Could land plant evolution have fed the marine revolution?

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Abstract. The advent of flowering plants on land has been suggested previously as a potential trigger for Cretaceous innovations in the marine realm by providing a greater energetic base for marine ecosystems through a more nutrient-rich terrestrial runoff. The scope of the angiosperm radiation certainly was unprecedented—flowering plants came to represent the large majority of species in all terrestrial floras in a geologically short span of time—and angiosperms possess much higher photosynthetic and hydraulic capacities than all other plants. Angiosperm evolution could have affected both the organic and inorganic content of terrestrial runoff, but the magnitude of these changes is in question. Angiosperms are more productive than other plants, suggesting an increase in organic matter runoff, but that quantity is small in comparison to native marine photosynthesis even in the modern angiosperm-dominated world. Changing the inorganic nutrient content of terrestrial runoff requires changing weathering rates, but angiosperms and earlier appearing vascular plants appear to be little different in this respect. Thus, the potential for angiosperms to have strongly influenced marine evolution may have been small. The greatest opportunity for angiosperms to have changed weathering rates may come from their impact on terrestrial climate. Their greatly elevated transpiration capacities feed rainfall and this enhancement of the hydrological cycle means that angiosperms may have increased weathering rates in aggregate even if they have little effect individually. The timing of the angiosperm radiation is both crucial and problematic, since their rise to ecological dominance is thought to lag significantly behind their increase in species diversity, thereby diminishing the correspondence with events in the marine realm.

Key words: Angiosperm, Cretaceous, Mesozoic marine revolution, precipitation, runoff, weathering

Introduction

Flowering plants dominate nearly all modern terrestrial environments, comprising at least 85% of the local diversity globally (Mutke and Barthlott, 2005). They combine a breathtaking array of structural diversity with unprecedented evolutionary facility: not only do they include woody and herbaceous plants, trees, climbers, succulents, herbs, geophytes, epiphytes, and aquatics, but they can encompass a surprising proportion of those habits in a single family or even genus (e.g., Judd *et al.*, 1994; Mabberley, 2008). As angiosperms spread from the tropics (Hickey and Doyle, 1977; Crane and Lidgard, 1989; Lupia *et al.*, 1999) after a Hauterivian first appearance (Hughes *et al.*, 1991), increase in species diversity was rapid (Lidgard and Crane, 1990). Their rise to ecological dominance was more protracted (Wing *et al.*, 1993; Wing and Boucher, 1998), although there is debate over how significantly ecological importance lagged behind the increase in species abundance (Lupia *et al.*, 1999). The evolution of angiosperms is correlated with broad changes in terrestrial faunas (Wing and Tiffney, 1987; Wang *et al.*,

2009). Flowering plants are speculated to have driven many of these changes through their increased productivity, palatability, and opportunity for specialization afforded both to herbivores and to biotic dispersal agents (Wing and Tiffney, 1987; Coe *et al.*, 1987; Tiffney, 1997; Boyce *et al.*, 2009; Brodribb and Feild, 2010; Boyce *et al.*, 2010). Flowering plants may also have altered terrestrial faunal diversity through their impact on climate (Boyce and Lee, 2010).

As with the earlier radiation of vascular plants (Berner, 1997; Algeo and Scheckler, 1998; Bambach, 1999; Beerling and Berner, 2005), the impact of flowering plant evolution may have reached beyond terrestrial ecosystems. The evolution of angiosperm mangroves and sea grasses would have directly provided novel habitats and increased productivity in near-shore environments, but changes wrought by angiosperms on land may also have reached the marine realm through the increased delivery of inorganic nutrients to bolster marine productivity and of organic matter for direct heterotrophic consumption (Bambach, 1993, 1999; Martin, 1996). Thus, angiosperm evolution on land may have bolstered marine biomass and energetics. The appearance of key

evolutionary innovations that restructured marine ecosystems over the Cretaceous, which have been collectively referred to as the Mesozoic marine revolution, have been attributed to an increased energetic base that may have been at least partially provided by terrestrial flowering plants (Vermeij, 1987, 1995, this volume; Bambach, 1993, 1999). Here, the possible specific impacts of angiosperm evolution on marine communities above and beyond the effects of earlier vascular and seed plant radiations are considered in more detail.

