

Letters

Xylem hydraulic evolution, I. W. Bailey, and Nardini & Jansen (2013): pattern and process

Introduction

Scientific fields flourish when they enjoy an abundance of important hypotheses to test. It is hard for a field to grow if its aspiring students do not know what its main hypotheses are and where to find them. Notwithstanding, there is a persistent tradition in the comparative wood anatomical literature of attributing major causal evolutionary hypotheses to the prominent wood anatomist I. W. Bailey and his associates, even when their entire body of work of four decades (1918–1957) in fact contains no such hypotheses (Baas, 1976; Olson, 2012a). Sending aspiring students of xylem to Bailey for inspiration and direction does them a disservice because they will look in vain for the hypotheses in need of testing. For xylem studies to draw on a solid foundation, it is essential to understand what Bailey did accomplish as well as what he did not. A recent commentary (Nardini & Jansen, 2013, on Feild & Brodribb, 2013) raises an opportunity to examine the missing-in-action hypotheses in Bailey's work regarding the evolutionary transition between scalariform and simple perforation plates. To examine this issue, I briefly summarize Bailey's thinking and contrast it with the main causal hypothesis that has been proposed to explain the scalariform-simple transition. I mention some of the important themes from Bailey's work that find parallels in current xylem studies, comment on how to frame questions of evolutionary causes, and conclude by emphasizing that there are many interesting open questions in the study of the functional significance of variation in xylem structure.

In 1918, Bailey and collaborator W. W. Tupper published a much-cited and rarely-read paper purporting to examine the relationship between cell size and trunk size across the woody plants. The study was burdened by the inconvenience that the authors neglected to gather the requisite stem size data. They noticed an interesting thing, though: the vessel elements that had scalariform perforation plates tended to be very long and narrow, whereas those with simple perforation plates were often very short and wide. By picking and choosing from across the 'dicots', Bailey and his associates found that they could line vessel elements up in a continual graded series from the longest scalariform plated elements to the shortest simple plated ones. Over a series of subsequent studies, they interpreted this long scalariform → short simple series as a ladder of evolutionary progress, concluding that simple perforation plates evolved via a progressive loss of bars from scalariform perforation plates (e.g. Frost, 1930). Simple

perforation plates very well may have evolved from scalariform ones, meaning that Bailey and his associates arrived at what could be a correct and important conclusion.

While unquestionably an admirable inference, Bailey arrived at his conclusion via reasoning that was largely decades out of date even in 1918. Despite working in the early twentieth century, a time of much debate regarding the mechanisms of evolution (Gould, 2002; Shanahan, 2004), Bailey's thinking was unaccountably pre-Darwinian. He believed fervently in 'Haeckel's law' that ontogeny recapitulates phylogeny (Bailey, 1910; Frost, 1930). That doctrine had been conclusively rejected as a universal generalization by Bailey's time (e.g. see the historical accounts of Russell, 1916 or De Beer, 1930). Bailey believed that evolution progressed via linear series more at home in Medieval notions of the Great Chain of Being rather than the branching phylogenetic bush that had been *de rigueur* in evolutionary thinking for over 60 yr (Lovejoy, 1936; O'Hara, 1992; Bryant, 1995). He thought about the drivers of evolution in terms of murky notions of progress rather than mechanisms such as natural selection. Hardly justifiable notions even a century ago.

Despite his shaky conceptual base, Bailey seems to have arrived at a potentially correct inference of the polarity of the scalariform → simple transition (though see Wheeler & Lehman, 2009). He anchored his inference of evolutionary transition in a case that just happened to fit his conceptual scheme. There are many plants that have scalariform perforation plates in the primary and first-formed secondary xylem but not in the later secondary xylem (many monocots, some Myristicaceae, etc.). That is, the ontogenetic transitions parallel the phylogenetic ones (see Mabee, 1989; Bryant, 1995). Bailey also employed what is now known as outgroup comparison, which reasons that given variation in the group of interest, the ingroup, the state not shared with the outgroup is the derived one (Kitching *et al.*, 1998). In the flowering plants we find both vessel bearing and tracheid-bearing plants. The conifers have tracheids, so the possession of vessels in the flowering plants must be derived. Long scalariform-plated vessel elements look a lot like angiosperm tracheids, suggesting that the scalariform condition must be ancestral and the simple the derived one. The inference certainly seems a plausible one, even though in general ontogeny does not infallibly recapitulate phylogeny and even though evolution is manifestly not an inexorable linear progress. If evolution is not inexorable, then something must drive it. To look for a cause driving the scalariform-simple trend, we can now return to Nardini & Jansen (2013).

