

TECHNICAL COMMENT

Appraising the roles of nutrient availability, global change, and functional traits during the angiosperm rise to dominance

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Abstract

To explain the rise of angiosperms during the Cretaceous, Berendse & Scheffer (*Ecol. Lett.*, 12, 2009, 865) invoke feedbacks between leaf litter, soil nutrients, and growth, overlooking other factors affecting resource acquisition by Cretaceous plants. We evaluate their hypothesis, highlight alternative explanations, and emphasize use of a broader framework for understanding the angiosperm radiation.

Keywords

Climate change, CO₂, evolution, gymnosperm, leaf, mycorrhizal fungi, nitrogen, phylogeny, roots, water.

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The expansion of angiosperms during the Cretaceous period has invited much speculation on its causes. Berendse & Scheffer (*Ecol. Lett.*, 12, 2009, 865) offer another ‘ecological explanation’ for the angiosperm rise to dominance (with respect to abundance and distribution). They posit that ancient gymnosperms produced leaf litter with low nutrient concentrations and slow decomposition, resulting in nutrient-poor soils upon which angiosperms were poor competitors. They suggest angiosperms, after a limited expansion driven by other factors, rose to dominance via a positive feedback on soil nutrient status and growth through production of leaf litter with higher nutrient concentrations and enhanced decomposition. Our question is ‘is the hypothesis well-supported?’

The examples of leaf litter feedbacks provided by Berendse and Scheffer lack gymnosperms, leaving their hypothesis without direct support. Instead, they suggest contrasting feedbacks of angiosperms and gymnosperms are expected based on well-documented differences in leaf traits and leaf litter decomposition between living angiosperms and gymnosperms. However, fine root traits, particularly nitrogen concentration, can have greater impacts on soil nutrients than leaf litter (Hobbie *et al.* 2007; Parton *et al.* 2007) and can be uncorrelated with aboveground traits (Withington *et al.* 2006; Hobbie *et al.* 2010). Also, as living angiosperms and gymnosperms generally dominate in contrasting soil types and climates, leaf and root trait

variation among these plant groups is not independent of climate or pre-existing soil variability. Thus correlations of litter traits with nutrient availability (e.g. litter lignin:nitrogen vs. nitrogen mineralization; Binkley & Giardina 1998) or of leaf traits with root traits (Newman & Hart 2006) across sites are confounded by variation in edaphic factors. Common garden experiments, though rare, control for climate and soil variability and offer direct, empirical evaluation of plant feedbacks. These experiments show woody gymnosperms often have equivalent or higher soil nutrient availability as compared to woody angiosperms (Table 1). Equivalent soil nutrient availability is also frequently observed in natural stands of angiosperms and gymnosperms on similar soils (e.g. Reich *et al.* 1997). Therefore, soil nutrient availability is not a simple function of leaf litter traits (Knops *et al.* 2002) and is not typically higher in angiosperm-dominated stands when compared with gymnosperm stands on similar soils – making Berendse and Scheffer’s hypothesis tenuous.

Berendse and Scheffer emphasize positive litter feedbacks on soil nutrient availability, but neglect other mechanisms of increasing nutrient supply to fast-growing angiosperms, including large-scale disturbances (e.g. pest/pathogen outbreaks, fire, volcanism) that likely accompanied the fluctuating climatic and tectonic conditions of the Cretaceous (McElwain *et al.* 2005; Tylianakis *et al.* 2008). Angiosperm dominance may also have been facilitated by evolution of

Table 1 Soil nitrogen availability* at common garden experiments that include both woody angiosperms and gymnosperms†