How might angiosperms have impacted the marine realm?

Marine flux of terrestrial organic matter

All other things being equal, an increase in primary productivity on land should result in an increase in organic matter export to the oceans (Bambach, 1993). Among extant plants, angiosperms are generally more productive than non-angiosperms and recent work has extended that assessment to the fossil record as well (Boyce *et al.*, 2009). As CO_2 for photosynthesis diffuses into leaves through their stomatal pores, H_2O diffuses out from internal leaf tissues. If the leaf cannot keep up with the replacement of this water loss, then the stomata must shut and CO_2 absorption and photosynthesis cease (Sack and Holbrook, 2006). Thus, photosynthetic capacity is intimately related to hydraulic capacity. Leaf vein density (the total length of vein per unit area of leaf lamina) has been identified as a crucial component of hydraulic capacity that closely correlates with photosynthetic potential (Brodribb *et al.*, 2007; Boyce *et al.*, 2009; Brodribb and Feild, 2010). Angiosperms possess mean and maximum vein densities about four times higher than any other plants, living or extinct, suggesting at least a doubling of primary production capacity with angiosperm evolution (Boyce *et al.*, 2009; Figure 1, top panel).

The above assessment of productivity increases with angiosperm evolution is based upon modern atmospheric CO_2 concentrations–significantly lower than those of the Cretaceous (Berner and Kothavala, 2001; Royer *et al.*, 2004; Berner, 2006)–and there has been some suggestion that the advantages of high vein density may saturate at high CO_2 concentrations (Brodribb and Feild, 2010). Furthermore, some fertilization effect is to be expected with increasing CO_2 concentration (Bazzaz, 1990; Berner and Kothavala, 2001; Beerling and Woodward, 2001; Jahren *et al.*, 2008; Brodribb and Feild, 2010; Adams, 2010), although it is unclear how applicable short-term experiments demonstrating CO_2 fertilization in living plants are to evolutionary timescales (Bazzaz, 1990) and estimates of how much fertilization should be expected for the deep past vary widely. Thus, in theory, terrestrial primary production could have declined over the Late Cretaceous and early Cenozoic with declining atmospheric CO_2 even as the productivity potential of

the plants was increasing with the angiosperm radiation. On balance, primary production likely increased over the Cretaceous, but assigning a number to that increase would be highly conjectural.

Any change in terrestrial primary production that did occur over the Cretaceous must be evaluated against the relative importance of the terrestrial organic flux to marine ecosystems. The annual riverine input of organic matter to the oceans of 0.4 gigatons (Gt, 1 Gt $= 1 \times 10^{15}$ g) of carbon is certainly significant considering that standing marine biomass is only about 3 Gt C, but that riverine input is still small relative to the 50 Gt of organic carbon generated each year by marine photosynthesis (Longhurst *et al.*, 1995; Hedges *et al.*, 1997). Thus, any increases in terrestrial organic input that accompanied increased angiosperm productivity would still represent only a fraction of a percent of the total marine budget. Coastal marine environments merit special attention as the most productive marine environments, as the site of terrestrial runoff, and as the source of the bulk of the paleontological record. However, coastal productivity is only 2.5 to 4.0 times lower than that of the ocean as a whole (Longhurst *et al.*, 1995). So, even if coastal environments are considered alone, any incremental change in organic runoff with angiosperm evolution could represent a difference at the very most of a few percent in the carbon budget of coastal ecosystems.