In implying that Bailey 'accounts for' patterns of xylem evolution, Nardini & Jansen (2013) give readers the incorrect notion that there was any causal evolutionary content in Bailey's thinking. Evolutionary biologists study patterns in nature and try to infer something about the processes that generated them (e.g. Eldredge & Cracraft, 1980). The remarkable fit between

organismal form and function is a pattern. Natural selection, a process, is usually invoked to explain the pattern. This is the correct form of a causal evolutionary explanation: process causing pattern, pattern diagnosing process. Explaining a pattern by reference to another pattern is incorrect evolutionary reasoning (cf. Blomberg & Garland, 2002, on the pattern often called ‘phylogenetic inertia’ and Crisp & Cook, 2012, on the pattern known as ‘niche conservatism’). If there is no hypothesized process in Bailey’s writings, then citing the Baileyan trends attempts to explain a pattern by reference to another pattern, effectively stating that ‘simple perforation plates are derived from scalariform ones (the pattern to be explained) because simple perforation plates are derived from scalariform ones (Bailey).’ Instead, thinking in pattern–process terms leads to Carlquist’s Ratchet rather than Bailey’s Inexorable Progress of unspecified causation.

Bailey’s inexorable progress vs Carlquist’s Ratchet

Wood anatomists dedicated themselves wholesale to the study of Baileyan trends for five decades following Bailey and Tupper, without a single time citing any cause at all for the trends. Instead, they were consumed in efforts to identify whether this plant was on a ‘higher plane of phylogenetic specialization’ than that plant, a pointless exercise driven by the Baileyan notions of linear progress (Olson, 2012a). This began to change in 1966 with the publication of Carlquist’s ‘Wood anatomy of Compositae: a summary with comments on factors controlling wood evolution’, the paper that quietly founded the field of ecological wood anatomy. Ecological wood anatomy is the effort to understand wood anatomy–environment associations and structure–function adaptation in the xylem (Olson, 2005). Several workers before had postulated adaptive hypotheses regarding wood–environment associations (e.g. McDougall & Penfound, 1928, or Webber, 1936). However, they made few generalizations and attracted no followers. By contrast, Carlquist’s work aimed to explain global patterns of wood anatomical variation: why some plants have wide vessels and others narrow ones, why some plants have grouped vessels and others solitary ones, and why some woods have tracheids but others fibers (Carlquist, 1985; Rosell *et al.*, 2007). His broad scheme was fleshed out in subsequent publications (e.g. Carlquist, 1975, 1980, 1996, 2001), and attracted followers active to this day (e.g. Baas, 1976; Baas *et al.*, 1983; Alves & Angyalossy-Alfonso, 2000; Lens *et al.*, 2004; Crivellaro *et al.*, 2012, etc.). Significantly for our discussion here, Carlquist’s framework also contains a causal mechanistic scenario that might have driven the scalariform → simple perforation plate transition at the heart of the Baileyan scheme, something I call ‘Carlquist’s Ratchet’.

Carlquist’s Ratchet is a hypothesis explaining why plants seem repeatedly to have made the scalariform → simple perforation plate transition, and why this transition seems to be largely unidirectional. It goes like this (see Carlquist, 2001, for a summary; also Carlquist, 1975, 1996). Vessels arose in ever-moist locales via lysis of most or all of the primary membrane in the grouped pits of tracheid endwalls, leading to the formation of scalariform perforation plates. Plants that conduct more water with a given unit of solar energy input should, all things being equal, fix more carbon

and make greater investments in vegetative growth and reproduction. In cool, ever-moist areas like highland tropical cloud forests, conduction is more or less constant and always low. In such habitats there is no major selective disadvantage in having conduction-impeding bars jutting across vessel perforations. However, these bars appear to be a major disadvantage in areas with marked seasonal fluctuations in water availability. In these situations, selection would favor the variants in a population with the highest peak rates, because it is these individuals that would be able to fix the maximal amount of carbon per year, with simple perforation plates conducting far more water per unit time (Christman & Sperry, 2010). So today we find the majority of plants with scalariform perforation plates in cool, ever-wet places like the highland tropics, and as a rule there are few plants with scalariform perforation plates in highly seasonal habitats such as warm deserts or tropical dry forests (Baas, 1976). The ‘ratchet’ comes in when plants with simple perforation plates reinvade cool, moist habitats, taking up residence beside plants with scalariform plates whose ancestors presumably never left the cloud forest. In these situations there is no selective disadvantage to having simple plates, and thus no pressure to reevolve scalariform ones (even though the developmental potential to do so is certainly present; many anatomists have documented the odd anomalous scalariform like plate in otherwise simple-plated clades, cf. Olson, 2012b). When plants lose the scalariform plate, they do not regain it, hence a ratchet. This is the first causal hypothesis proposed to explain the scalariform–simple transition and its apparent irreversibility. This hypothesis is not to be found anywhere in the 50+ yr of Baileyan writings following Bailey & Tupper (1918). The Baileyan scheme makes no reference to any real process, so there is no way that it can ‘account for’ the origin of any xylem trait.