Location (duration, year)	Angiosperm species	Gymnosperm species	Results (N_m = nitrogen mineralization; N_{ext} = extractable $NH_4 + NO_3$)	Reference
Wisconsin, USA (~35)	<i>Acer saccharum</i> , <i>Betula papyrifera</i>	<i>Picea glauca</i> , <i>Pinus resinosa</i> , <i>Pinus strobus</i>	Mineral soil (0–10 cm): N_m was highest under <i>P. strobus</i> , intermediate under <i>Acer</i> , <i>Betula</i> , and <i>Picea</i> , lowest under <i>P. resinosa</i>	1
Connecticut, USA (50)	<i>Fraxinus pennsylvanica</i>	<i>Picea abies</i> , <i>Pinus strobus</i>	Mineral soil (0–15 cm): N_m was highest under <i>P. strobus</i> , intermediate under <i>Picea</i> , lowest under <i>Fraxinus</i>	2
Wisconsin, USA (28)	<i>Quercus rubra</i>	<i>Larix decidua</i> , <i>Picea abies</i> , <i>Pinus strobus</i> , <i>Pinus resinosa</i>	Top 20 cm (O and mineral): N_m was highest under <i>P. strobus</i> and <i>Larix</i> , lower (and similar) under <i>Quercus</i> , <i>Picea</i> , and <i>P. resinosa</i>	3
Denmark (28)	<i>Fagus sylvatica</i> , <i>Quercus robur</i>	<i>Picea abies</i> , <i>Pseudotsuga menziesii</i>	O horizon: N_{ext} was highest under <i>Picea</i> at one site; highest under <i>Pseudotsuga</i> at another site	4
Denmark (~30)	<i>Fagus sylvatica</i> , <i>Quercus robur</i>	<i>Pseudotsuga menziesii</i> , <i>Picea abies</i> , <i>Picea sitchensis</i>	O horizon: N_{ext} was higher under all gymnosperms at one site; similar among species at another site (<i>Picea</i> was the lowest); gymnosperms were intermediate between <i>Quercus</i> (highest) and <i>Fagus</i> (lowest) at another site	5
New York, USA (36–38, O horizon) (42–44 mineral soil)	<i>Acer saccharum</i> , <i>Fraxinus americana</i> , <i>Quercus rubrum</i>	<i>Picea abies</i> , <i>Pinus resinosa</i>	O horizon‡: N_m was highest under <i>Acer</i> , lower under gymnosperms (<i>Fraxinus</i> and <i>Quercus</i> not tested, Ref. 6)	6,7
Finland (23–24)	<i>Betula pendula</i>	<i>Picea abies</i> , <i>Pinus sylvestris</i>	Mineral soil (0–4 cm): N_m under <i>Picea</i> , <i>Pinus</i> , and <i>Acer</i> was statistically equivalent and higher than <i>Quercus</i> and <i>Fraxinus</i> (Ref. 7)	8
Finland (~60)	<i>Betula pendula</i>	<i>Picea abies</i> , <i>Pinus sylvestris</i>	Mineral soil (0–10 cm): N_m and N_{ext} were similar among species O horizon‡: N_{ext} under <i>Betula</i> was higher than gymnosperms at one site and highest under <i>Picea</i> at another site; same pattern for N_m	9
			Mineral soil (0–6 cm): N_{ext} under <i>Betula</i> was higher than gymnosperms at both sites; N_m was higher under gymnosperms at one site and highest under <i>Betula</i> at the other	

Table 1 *continued*

Location (duration, year)	Angiosperm species	Gymnosperm species	Results (N_m = nitrogen mineralization; N_{ext} = extractable $NH_4 + NO_3$)	Reference
British Columbia, Canada (25)	<i>Betula papyrifera</i>	<i>Pinus contorta</i> , <i>Pseudotsuga menziesii</i>	O horizon†: N_m and N_{ext} was highest under <i>Pseudotsuga</i> , intermediate under <i>Betula</i> , and lowest under <i>Pinus</i> Mineral soil (0–12 cm): N_m and N_{ext} was highest under <i>Betula</i>	10
Siberia (31–32)	<i>Betula pendula</i> , <i>Populus tremula</i>	<i>Larix siberica</i> , <i>Picea abies</i> , <i>Pinus siberica</i> , <i>Pinus sylvestris</i>	Mineral soil (0–10 cm): N_{ext} was highest under <i>Larix</i> and <i>P. siberica</i> , intermediate under <i>Betula</i> and <i>Populus</i> , and lowest under <i>P. sylvestris</i> and <i>Picea</i> ; same pattern for N_m	11
United Kingdom (25)	<i>Betula ermannii</i>	<i>Picea sitchensis</i> , <i>Pinus contorta</i>	O horizon (peat): N_{ext} under <i>Betula</i> and <i>Pinus</i> were similar, with <i>Picea</i> the lowest; N_m was similar among species in upper and middle peat layers and higher under <i>Betula</i> in the lower layer	12
France (25)	<i>Fagus sylvatica</i> , <i>Quercus petraea</i>	<i>Picea abies</i> , <i>Pinus laricio</i> , <i>Pseudotsuga menziesii</i>	Mineral soil (A and E horizons): N_{ext} under <i>Pinus</i> was highest, lower (and similar) under <i>Betula</i> and <i>Picea</i> ; N_m was similar among species in the E horizon but higher under <i>Betula</i> in the A horizon	12,13
Florida, USA (7)	<i>Populus deltoides</i> , <i>Quercus falcata</i> , <i>Platanus occidentalis</i>	<i>Pinus taeda</i>	Mineral soil (0–5 cm)§: N_m was highest under <i>Fagus</i> and lowest under <i>Quercus</i> with gymnosperms intermediate (Ref. 12); N_{ext} was highest under <i>Fagus</i> (<i>Quercus</i> and <i>Pinus</i> not reported, Ref. 13)	14
			Mineral soil (0–10 cm): N_m was higher under <i>Quercus</i> and <i>Populus</i> than <i>Platanus</i> and <i>Pinus</i> (which were statistically equivalent)	