Although the bulk of terrestrial input is focused on coastal regions, its proportional importance is actually greater in the open ocean where native marine productivity is lower (Zafiriou *et al.*, 1985; Hedges *et al.*, 1997). This input of wind-blown terrestrial debris may have actually decreased substantially over the Cretaceous and early Cenozoic as the gymnospermous seed plants and seedless vascular plants that produce abundant wind-dispersed pollen and spores were replaced by the predominantly insect-pollinated angiospermous seed plants. Thus, any increases in organic matter delivery to the oceans that accompanied the angiosperm radiation would have been focused on coastal environments and likely at the expense of the open oceans.

Weathering and nutrient runoff

To the extent that phosphorus and other key nutrients are derived from the weathering of terrestrial rocks, the impact of angiosperm evolution on marine energetics may have been less through the runoff of organic matter directly and more through the delivery of nutrients vital for native marine photosynthetic production (Bambach, 1993, 1999). The litter produced by eudicot angiosperms does decay substantially faster than that of extant non-angiosperms (Cornwell *et al.*, 2008). The angiosperm combination of rapid decay with high rates of nutrient uptake have even led to the hypothesis that the ecological spread of angiosperms was dependent on a positive feedback in which they modified their environment
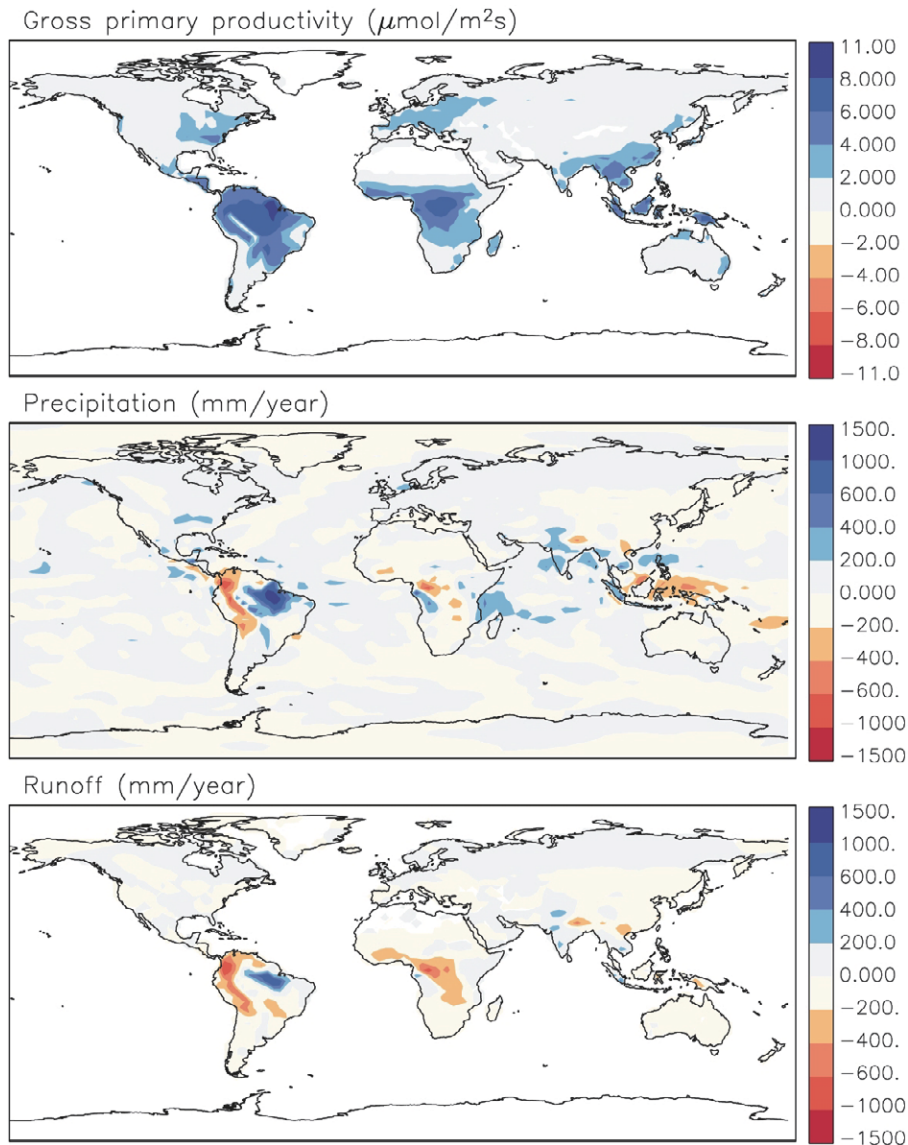
Figure 1. Climate modeling of the differences in a world with angiosperms relative to a world without them. Following Boyce *et al.* (2009), absence of angiosperms was simulated with a four-fold drop in the maximum carboxylation rate when intercellular air space is saturated with CO_2 (V_{max}), which decreases the effective photosynthetic/transpirational capacity. All other factors were held as fixed at modern values, including sea surface temperatures, geography, and vegetative biomass. For detailed methods, see Boyce and Lee (2010), Lee and Boyce (2010). Local reductions in precipitation with the increased transpiration of angiosperms reflect changes in atmospheric moisture convergence patterns.