Carlquist’s Ratchet was the first hypothesis that postulated a plausible evolutionary cause for the Baileyan perforation plate trends. Like any good hypothesis, it has spun off many additional questions that continue to be debated to the present day. For example, why are scalariform perforation plates present in so many lineages (Fig. 1)? It is not at all clear what process of diversification through time would lead to the pattern observed today. Certainly a simple linear scale of Baileyan progress cannot explain it. Does study of scalariform plates in the ‘basal’ angiosperms necessarily reveal anything about early angiosperm evolution simply by virtue of their phylogenetic position (Feild & Wilson, 2012)? What is the role of embolism resistance vs conductive efficiency in the evolution of perforation plate morphology (Sperry *et al.*, 2007; Christman & Sperry, 2010)? Although there are few scalariform-plated species in hot places, in cold temperate areas, scalariform plates might occasionally have been adaptively co-opted, with bars potentially sieving out gas bubbles post-freezing, facilitating refilling (Zimmermann, 1983; Sperry, 2003). In some mangroves, thick bars might help resist vessel deformation (Carlquist, 1975). Is there a ratchet at all, or have scalariform plates reevolved from simple plated ancestors (Feild & Wilson, 2012)? For that matter, are simple perforation plates always derived evolutionarily from scalariform ones? Whereas one of the two earliest known vessel-bearing wood types, *Icacinoxylon*, did have scalariform plates, the contemporaneous *Paraphyllanthoxylon* type had simple perforation

