundation for speculation about how angiosperms drove sweeping ecological and biogeochemical change during the Cretaceous. However, there is no empirical evidence that angiosperms evolved highly photosynthetically active leaves during the Cretaceous. Using vein density (D_v) measurements of fossil angiosperm leaves, we show that the leaf hydraulic capacities of angiosperms escalated several-fold during the Cretaceous. During the first 30 million years of angiosperm leaf evolution, angiosperm leaves exhibited uniformly low vein D_v that overlapped the D_v range of dominant Early Cretaceous ferns and gymnosperms. Fossil angiosperm vein densities reveal a subsequent biphasic increase in D_v . During the first mid-Cretaceous surge, angiosperm D_v first surpassed the upper bound of D_v limits for nonangiosperms. However, the upper limits of D_v typical of modern megathermal rainforest trees first appear during a second wave of increased D_v during the Cretaceous-Tertiary transition. Thus, our findings provide fossil evidence for the hypothesis that significant ecosystem change brought about by angiosperms lagged behind the Early Cretaceous taxonomic diversification of angiosperms.

angiosperm evolution | plant evolution | transpiration | tropical rainforest | venation

Photosynthesis and transpiration by leaves fundamentally influence the cycling of carbon and water in the terrestrial realm. Consequently, evolutionary changes in the rates at which leaves exchange water for carbon bear on the origin and maintenance of biodiversity by varying the size and resource stoichiometry of the primary productivity base. How leaves exchange gases also shape climate and atmospheric gas composition by changing the amounts of water vapor and carbon in the atmosphere (1–3). Recent evidence has suggested that the evolution of flowering plants involved a sharp rise in the capacity of leaves to transport water and extract CO₂ from the atmosphere (4, 5).

The evolution of unrivaled CO₂ uptake and transpirational output by angiosperm leaves form the mechanistic cornerstone for a multitude of hypotheses citing angiosperms as agents of expansive ecosystem change during the Cretaceous (6–8). These hypotheses include (i) intensified mineral weathering by angiosperms that decreased global atmospheric CO₂ concentration; (ii) heightened transpirational input to the atmosphere that increased regional rainfall and favored the spread and diversity of tropical rainforest vegetation; (iii) the nearly complete competitive exclusion by angiosperms of diverse gymnosperms and ferns from high-productivity sites worldwide; and (iv) the spread of novel fire regimes that entrained a positive feedback on angio-

sperm takeover (3, 4, 6, 9–15). In addition, increasing terrestrial productivity furnished by the rise of angiosperms with highly photosynthetically active leaves has been posited as a large-scale driver for the mid-Cretaceous turning point when terrestrial biodiversity eclipsed that of the marine realm (16). However, the actual timing for when angiosperms first evolved their high capacities for leaf photosynthetic gas exchange remains poorly resolved (4, 5, 17–19).

A fundamental shift in how angiosperm leaf venation functions has been proposed as a key mechanism in the evolution of high photosynthetic gas exchange potential (4, 5). Evidence for a shift in angiosperm venation structure was reconstructed from living phylogenetic diversity as a surge in the vein length density (D_v) of angiosperm leaves that rose above the densities found across all other vascular plants during the mid-Cretaceous (5). In contrast to nonangiosperms, leaves of modern ecologically dominant angiosperms routinely exhibit tremendous vein lengths, which are evenly reticulated through the lamina (8). Leaves of tropical pioneer angiosperms, which operate at the upper limits of C₃ gas exchange for woody vegetation, possess an average of 13 mm and a maximum of 20 mm of vein length within a single square millimeter of leaf area (4). By comparison, all known extant and extinct nonangiosperm leaves fall within the range of 0.1–6 mm of vein length per square millimeter (4). Increased vein branching furnishes greater photosynthetic capacity because adding more veins brings the xylem-based water supply closer to the sites of evaporation in the leaf. Hence, D_v defines the hydraulic supply limit of water vapor exchange that secondarily constrains maximum CO₂ assimilation by leaves (4, 5, 8, 20, 21).

