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The evolutionary origins and subsequent histories of soils and trees

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ABSTRACT

The evolutionary relationships between forests, grasslands and humans have exerted profound terraforming influences, not just on and through readily visible landscapes but also (and perhaps especially) below ground. This paper examines how these interactions have played out at various points in the history of the land flora and the arrival of hominins, and their implications for soil sustainability.

KEYWORDS

forest; roots; weathering; carbon cycle; competition

A brief overview of terrestrial plant evolution

Almost half a billion years ago small, twiggy, rootless, leafless plants began to make the transition from the aquatic to the terrestrial environment (Plackett & Coates, 2016). In a comparatively short time, geologically speaking, evolution solved the problems of life out of water and the pioneer plants went on to become giants: by the Devonian period the trees had arrived. Forests became the dominant global vegetation type from the mid Devonian (around 380 Mya; Berner, 1997). Very few representatives of the early forest pteridophytes exist today (an example of a “living fossil” is Ginkgo; Gordenko & Broushkin, 2015).

Broadly speaking, with the appearance of seed and flowering plants (140 Mya or earlier; Herendeen, Friis, Pedersen, & Crane, 2017; Wikström, Savolainen, & Chase, 2001) came a trend leading from the long-lived tree and clonal habit to plants that, by displaying persistent juvenile characters and precocious reproductive development, obeyed the Romano Rule (live fast, die young; Thomas, 2017a). Monocots and dicots diverged more than 100 Mya (Doyle, Endress, & Upchurch, 2008) and grasses appeared later, about 60–70 Mya (Prasad et al., 2011). Grass-dominated biomes expanded from about 50 Mya. Hominids arrived within the last 3–7 million years (Raven & Thomas, 2010). Ancestors of the grass species that feed the human race today can be traced to the time when the first hominins were beginning to emerge, setting the scene for the rise of agriculture (Thomas, 2017a).

The key factor in the developing relationship between grassland, and later cereal, species and human evolution was sugar. Starch provides a high-glycaemic hit and profoundly influenced hominin brain size, the form of the skull and digestive tract and, consequentially, behaviour and culture (Hardy, Brand-Miller, Brown, Thomas, & Copeland, 2015). Starch is only the second most abundant source of sugar: about half of global biomass is accounted for by cellulose. Humans cannot directly digest and utilise cellulose; but grasslands are extensively populated by animals that can. Meat and dairy are sources of protein and fat but,

more significantly, hunting, herding and livestock farming allow access to cellulose (Thomas, 2017b). One of many possible definitions of the Anthropocene (Lewis & Maslin, 2015) is the era of human dependence on starch and cellulose.

“Enlightened” cultures may revere trees and deplore deforestation and environmental degradation. But the fact is, the vast majority of humanity does not share these attitudes and is merrily slashing and burning for all it is worth (Figure 1). Over the course of human history an estimated $2.4\text{--}3.4 \times 10^9$ ha (42–51%) of forest cover has been lost. The present-day area of cropland is of the same order of magnitude, about 5×10^9 ha (Thomas, 2017a). Although it is not as simple as a case of one kind of land use replacing another, the food, feed, fibre and fuel needs of humanity are certainly among the most potent drivers of deforestation. This can be traced back to the dawn of human evolution, when grasses enlisted us as mercenaries in their war on trees, and we took the King’s Shilling in the form of polymerised glucose. All of us, from the most powerful down, remain enslaved by grass – not just as a source of food but for our leisure and entertainment too (Thomas, 2017a).

The earliest soils and the earliest roots of the earliest terrestrial plants

In order to survive on land, the newly arrived plants needed to develop structural support and anchorage, waterproofing and the means to acquire and translocate nutrients and