with high nutrient litter in a way that enabled their high nutrient requirements and rates of uptake (Berendse and Scheffer, 2009). However, such a system could not produce a steady-state increase in nutrient availability (and runoff flux to the oceans) unless angiosperms also increased weathering rates. In order for angiosperm nutrient cycling to have an impact on either their own evolution or upon marine ecosystems, they must alter the rate of introduction of new nutrients into the ecosystem from rock reservoirs, not just increase the cycling of the existing nutrient pool within ecosystems. Increased cy-

cling without an increased flux from the nutrient source can only lead to no change in availability or a bleeding of nutrients from terrestrial systems, leading to a short-term increase of availability in marine systems, but cannot result in a sustained steady-state increase in availability. This requirement for increased weathering is problematic because study of living trees suggests that the impact of angiosperm evolution on weathering rates is likely to have been small or neutral (Andrews *et al.*, 2008; Adams, 2010). The Paleozoic evolution of arborescent vascular plants had a profound impact on weath-

ering rates (Berner, 1997), but the later substitution of one group of vascular plant trees for another with the angiosperm replacement of gymnosperms is likely to have had little additional effect. If anything, concurrent evolution of different lineages of mycorrhizal fungi may have been more relevant (Taylor *et al.*, 2009).

The greatest chance for angiosperm evolution to have appreciably affected marine ecosystems may come not through their individual biology, but their cumulative effect on climate. Flowering plants possess transpirational capacities much larger than any other plant groups (Boyce *et al.*, 2009) and recycling of this transpiration feeds convective rainfall, particularly in the tropics (Boyce and Lee, 2010; Lee and Boyce, 2010; Figure 1, middle panel). Although modest overall gains in runoff are possible due to more moisture being drawn in from the oceans with the increased atmospheric convergence over land (Figure 1, bottom panel), the additional precipitation accompanying angiosperm evolution could not have resulted directly in additional runoff, because of the recycling involved. Indeed, increased transpiration has actually been suggested as a potential cause in cases of decreased runoff (Gedney *et al.*, 2006; Betts *et al.*, 2007), as supported by some regions in Figure 1. However, the additional precipitation in angiosperm ecosystems represents a substantial enhancement of hydrological cycling that should translate to greater chemical weathering rates (Stewart *et al.*, 2001; Berner and Kothavala, 2001; West *et al.*, 2005). Thus, angiosperm-dominated ecosystems may tend to have higher weathering rates than gymnosperm-dominated ecosystems, even if comparison of individual trees did not show such an effect, and the nutrient load of terrestrial runoff might have increased with angiosperm evolution, even if the runoff volume stayed relatively constant. As conjectural as this mechanism is, it may be the most viable remaining opportunity for angiosperms to have influenced marine events, given the arguments against other potential mechanisms outlined above.