Vein density evolution in the angiosperms has been argued to represent an innovation that transformed global terrestrial biogeochemistry and biodiversity (3–5, 15, 16). However, evidence for the timing of this Earth-changing shift in leaf function remains untested in the fossil record and is limited to phylogenetically based reconstruction of vein evolution from living angiosperms (5). Clarifying when densely veined angiosperm leaves became the dominant fixture of the vegetation is critical for disentangling how Mesozoic environmental change affected angiosperm evolution and how innovations in early angiosperm function restructured Cretaceous ecosystem function (6, 11–16). Fossil angiosperm leaves of Cretaceous age often faithfully

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preserve the fine details of leaf venation (17, 22). Thus, vein densities of fossil leaves may offer signatures for ancient maximal leaf hydraulic limits and their evolutionary changes during the early angiosperm radiation (4). Interestingly, there are reports that early angiosperms possessed low vein densities, but when high D_V leaves that dominate modern angiosperm forests first appear remains unknown (22). In this paper, we analyze fossil angiosperm leaves through the Cretaceous to determine the evolutionary timing of angiosperms' D_V innovation. We measured vein densities of 307 taxa (approximate morphotypes) of fossil early angiosperm leaves as well as diverse gymnosperms and ferns from the early phases of angiosperm diversification and ecological expansion (Early Cretaceous to earliest Tertiary) and plotted vein density patterns through this crucial period.

Results

D_V values of the oldest angiosperm fossil leaves sampled (Hauterivian to Early Albian, 136–112 Ma) averaged $3.31 \text{ mm mm}^{-2} \pm 0.93 \text{ SD}$ ($n = 29$). These angiosperm leaf fossils nested within the range of diverse co-occurring and coeval gymnosperms and ferns (Fig. 1). In contrast with nonangiosperm fossil vein densities, which remained uniform through the Cretaceous to Paleogene (mean = $2.43 \text{ mm mm}^{-2} \pm 1.19 \text{ SD}$; $n = 107$), angiosperm D_V values first increased above the nonangiosperm range by the

Middle-Late Albian (106–100 Ma; Fig. 1). At 108–94 Ma (Late Albian-Cenomanian), mean angiosperm D_V ($5.55 \text{ mm mm}^{-2} \pm 1.79 \text{ SD}$, $n = 72$) became $\sim 2\times$ greater than that of nonangiosperms. Maximum D_V values for Late Albian-Early Cenomanian angiosperms increased to $\sim 40\%$ greater than the highest D_V values ($\sim 6 \text{ mm mm}^{-2}$) measured for nonangiosperms and were nearly $4\times$ greater than the nonangiosperm mean. The timing and magnitude for increased fossil angiosperm D_V during the mid-Cretaceous compared well to previous ancestral state reconstructions of D_V evolution across extant angiosperms (Fig. 2).

By the latest Cretaceous (Maastrichtian)-Paleocene, mean D_V values of angiosperms (mean = $9.76 \text{ mm mm}^{-2} \pm 3.0 \text{ SD}$; $n = 78$) increased 74% above the nonangiosperm sample through time, and the mean was 66% greater than the Hauterivian-Early Albian angiosperm mean. Several angiosperm D_V values from this timeframe became comparable to the vein densities found across extant canopy-dominants of the megathermal rainforest biome (Fig. 1).

Discussion

Fossil Evidence for a Cretaceous Surge in Angiosperm Vein Density.

Our measurements show fossil evidence that leaf hydraulic function changed dramatically during the Cretaceous radiation of angiosperms. We show that Early Cretaceous fossil angiosperm leaves shifted from possessing low vein densities to very high vein densities by the close of the Cretaceous. During the first 30 Myr of angiosperm leaf evolution seen in the fossil leaves from Brazil, China, and Europe, as well as North and South America across a large paleolatitudinal gradient (Dataset S1), angiosperm leaves exhibited uniformly low vein densities that fell in the range of dominant Early Cretaceous ferns and gymnosperms. These results support the conclusion that a widespread pattern of low leaf hydraulic potential existed for pre-Early Albian angiosperms (22).