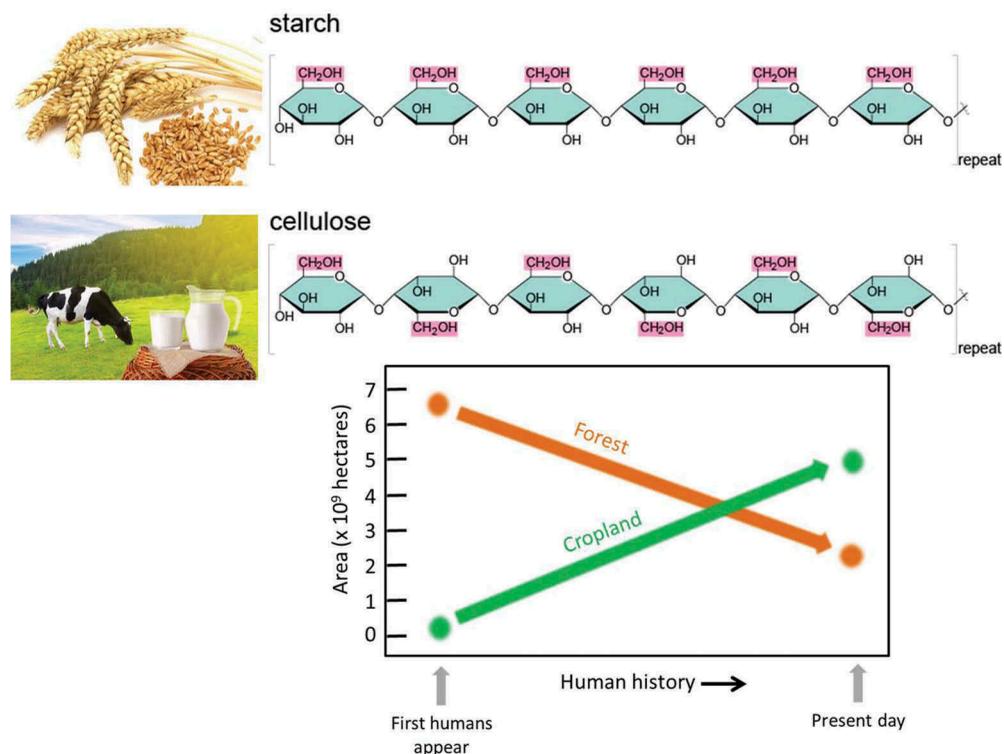


Figure 1. Forests pay the price for human addiction to the sugar in starch and cellulose. About 50% of global forest cover has been lost as human population and area of cropland expanded.

water. But significant beyond plant adaptation to the new environment was the development of roots (Bardgett, Mommer, & De Vries, 2014). The first land plants (such as those of the Rhynie flora, dated to 407 Mya; Edwards, Kenrick, & Dolan, 2018) lacked roots, relying on rhizomes and corm-like structures with rhizoids for attachment and uptake of nutrients and water. Plant-fungus alliances date from the earliest period of life on land (Strullu-Derrien, Selosse, Kenrick, & Martin, 2018). Arbuscular mycorrhiza-like associations have been identified in bryophytes and early vascular plants, and mycorrhization and arborescence are tightly connected. Overall, the importance of soil fungi and mycorrhizal systems for plant evolution and global change cannot be overstated.

Roots evolved in a piecemeal, stepwise fashion and independently in several major clades through the Devonian period (416–360 Mya), when functionality and complexity rapidly expanded (Hetherington & Dolan, 2018). Roots facilitated weathering, pedogenesis (soil formation) and positive feedback effects on plant development, with global consequences (Algeo & Scheckler, 1998). Short-term outcomes include intensified pedogenesis, nutrient release, eutrophication, anoxia and organic carbon sequestration (Figure 2). Over the longer-term, there was a trend towards the tree lifeform, profound changes in landscape and soil profiles, large-scale transfer of atmospheric carbon to soils and carbonate sediments (think of the white cliffs of Dover for example), and episodes of glaciation and extinctions.