Discussion

Although often more broadly inclusive, the focus on evolutionary innovation in the marine realm is most frequently concentrated on the later half of the Cretaceous (Vermeij, 1977, 2008, this volume). How do the potential impacts of the angiosperm radiation match up with this time frame? Angiosperm species diversity certainly increases dramatically over this period, but establishment of ecological dominance is more important as far as influencing marine nutrient delivery and terrestrial weathering. The potential impact of angiosperms on productivity and weathering rates are differentially impacted by the lag in angiosperm ecological importance. In the case of productivity, any incremental increase in angiosperm abundance should translate into an increase in overall productivity and, thereby, organic runoff to the

oceans. However, it should be noted that the high leaf vein density that signals high photosynthetic capacity is not a trait of angiosperms as a whole, but something absent from basal angiosperms and independently derived in the magnoliid, monocots, and eudicot angiosperms, with elevated vein densities first appearing around the Cenomanian, about 30 million years after the first appearance of angiosperms (Boyce *et al.*, 2009; Brodribb and Feild, 2010). Impacts on weathering rates through increasing precipitation are more dependent on angiosperms achieving ecological dominance and a large proportion of the biomass (supplemental figures of Boyce and Lee, 2010). Estimates concerning when this dominance was achieved vary widely over the Late Cretaceous and into the early Cenozoic (Wing *et al.*, 1993; Wing and Boucher, 1998; Lupia *et al.*, 1999), resulting in a variable degree of asynchrony with marine events.

The emphasis here has been on changes associated with the spread of the angiosperms that may have coincided with important changes in marine ecosystems during the Cretaceous, but it is important to note that other long-term trends affecting the delivery of terrestrial nutrients to the marine realm may well exist with complex and difficult to quantify net effects. For example, the establishment of abundant vertebrate herbivory towards the end of the Permian may have presented a discrete and permanent decrease in the organic matter flux to the oceans due to more efficient cycling within terrestrial ecosystems (such a decrease also could have accompanied the increased palatability of angiosperms). However, the progressive rise in importance of deciduous leaves over the Phanerozoic might provide a slowly but more or less steadily increasing supply of readily transportable organic matter at a macroscopic scale. Since disturbed environments more poorly retain their nutrients (Vitousek and Reiners, 1975), increased nutrient delivery to the oceans may have resulted from the enhanced disturbance potential of large dinosaurs during the Jurassic and Cretaceous. The summation of these poorly quantifiable factors along with those induced by the angiosperms may be too complex to compare properly their potential for affecting global change against that of the various abiotic influences on marine nutrient availability, including volcanism, mountain building, continental fragmentation, atmospheric CO_2 concentrations, wildfire rate due to atmospheric O_2 fluctuations, upwelling, sea level, glaciation, and temperature.

Acknowledgments

References

Adams, J., 2010: *Vegetation-climate interaction*, 266 p. Springer Praxis, Chichester.

Algeo, T. J. and Scheckler, S. E., 1998: Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society of London B*, vol. 353, p. 113–130.

Andrews, M. Y., Ague, J. J. and Berner, R. A., 2008: Weathering of soil minerals by angiosperm and gymnosperm trees. *Mineralogical Magazine*, vol. 72, p. 11–14.

Bambach, R. K., 1993: Seafood through time: changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology*, vol. 19, p. 372–397.

Bambach, R. K., 1999: Energetics in the global marine fauna: a connection between terrestrial diversification and change in the marine biosphere. *Geobios*, vol. 32, p. 131–144.

Bazzaz, F. A., 1990: The responses of natural ecosystems to the rising global CO_2 levels. *Annual Review of Ecology, Evolution, and Systematics*, vol. 21, p. 167–196.

Beerling, D. J. and Berner, R. A., 2005: Feedbacks and the coevolution of plants and atmospheric CO_2. *Proceedings of the National Academy of Sciences of the United States of America*, vol. 102, p. 1302–1305.

Beerling, D. J. and Woodward, F. I., 2001: *Vegetation and the Terrestrial Carbon Cycle. Modelling the First 400 Million Years*, 405 p. Cambridge University Press, Cambridge.