Table 1 continued

Location (duration, year)	Angiosperm species	Gymnosperm species	Results (N_m = nitrogen mineralization; N_{ext} = extractable $NH_4 + NO_3$)	Reference
Poland (32–33)	<i>Acer platanoides</i> , <i>A. pseudoplatanus</i> , <i>Betula pendula</i> , <i>Carpinus betulus</i> , <i>Fagus sylvatica</i> , <i>Quercus robur</i> , <i>Q. rubra</i> , <i>Tilia cordata</i>	<i>Abies alba</i> , <i>Larix deatida</i> , <i>Picea abies</i> , <i>Pinus nigra</i> , <i>P. sylvestris</i> , <i>Pseudotsuga menziesii</i>	Top 20 cm (O and mineral): N_m was highest under <i>Acer</i> sp., slightly lower under <i>Betula</i> and <i>Picea</i> , intermediate beneath <i>Fagus</i> and <i>Q. robur</i> , lower beneath <i>Larix</i> , <i>Pinus</i> sp., <i>Pseudotsuga</i> , <i>Abies</i> , <i>Carpinus</i> , and <i>Tilia</i> , lowest under <i>Q. rubra</i>	15

*Nitrogen mineralization (via laboratory or in situ incubations) and extractable nitrogen ($NH_4 + NO_3$) were used as indices of soil nitrogen availability.

†We used ISI Web of Science to find relevant studies using the following terms in two separate searches: (1) 'common garden' or plantation or stand or monoculture AND species or angiosperm or gymnosperm or evergreen or deciduous or conifer or woody AND soil AND nitrogen; (2) 'common garden' or plantation or stand or monoculture or species or angiosperm or gymnosperm or evergreen or deciduous or conifer or woody AND soil AND 'N mineralization' or 'N availability' or 'extractable N' or 'exchangeable N' or 'N transformations'. For brevity we have omitted plural forms of each search term, although most plural forms were included (exceptions being plural forms of the nitrogen terms, 'woody', 'deciduous' and 'common garden'. For search 2 we also used the letter 'N' as a replacement for nitrogen in each of the nitrogen availability terms, e.g. 'N mineralization'). Only studies that included angiosperm and gymnosperm stands that met the following additional criteria were included: stands must be of similar age, growing on the same soil type and topography, in close proximity, derived from plantings, and having similar forest management (e.g. thinning).

‡ N_m and/or N_{ext} were reported per unit organic matter or soil mass. N_m of conifers is likely to increase relative to that of hardwoods if differences in forest floor mass were taken into account.

§ N_m calculated by isotope dilution during a short (5 days) incubation yielded different results, with spruce having the highest N_m and beech the lowest.

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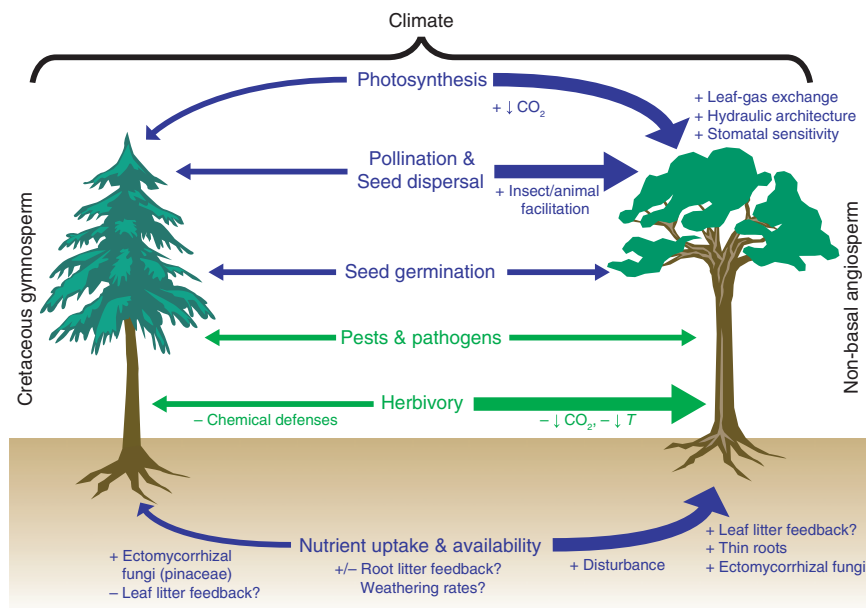