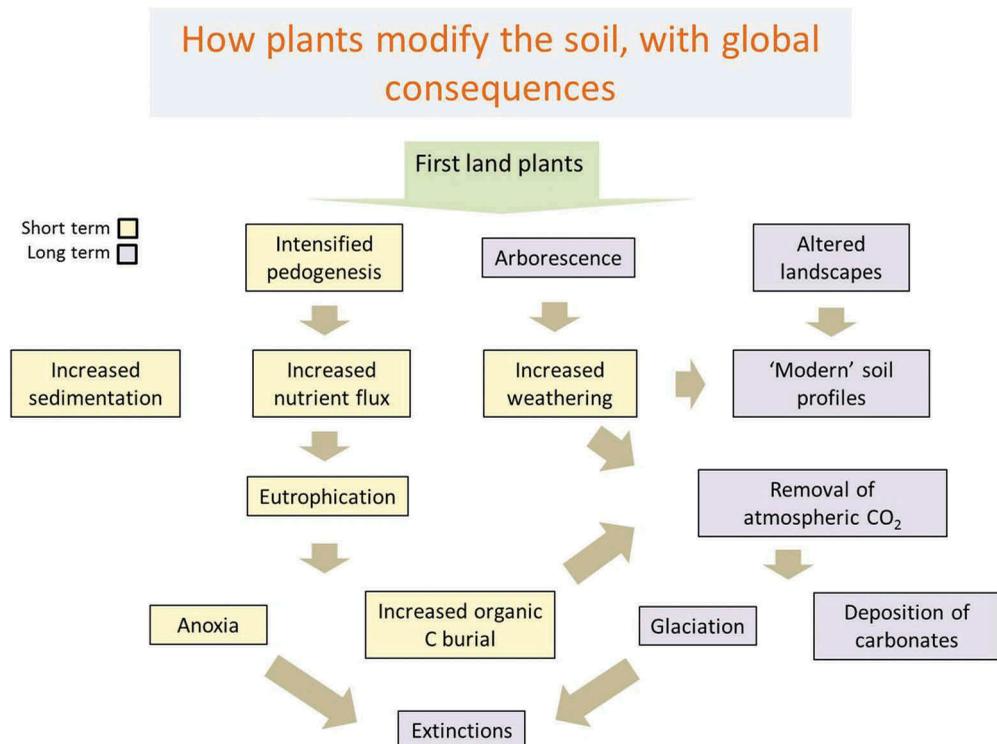


Figure 2. The joint venture between plants and soil during the evolution of life on land had global implications.

Terraformation by Devonian trees

A step change in plant size occurred in the Devonian (Algeo & Scheckler, 1998). Trees are big and tough, as a consequence of the fact that most of their cells (more than 95%) are dead (Thomas, 2016). Devonian forests were home to a range of tree forms (Kenrick & Strullu-Derrien, 2014). The bases of cladoxylopid trunks (Gilboa trees) had mangrove-like aerial root mantles that probably functioned in water conduction and support, as well as absorption (Driese, Mora, & Elick, 1997). Other Devonian tree forms had larger and deeper root systems (Morris et al., 2015). Tree roots are immensely strong, capable of breaking the toughest rocks and physically agitating the soil (Pawlik, Phillips, & Šamonil, 2016); as unfortunate householders faced with the problem of subsidence sometimes learn to their cost. Programmed disposal of cells, tissues and organs, and the throw-away lifestyle are the essence of tree development and adaptation (Thomas, 2017a). Plant litter contributed greatly to evolutionary and geochemical changes in the Devonian and beyond (Algeo & Scheckler, 1998).

At the beginning of life on land, atmospheric CO₂ concentration was 20 times higher than at present. The rise of forests in the Devonian was a leading cause of declining atmospheric CO₂ towards the Carboniferous and Permian. This reverse greenhouse effect resulted in a prolonged glaciation period (Royer, Berner, Montañez, Tabor, & Beerling, 2004).

Tree-grass warfare goes underground

The grass life-form arose about 70 Mya and differs fundamentally from that of trees (I call grasses “anti-trees”), particularly in shoot and root architecture and the location of growing points. Grassland ecosystems expanded greatly from about 50 Mya (Strömberg, 2011). Grasses, unlike forest trees, are adapted for grazing and trampling. The distinctive biologies and ecologies of grassland plant species, and the animals that graze them, are the outcome of antagonistic coevolution (Pennington & Hughes, 2014). Fire favours grassland species over forests. It is a natural and essential environmental factor in many regions of the world and has been called a “global herbivore” (Bond & Keeley, 2005). Some woody species in fire-prone habitats have adapted by going subterranean – for example the geoxyles that form the South African “underground forests” (Maurin et al., 2014).