By the latest Albian-Cenomanian (108–94 Ma), a rapid and sharp increase in angiosperm D_V became evident. Angiosperm D_V surpassed the upper bound of the physiological vein morphospace for living and fossil nonangiosperm vascular plant lineages during the mid-Cretaceous surge (4, 5). The highest fossil angiosperm D_V measured during the Late Albian approached 8 mm mm^{-2} and occurred in extinct platanoids (*Sapindopsis*) and Laurales. That these taxa defined the upper limits of mid-Cretaceous angiosperm vein densities supports earlier paleoecological evidence that platanoids and lauroids functioned with the most weedy, nonherbaceous ecologies at the time (17, 23). Interestingly, the timing and the amount of D_V increase found in mid-Cretaceous angiosperm fossils compared well to the pattern reconstructed from

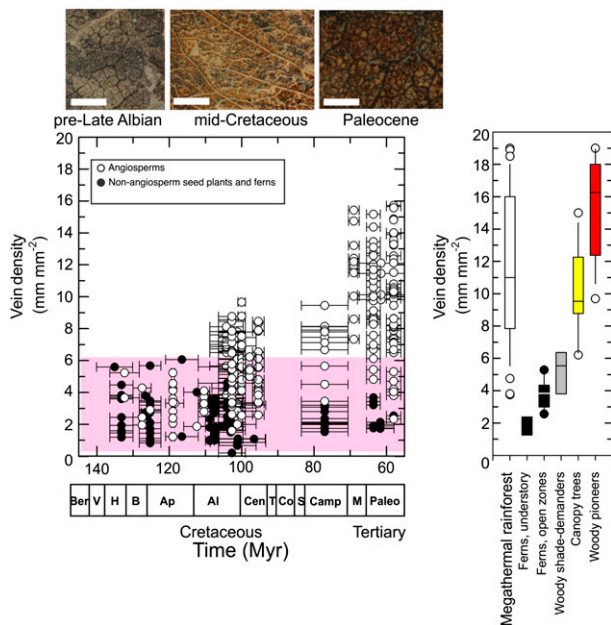


Fig. 1. Escalation in angiosperm D_V from Cretaceous to earliest Tertiary angiosperm fossil leaves (140–58 Ma). Angiosperm (○) and nonangiosperm (●) fossils represent mean D_V values per morphotype. Angiosperm D_V first increases above the nonangiosperm maximum at ~ 100 Ma (Late Albian). A second phase of angiosperm D_V increase occurred during the latest Cretaceous/earliest Tertiary (68–58 Ma). The fossil angiosperm D_V values during the second phase represent the earliest known densities comparable to the range of extant megathermal rainforest (Right box plot represents 25 species of woody plants across diverse regeneration guilds from Madang, Papua New Guinea). Representative fossil angiosperm leaves represent the pre-Late Albian (sparse D_V , *Ficophyllum crassinerve* = 3.5 mm mm^{-2}), mid-Cretaceous (moderately high D_V , *Sapindopsis magnolifolia* = 7.8 mm mm^{-2}), and Paleocene (dense D_V , morphotype CJ40 = 13.9 mm mm^{-2}) vein density shifts through time. Horizontal error bars around all data points represent the SD around the mean values for fossil ages. Geological ages: Ber, Berriasian; V, Valanginian; H, Hauterivian; B, Barremian; Ap, Aptian; Al, Albian; Cen, Cenomanian; T, Turonian; Co, Coniacian; S, Santonian; Camp, Campanian; M, Maastrichtian; Paleo, Paleocene. The shaded pink area denotes the range of D_V for all nonangiosperms, living and extinct (4). (Scale bar, 1 mm.)

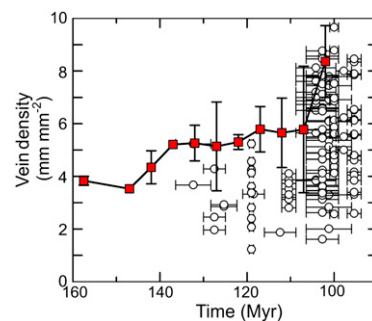


Fig. 2. The mid-Cretaceous increased angiosperm vein density based on fossil leaves (open circles) is comparable to the reconstructed vein density evolution based on ancestral states across extant angiosperm phylogeny (red squares) (5). Ancestral state values were averaged over 10-Myr slices with SD illustrated. Horizontal error bars around the fossil angiosperm data represent the SD around the mean values for fossil ages.

age-calibrated ancestral state analyses of D_V evolution based on living angiosperms (5) (Fig. 2). Thus, our fossil evidence shows that time-calibrated phylogenies of living angiosperms offer accurate evolutionary signals for an ancient hydraulic transition during the early angiosperm radiation.