Figure 1 A conceptual framework of the biotic and abiotic factors that influenced fitness and competitive interactions of Cretaceous angiosperms and gymnosperms. Processes that have a positive impact on plant fitness are highlighted in blue and processes that have a negative impact are highlighted in green. Differences in the width of arrows indicate where disproportionate effects of a given process on Cretaceous angiosperms and gymnosperms are expected. Plant traits or abiotic factors controlling these disproportionate effects are labelled next to the arrow of the relevant process; ‘+’ or ‘-’ signs indicate the direction of the modifying effect of those plant traits or abiotic factors. Where arrows have equal width, disproportionate effects are possible, but not currently hypothesized (to our knowledge). Climate and global change can have direct, indirect, and unexpected effects on each aspect of plant fitness that are not shown. We highlight effects of the long-term decline of CO₂ during the mid- to late-Cretaceous (as mediated by plant traits) as a more plausible explanation related to resource acquisition than the nutrient feedbacks proposed by Berendse & Scheffer (2009). Decreasing CO₂ could directly favour non-basal angiosperms via their higher leaf-gas-exchange capacity, which would reduce stomatal and CO₂ limitations on photosynthesis. Declining CO₂ could also lead to increased leaf nitrogen concentrations and decreased temperature, both of which could reduce herbivory and indirectly benefit angiosperms by releasing them from disproportionate top-down control by herbivores. Other plant traits and their interactions with environmental changes (e.g., climate change, tectonic activity, volcanism) were likely important but are not shown here.

root traits or fungal symbioses (Brundrett 2002). Thin, fast-growing roots are more common within angiosperms and can be superior for nutrient uptake relative to thick, slow-growing roots of more ancient plants (Comas & Eissenstat 2009). Ectomycorrhizal fungi, which evolved independently in the Pinaceae and several angiosperm lineages during the Cretaceous, confer greater access to organic nitrogen than the arbuscular mycorrhizal fungi of Jurassic and Cretaceous gymnosperms (Brundrett 2002).

To justify their emphasis on nutrients, Berendse and Scheffer suggest high atmospheric CO₂ during the Cretaceous would have reduced the role of water stress relative to soil nutrients in limiting plant growth. Yet they do not discuss the apparent long-term decline in atmospheric CO₂ that dominates the Cretaceous and which may have increased plant demand for water. To prevent reductions in carbon assimilation under decreasing CO₂, plants would likely increase stomatal conductance and associated water losses, favouring angiosperms with more responsive stomata and greater capacity to conduct water (McElwain

et al. 2005; Brodribb & Feild 2010). Evolution of high leaf vein density within non-basal angiosperms was likely a critical step enabling increased carbon assimilation (Brodribb & Feild 2010), particularly when coupled to other advances in hydraulic architecture and resource acquisition by roots.

Given the abundance of hypotheses for the angiosperm rise to dominance and the difficulty in testing them, each hypothesis must be presented and evaluated in light of alternatives and multiple aspects of plant fitness (Fig. 1). In presenting their hypothesis, Berendse and Scheffer ignore other factors that influence nutrient availability or uptake and they overlook better-supported, competing hypotheses (e.g. declining atmospheric CO₂ coupled with superior angiosperm leaf-gas-exchange capacity), resulting in a skewed perspective. As most hypotheses are based on trait variation and competition among living plants, studies that characterize the nature of Cretaceous plants are required, including retrospective studies of the geologic record and studies that map contemporary trait variation onto relevant

branches and nodes of plant phylogenetic trees (Brodribb & Feild 2010; Comas & Eissenstat 2009). Finally, as global change has unexpected and variable consequences for biotic interactions (Tylianakis *et al.* 2008), future studies must consider effects of Cretaceous global change (Brodribb *et al.* 2009), including the timing of global change events relative to evolution of plant traits and community composition (McElwain *et al.* 2005; Brodribb & Feild 2010).

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