Grasses avidly mine the soil for silicates, depositing them as resistant surface structures (phytoliths). As grasslands expanded, phytoliths released by fire, grazing and decay began to appear in the marine record and there was a consequent surge in populations of siliceous diatoms and in ocean productivity (Falkowski et al., 2004). This in turn sucked more CO₂ out of the atmosphere and contributed to another period of glaciation. Such global consequences of plant-soil interactions are recurrent themes during evolution.

The savanna ecosystem is an example of how trees and grasses coexist and compete. Savanna trees grow within extensive areas of pyrogenic grasses and, in contrast to forest trees, have become adapted to fire and browsing above ground and competition for resources below. Establishment of forest trees is deterred by herbivory, but conversely such trees can deploy shading to overcome resistance to intrusion (Priyadarshini et al., 2016). Modelling the relationship between forest trees and savanna trees and grasses leads to the rather counter-intuitive conclusion that by moderating their potential to out-compete their grass neighbours,

savanna trees can keep encroachment by aggressive forest trees at bay. Ratajczak, D’Odorico, and Yu (2017) call this the “enemy of my enemy” hypothesis. Below-ground competition is a major determinant of ecosystem composition and is played out through a complex network of plant traits and soil cycles (Figure 3). At one extreme are the fast-moving grassland types, at the other the more conservative forest components, with nutrient status and herbivory among the most influential drivers (Bardgett, 2018). These considerations are of much current climate-change interest as the need for carbon-sequestration strategies becomes ever more urgent.

Lessons about sustainable soils from (pre-) history

Throughout the history of life on land, soils and plants have formed a creative partnership that not only built and sustained the terrestrial environment, but also geo-engineered profound changes in the atmosphere and oceans. Now we see the world’s population increasing by about 80 million a year. At the same time, 10 million hectares of cropland worldwide have been abandoned annually due to soil erosion and a further