Berendse, F. and Scheffer, M., 2009: The angiosperm radiation revisited, an ecological explanation for Darwin's 'abominable mystery'. *Ecology Letters*, vol. 12, p. 865–872.

Berner, R. A., 1997: The rise of plants and their effect on weathering and atmospheric CO_2. *Science*, vol. 276, p. 544–546.

Berner, R. A., 2006: GEOCARBSULF: A combined model for Phanerozoic atmospheric O_2 and CO_2. *Geochimica et Cosmochimica Acta*, vol. 70, p. 5653–5664.

Berner, R. A. and Kothavala, Z., 2001: GEOCARB III: a revised model of atmospheric CO_2 over Phanerozoic time. *American Journal of Science*, vol. 301, p. 182–204.

Betts, R. A., Boucher, O., Collins, M., Cox, P. M., Falloon, P. D., Gedney, N., Hemming, D. L., Huntingford, C., Jones, C. D., Sexton, D. M. H. and Webb, M. J., 2007: Projected increase in continental runoff due to plant responses to increasing carbon dioxide. *Nature*, vol. 448, p. 1037–1041.

Boyce, C. K., Brodribb, T., Feild, T. S. and Zwieniecki, M. A., 2009: Angiosperm leaf vein evolution was physiologically and environmentally transformative. *Proceedings of the Royal Society of London B*, vol. 276, p. 1771–1776.

Boyce, C. K. and Lee, J.-E., 2010: An exceptional role for flowering plant physiology in the expansion of tropical rainforests and biodiversity. *Proceedings of the Royal Society of London B*, vol. 277, p. 3437–3443.

Boyce, C. K., Lee, J.-E., Feild, T. S., Brodribb, T. and Zwieniecki, M. A., 2010: Angiosperms helped put the rain in the rainforests: The impact of plant physiological evolution on tropical biodiversity. *Annals of the Missouri Botanical Gardens*, vol. 97, p. 527–540.

Brodribb, T. J. and Feild, T. S., 2010: Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. *Ecology Letters*, vol. 13, p. 175–183.

Brodribb, T. J., Feild, T. S. and Jordan, G. J., 2007: Leaf maximum photosynthetic rate and venation are linked by hydraulics. *Plant Physiology*, vol. 144, p. 1890–1898.

Coe, M. J., Dilcher, D. L., Farlow, J. O., Jarzen, D. M. and Russell, D. A., 1987: Dinosaurs and land plants. *In*, Friis, E. M., Chaloner, W. G. and Crane, P. R. *eds.*, *The Origins of Angiosperms and their Biological Consequences*, p. 225–258. Cambridge University Press, Cambridge.

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D. E.,

Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V. and Westoby, M., 2008: Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, vol. 11, p. 1065–1071.

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

Gedney, N., Cox, P. M., Betts, R. A., Boucher, O., Huntingford, C. and Stott, P. A., 2006: Detection of a direct carbon dioxide effect in continental river runoff records. *Nature*, vol. 439, p. 835–838.

Hedges, J. I., Keil, R. G. and Benner, R., 1997: What happens to terrestrial organic matter in the ocean? *Organic Geochemistry*, vol. 27, p. 195–212.

Hickey, L. J. and Doyle, J. A., 1977: Early Cretaceous fossil evidence for angiosperm evolution. *Botanical Review*, vol. 43, p. 2–104.

Hughes, N. F., McDougall, A. B. and Chapman, J. L., 1991: Exceptional new record of Cretaceous Hauterivian angiospermid pollen from southern England. *Journal of Micropalaeontology*, vol. 10, p. 75–82.

Jahren, A. H., Arens, N. C. and Harbeson, S. A., 2008: Prediction of atmospheric $\delta^{13}CO_2$ using fossil plant tissues. *Review of Geophysics*, vol. 46, p. RG1002.