Our results indicate that after the Late Albian-Cenomanian, angiosperm D_V continued to increase. By the latest Cretaceous-Paleocene, angiosperm D_V exhibited peak values comparable with the very high vein densities typical of hyperproductive modern megathermal rainforest angiosperm trees, averaging ~ 10 (and up to 16) mm mm^{-2} . The magnitude of vein branching measured for Late Cretaceous angiosperm leaf fossils represents the arrival of leaves capable of very high gas exchange capacities that today characterize hyperproductive megathermal rainforest angiosperms (4, 5, 7, 8).

Escalation of Leaf Angiosperm Hydraulic Potential. Broadly, the pattern of angiosperm D_V evolution supplies fossil evidence that the maximum potential for hydraulic capacity by angiosperm leaves escalated tremendously during the Cretaceous (6, 9, 16, 24). Although connecting changes in maximal leaf hydraulic capacity to competitive ability and ecosystem productivity remains a thorny issue for Cretaceous angiosperm macroevolution (13, 19, 24), the dynamics of fossil angiosperm D_V through time adds a new quantitative functional dimension to several critical turning points in early angiosperm ecological evolution.

For example, the Late Albian-Cenomanian pulse of increased angiosperm D_V coincides with a landmark ecological event—the first appearance of large angiosperm trees. Fossilized logs up to 1 m in diameter with the xylem plumbed by large-diameter ($\geq 200 \mu\text{m}$) vessels and simple perforation plates are first found in the mid-Cretaceous (23, 25–28). That a large shift in angiosperm body size, wood hydraulic efficiency, and, as we now show, moderately high D_V emerged synchronously points to a coordinated whole plant transformation in angiosperm hydraulic capacity during the mid-Cretaceous (19–21). Although angiosperms first entered the forest canopy and diversified at moderately high D_V by the Cenomanian, global inventories of angiosperm fossil abundance and diversity indicate that mid-Cretaceous angiosperms occupied subordinate ecological roles relative to conifers and ferns (13, 14, 23). Indeed, fossilized wood depositional environments, inferred from facies analyses, suggested that mid-Cretaceous angiosperm trees remained restricted to early successional floodplain zones (17, 27).

The second Maastrichtian-Paleocene surge in angiosperm D_V corresponds with the key time interval for when (i) angiosperms radiated into and dominated diverse environments, including late successional zones of mesothermal forests and megathermal peat- and coal-forming environments; and (ii) when angiosperm ecological abundance first eclipsed ferns and conifers across several biomes (13, 14, 23, 24, 28, 29). These fossil patterns are consistent with a major expansion in angiosperm competitive ability, which is supported by our finding that D_V values associated with the most productive extant angiosperm forests first emerge during the Late Cretaceous (1). In light of recent research that tropical angiosperm trees can strongly modify their climates by virtue of their densely veined leaves (3), the second wave of increased angiosperm D_V provides new time constraints for a possible major transition in vegetation-atmosphere interactions. High leaf transpiration, enabled by high D_V values in the range of 12–16 mm mm^{-2} and coupled to high forest cover, intensifies the hydrological cycle through the recycling of precipitation in ways that fostered the origin and diversity of disparate tropical organisms (2–4). Thus, our findings on fossil angiosperm veins through time show that the leaf hydraulic basis for how megathermal rainforest climate, transpiration, and productivity operate today was not explored by angiosperm leaf evolution until the latest Cretaceous (1, 3).