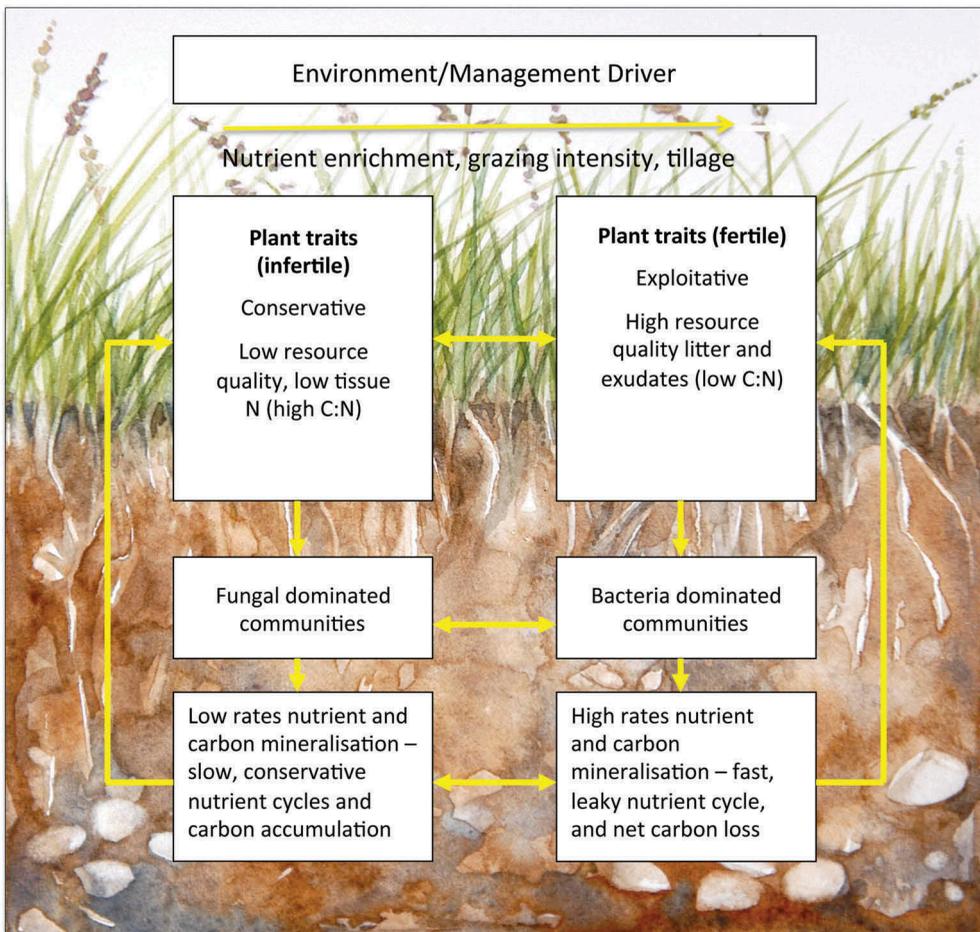


Figure 3. Plant traits influence carbon and nutrient cycles in forest and grassland soils (reproduced with permission from Bardgett, 2018).

10 million hectares are critically damaged each year by salinity. In 1960, each member of the world's population was supported by an average of 0.5 ha of agricultural land; today the figure is 0.23 ha and falling. At the same time the tide of deforestation shows no sign of turning, exerting even more pressure on soil resources. In the global carbon cycle, soil is one of the largest repositories (an estimated 2.5 trillion tons of carbon), and root turnover, determined by the lifespan of fast-cycling absorptive roots, is a major factor in the carbon, nutrient, and water cycles for plants and whole-ecosystems. Evolutionary history tells us that we need to nurture our soils, not just to feed us, but to calm the raging environmental and climatic fevers that threaten the future of humanity itself (Gosling, Gast, & Bending, 2017; McCormack, Eissenstat, Prasad, & Smithwick, 2013).

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Disclosure statement

No potential conflict of interest was reported by the author.

Notes on contributor

Howard Thomas was born and educated in Wales and, after a research career including visiting professorships at Universities in Japan, the United States and Switzerland, he is now emeritus Professor of Biology at Aberystwyth University. He has published extensively on plant development and has a special interest in the science-humanities connection. He is a Fellow of the Learned Society of Wales, a Trustee of the New Phytologist and co-author of *The Molecular Life of Plants* (2013, Wiley) and *Food and the Literary Imagination* (2014, Palgrave). His most recent books are *Senescence* (2016), *The War Between Trees and Grasses* (2017) and *The Tale of the Three Little Pigments* (2018).

References

- Algeo, T. J., & 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: Biological Sciences*, 353, 113–130.
- Bardgett, R. D. (2018). Plant trait-based approaches for interrogating belowground function. *Proceedings of the Royal Irish Academy*. Retrieved from www.jstor.org/stable/10.3318/bioe.2018.05pr.
- Bardgett, R. D., Mommer, L., & De Vries, F. T. (2014). Going underground: Root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, 29, 692–699.
- Berner, R. A. (1997). The rise of plants and their effect on weathering and atmospheric CO₂. *Science*, 276, 544–546.
- Bond, W. J., & Keeley, J. E. (2005). Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, 20, 387–394.
- Doyle, J. A., Endress, P. K., & Upchurch, G. R. (2008). Early cretaceous monocots: A phylogenetic evaluation. *Acta Musei Nationalis Pragae, Series B, Historia Naturalis*, 64, 59–87.
- Driese, S. G., Mora, C. I., & Elick, J. M. (1997). Morphology and taphonomy of root and stump casts of the earliest trees (Middle to Late Devonian), Pennsylvania and New York, USA. *Palaios*, 12, 524–537.