Judd, W. S., Sanders, R. W. and Donoghue, M. J., 1994: Angiosperm family pairs: preliminary phylogenetic analyses. *Harvard Papers in Botany*, vol. 5, p. 1–51.

Lee, J. E. and Boyce, C. K., 2010: Impact of the hydraulic capacity of plants on water and carbon fluxes in tropical South America. *Journal of Geophysical Research*, vol. 115, p. D23123.

Lidgard, S. and Crane, P. R., 1990: Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. *Paleobiology*, vol. 16, p. 77–95.

Longhurst, A., Sathyendranath, S., Platt, T. and Caverhill, C., 1995: An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research*, vol. 17, p. 1245–1271.

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

Mabberley, D. J., 2008: *Mabberley's Plant-Book*, 1040 p. Cambridge University Press, Cambridge.

Martin, R. E., 1996: Secular increase in nutrient levels through the Phanerozoic: implications for productivity, biomass, and diversity of the marine biosphere. *Palaios*, vol. 11, p. 209–219.

Mutke, J. and Barthlott, W., 2005: Patterns of vascular plant diversity at continental to global scales. *Biologiske Skrifter*, vol. 55, p. 521–531.

Royer, D. L., Berner, R. A., Montañez, I. P., Tabor, N. J. and Beerling, D. J., 2004: CO_2 as a primary driver of Phanerozoic climate. *GSA Today*, vol. 14, p. 4–10.

Sack, L. and Holbrook, N. M., 2006: Leaf hydraulics. *Annual Review of Plant Biology*, vol. 57, p. 361–381.

Stewart, B. W., Capo, R. C. and Chadwick, O. A., 2001: Effects of rainfall on weathering rate, base cation provenance, and Sr isotope composition of Hawaiian soils. *Geochimica et Cosmochimica Acta*, vol. 65, p. 1087–1099.

Taylor, L. L., Leake, J. R., Quirk, J., Hardy, K., Banwart, S. A. and Beerling, D. J., 2009: Biological weathering and the long-term carbon cycle: integrating mycorrhizal evolution and function into the current paradigm. *Geobiology*, vol. 7, p. 171–191.

Tiffney, B. H., 1997: Land plants as food and habitat. *In*, Farlow, J. O. and Brett-Surman, M. K. *eds.*, *The Complete Dinosaur*, p. 352–370. Indiana University Press, Bloomington.

Vermeij, G. J., 1977: The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, vol. 3, p. 245–258.

Vermeij, G. J., 1987: *Evolution and Escalation*, 527 p. Princeton University Press, Princeton.

Vermeij, G. J., 1995: Economics, volcanoes, and Phanerozoic revolutions. *Paleobiology*, vol. 21, p. 125–152.

Vermeij, G. J., 2008: Escalation and its role in Jurassic biotic history. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 263, p. 3–8.

Vitousek, P. M. and Reiners, W. A., 1975: Ecosystem succession and nutrient retention: a hypothesis. *BioScience*, vol. 25, p. 376–381.

Wang, H., Moore, M. J., Soltis, P. S., Bell, C. D., Brockington, S. F., Alexandre, R., Davis, C. C., Latvis, M., Manchester, S. R. and Soltis, D. E., 2009: Rosid radiation and the rapid rise of angiosperm-dominated forests. *Proceedings of the National Academy of Sciences of the United States of America*, vol. 106, p. 3853–3858.

West, A. J., Galy, A. and Bickle, M., 2005: Tectonic and climatic controls on silicate weathering. *Earth and Planetary Science Letters*, vol. 235, p. 211–228.

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

Wing, S. L., Hickey, L. J. and Swisher, C. C., 1993: Implications of an exceptional fossil flora for Late Cretaceous vegetation. *Nature*, vol. 363, p. 342–344.

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

Zafiriou, O. C., Gagosian, R. B., Peltzer, E. T., Alford, J. B. and Loder, T., 1985: Air-to-sea fluxes of lipids at Enewetak Atoll. *Journal of Geophysical Research*, vol. 90, p. 2409–2423.