Though our findings indicate a biphasic rise in angiosperm D_V change through the Cretaceous, these results should be regarded as a hypothesis requiring future testing. For example, sampling of fossil angiosperm leaves from Turonian to Campanian sediments, where our sampling is sparse and limited to one middle paleolatitude site, may fill in the gap to reveal a steady rise in D_V . Nevertheless, the appearance of fossil D_V close to the modern limits of angiosperm leaf hydraulic capacity during the Cretaceous-Tertiary transition was consistently found among three fossil sites across a large paleolatitude gradient (11 °N to 36 °S) (30, 31) (Dataset S1). Such a pattern suggests that by the Maastrichtian-Paleocene, angiosperms bearing high D_V leaves became geographically significant. In addition, our measurements of very high D_V in the Cerrejon flora of Colombia extends systematic and paleoclimatic evidence in showing that the fossil flora functioned as the earliest known equatorial neotropical megathermal rainforest (31). The appearance of high angiosperm vein densities first in this zone during the Maastrichtian (Guaduas, Colombia) generate important questions about the ecophysiological modernization of the equatorial vegetational belt: (i) Do the high D_V values reflect colonization of a new megathermal wet environment by angiosperms that was opened up by tectonic and oceanic circulation change? or (ii) Did invading angiosperms with high D_V generate a hydrological feedback in situ to increase the geographic spread of tropical humid biomes (3).

Tuning the Angiosperm Venation Pipeline: Atmospheric and Conduit Change. The processes that drove the transformation of angiosperm venation during the Cretaceous remain unknown. However, an interplay of Cretaceous environmental opportunities and evolutionary novelty in angiosperm leaf hydraulics likely influenced the shifts in angiosperm leaf hydraulics through time (5, 19). A long-term decline in CO_2 and a rise in O_2 atmospheric concentrations during the Cretaceous indicate environmental pressures for increasing vein reticulation because both directions of atmospheric change favor increased vein density by increasing the transpirational cost for carbon uptake (5, 14, 32, 33). In this light, the broad decline in global CO_2 and rise in O_2 during the Cretaceous suggests an environmental opportunity that angiosperms were able to seize (5, 33). Indeed, an abrupt drawdown in global CO_2 associated with an ocean anoxic event (OAE2) during the mid-Cretaceous occurred at the same time as the first wave of increased angiosperm D_V (34). However, the possibility of a second wave of angiosperm D_V during the latest Cretaceous does not mirror current understanding of CO_2/O_2 dynamics through the Late Mesozoic (35, 36), which suggests that intrinsic innovations also bear on the evolution of angiosperm leaf gas exchange capacity.

Two functional conundrums of increased D_V by angiosperms are as follows: (i) only angiosperms evolved high D_V despite the fact that diverse nonangiosperm vascular plants also evolved through periods of low CO_2 , and several of these clades also possessed complex multiple-vein order designs or single-vein systems with accessory lignified tissues that are convergent with angiosperms (4, 8); and (ii) increasing D_V would, all else being equal, elevate leaf construction costs because veins, being lignified, are expensive (19, 21, 33). Therefore, gains in leaf photosynthetic potential by increasing D_V could be offset by inflated vascular plumbing costs (33). A hypothesis underlying the angiosperm monopoly of high D_V that requires future evaluation is that evolution of xylem vessels in angiosperm leaf veins provided an essential cost-mitigating mechanism (5, 19, 21). Vessels, through furnishing less-resistive flow compared with ancestral tracheids, may enable more vein reticulation and therefore faster rates of hydraulic supply for a given amount of vein volume (5, 19).

Conclusions

Our results indicate that a several-fold escalation in angiosperm leaf hydraulic capacity occurred during the Cretaceous. Increasing leaf hydraulic potential and linked high rates of transpiration by evolution of angiosperm vein densities exceeding those of nonangiosperms would have set in motion novel changes in the flows of carbon, water, and nutrients through the biosphere beginning in the mid-Cretaceous (3, 5, 15). However, the range of leaf hydraulic capacities representing the modern limits of woody angiosperm photosynthesis, which are those of capable of changing climates and foster today's enormous megathermal rainforest diversity and productivity, emerged long after angiosperm origin (3, 10, 13, 16, 19, 22, 23, 36, 37). Thus, our findings support previous interpretations of angiosperm paleoecology that despite tremendous phylogenetic diversification in the Early Cretaceous, transformative ecosystem change brought about by increased angiosperm productivity unfolded much later (24, 29).

Materials and Methods

D_v is the length of veins per unit leaf area (mm mm^{-2}). D_v was measured only on well-preserved compression fossils by tracing veins on fossil images

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