- Edwards, D., Kenrick, P., & Dolan, L. (2018). History and contemporary significance of the Rhynie cherts—Our earliest preserved terrestrial ecosystem. *Philosophical Transactions of the Royal Society B*, 373, 20160489.
- Falkowski, P. G., Katz, M. E., Knoll, A. H., Quigg, A., Raven, J. A., Schofield, O., & Taylor, F. J. (2004). The evolution of modern eukaryotic phytoplankton. *Science*, 305, 354–360.
- Gordenko, N. V., & Broushkin, A. V. (2015). Ginkgoales: Some problems of systematics and phylogeny. *Paleontological Journal*, 49, 546–551.
- Gosling, P., Gast, C., & Bending, G. D. (2017). Converting highly productive arable cropland in Europe to grassland:—A poor candidate for carbon sequestration. *Scientific Reports*, 7, 10493.
- Hardy, K., Brand-Miller, J., Brown, K. D., Thomas, M. G., & Copeland, L. (2015). The importance of dietary carbohydrate in human evolution. *Quarterly Review of Biology*, 90, 251–268.
- Herendeen, P. S., Friis, E. M., Pedersen, K. R., & Crane, P. R. (2017). Palaeobotanical redux: Revisiting the age of the angiosperms. *Nature Plants*, 3, 17015.
- Hetherington, A. J., & Dolan, L. (2018). Stepwise and independent origins of roots among land plants. *Nature*, 561, 235–238.
- Kenrick, P., & Strullu-Derrien, C. (2014). The origin and early evolution of roots. *Plant Physiology*, 166, 570–580.
- Lewis, S. L., & Maslin, M. A. (2015). Defining the anthropocene. *Nature*, 519, 171–180.
- Maurin, O., Davies, T. J., Burrows, J. E., Daru, B. H., Yessoufou, K., Muasya, A. M., ... Bond, W. J. (2014). Savanna fire and the origins of the ‘underground forests’ of Africa. *New Phytologist*, 204, 201–214.
- McCormack, M. L., Eissenstat, D. M., Prasad, A. M., & Smithwick, E. A. H. (2013). Regional scale patterns of fine root lifespan and turnover under current and future climate. *Global Change Biology*, 19, 1697–1708.
- Morris, J. L., Leake, J. R., Stein, W. E., Berry, C. M., Marshall, J. E., Wellman, C. H., ... Beerling, D. J. (2015). Investigating Devonian trees as geo-engineers of past climates: Linking palaeosols to palaeobotany and experimental geobiology. *Palaeontology*, 58, 787–801.
- Pawlik, Ł., Phillips, J. D., & Šamonil, P. (2016). Roots, rock, and regolith: Biomechanical and biochemical weathering by trees and its impact on hillslopes—A critical literature review. *Earth-Science Reviews*, 159, 142–159.
- Pennington, R. T., & Hughes, C. E. (2014). The remarkable congruence of New and Old World savanna origins. *New Phytologist*, 204, 4–6.
- Plackett, A. R. G., & Coates, J. C. (2016). Life’s a beach – The colonization of the terrestrial environment. *New Phytologist*, 212, 831–835.
- Prasad, V., Strömberg, C. A. E., Leaché, A. D., Samant, B., Patnaik, R., Tang, L., ... Sahni, A. (2011). Late Cretaceous origin of the rice tribe provides evidence for early diversification in Poaceae. *Nature Communications*, 2, 480.
- Priyadarshini, K. V., de Bie, S., Heitkönig, I. M., Woodborne, S., Gort, G., Kirkman, K. P., & Prins, H. H. (2016). Competition with trees does not influence root characteristics of perennial grasses in semi-arid and arid savannas in South Africa. *Journal of Arid Environments*, 124, 270–277.
- Ratajczak, Z., D’Odorico, P., & Yu, K. (2017). The enemy of my enemy hypothesis: Why coexisting with grasses may be an adaptive strategy for savanna trees. *Ecosystems*, 20, 1278–1295.
- Raven, J., & Thomas, H. (2010). Quick guide: Grasses. *Current Biology*, 20, R837–R839.
- Royer, D. L., Berner, R. A., Montañez, I. P., Tabor, N. J., & Beerling, D. J. (2004). CO₂ as a primary driver of phanerozoic climate. *GSA Today*, 14, 4–10.
- Strömberg, C. A. (2011). Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences*, 39, 517–544.
- Strullu-Derrien, C., Selosse, M.-A., Kenrick, P., & Martin, F. M. (2018). The origin and evolution of mycorrhizal symbioses: From palaeomycology to phylogenomics. *New Phytologist*, 220, 1012–1030.
- Thomas, H. (2016). *Senescence*. Aberystwyth: Thomas.
- Thomas, H. (2017a). *The war between trees and grasses*. Aberystwyth: Thomas.
- Thomas, H. (2017b). A green epoch in the evolutionary history of biological energy sources. *Nature Ecology and Evolution*, 1, 1214.
- Wikström, N., Savolainen, V., & Chase, M. W. (2001). Evolution of the angiosperms: Calibrating the family tree. *Proceedings of the Royal Society B*, 268, 2211–2220.