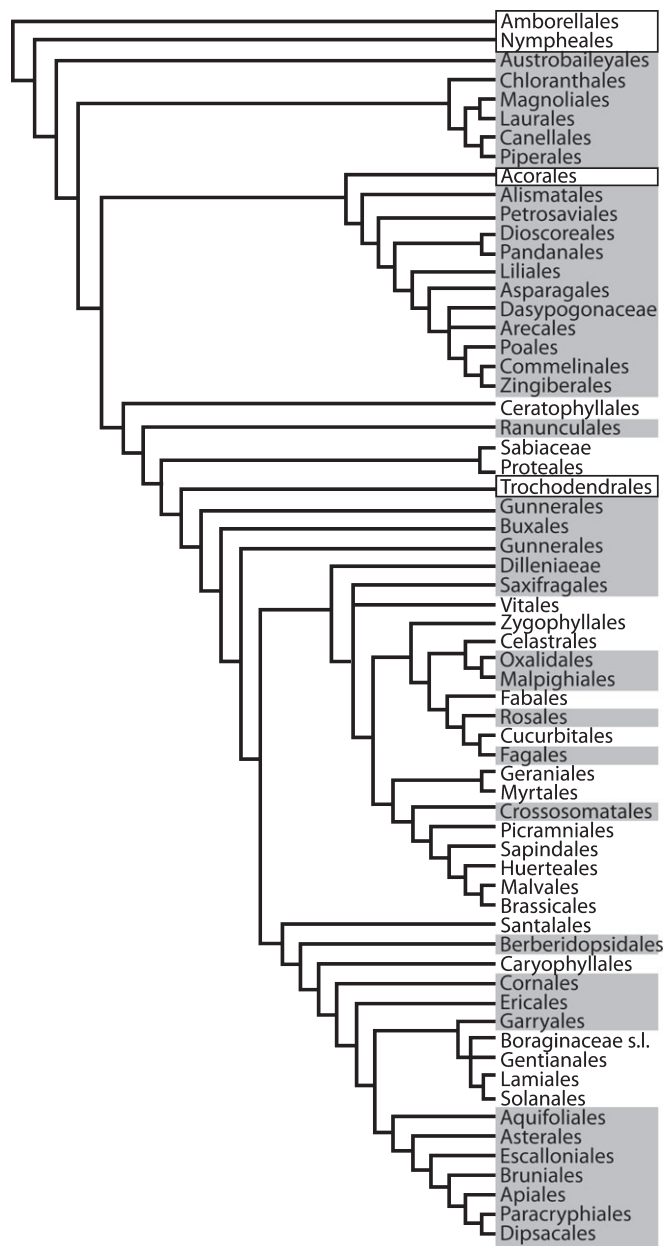


Fig. 1 Scalariform perforation plates and the ordinal-level phylogeny of Stevens (2001 onwards). Clades in which scalariform perforation plates are found (usually also in addition to simple perforation plates in other species, sometimes in addition to species with tracheid-only wood, as in Canellales) are shaded in gray. Vesselless clades are boxed. Shading refers to first-formed xylem in monocots, secondary xylem in the rest. How to tell the difference between vesselless plants and those with vessels is not always clear, and presence/absence mapping masks continuous variation within groups. But whatever the exact classification used, it is clear that scalariform perforation plates are scattered throughout the flowering plant phylogeny. A simple scheme of 'advancement' along a linear series provides no reason to predict the observed pattern. An inexorable trend of successive replacement of scalariform perforation plates by simple ones would lead to all modern plants having simple plates. Species that have scalariform perforation plates come from lineages that have for the most part never left ever-moist habitats. The plates are lost as lineages invade habitats where conductive rates vary markedly throughout the year.

plates (Wheeler & Lehman, 2009; Falcon-Lang *et al.*, 2012), hardly 'general support' for the Baileyan scalariform → simple pattern, *pace* Nardini & Jansen (2013; see also Takahashi & Suzuki, 2003, on greater antiquity in the fossil record as the smoking gun needed to identify scalariform plates as ancestral; they cite studies such as Wheeler & Baas (1991) as showing changes in relative abundance through time but not relative antiquity). My intention here is not to finger Carlquist's Ratchet or any other single explanation as the 'correct' one and call it a day. Instead, the goal here is to show that there are many interesting open causal questions found in the structural xylem literature, and that, importantly, none of them are to be found in the Baileyan literature. Bailey was a pioneer in his broad comparative approach spanning all of the 'dicots', for his insightful developmental studies of cambial activity, for his detailed studies of groups such as Icacinaceae and Cactaceae, and many other aspects. However, causal evolutionary hypotheses were not among his contributions.

An additional aspect of Baileyan writings that often confuses readers is a troublesome use of terminology. The moral for current students of xylem is to replace Baileyan terminological vagueness with conceptual rigor. Nardini & Jansen (2013) state that the Baileyan 'phylogenetic trends' of 'specialization' 'account for' the findings of Feild & Brodribb (2013). Bailey never explained what these key terms mean. With regard to 'phylogenetic trends', Bailey's tendency to think in linear terms about a branched phylogeny can only be attributed to a misunderstanding of evolution (see O'Hara's brilliant 1992 treatment of linear-vs-bush thinking). As to 'specialization', even Bailey did not know what he meant. Baileyans used the term in at least six (six!) different senses (Olson, 2012a), sloppy thinking that is no basis for building a firm field of structural xylem study. For anyone wanting to understand xylem evolution, Bailey's writings are foundational. But for foundational works like the Bible or Shakespeare, it is necessary to understand their context and limitations. Olson (2012a) is a guide to help readers navigate the confusing terms in the Baileyan literature.

Conclusion

Students of xylem must explain patterns via appeal to processes. In this regard Feild & Brodribb's (2013) study of leaf vein density and perforation plate type provide us with an example for studies of functional wood evolution. Feild & Brodribb (2013) looked for correlation between leaf xylem structure and vein density, and connected their observations to data on relative photosynthetic efficiency. The efficient conduction associated with simple perforation plates allows for very narrow leaf veins that can in turn pack densely, effectively energizing metabolically greedy tissue. Density in turn seems positively associated with photosynthetic rate. Finding that similar structural aspects are predictably associated with certain functional aspects regardless of ancestry leads to hypotheses of convergent evolution, one of the key sources of evidence for inferring adaptation. No notions of evolution as inexorable progress driven by a mysterious, never-specified force are needed. Carlquist's Ratchet might help explain the Baileyan trends, but readers will be disappointed if they look to Baileyan writings for anything resembling a real evolutionary mechanism, much less one

involving environmental selection pressures or any other process leading to pattern.

Nardini & Jansen (2013) are right: work such as that of Feild & Brodribb (2013) does help explain major evolutionary transitions in the structural evolution of plant hydraulic systems. Like all wood anatomists, I share Nardini & Jansen's admiration for Bailey's pioneering work. But Bailey was wrong about a great many things, including much of the reasoning that led to the things he was probably right about. Devoid as it was of process, the Baileyan scheme stifled decades of research on important subjects. Rather than participating in important evolutionary debates for much of the twentieth century, wood anatomists were busy searching for things that were not there, such as inexorable progress along the levels of linear hierarchies (Olson, 2012a). To build a firm link between the study of xylem structure and function, it is important to understand what Bailey did accomplish, as well as where the shortcomings of the Baileyan literature lie. If we xylem aficionados let our admiration of Bailey cloud our thinking, we mistake the content of Baileyan writings, ignore the literature on the adaptive mechanisms driving wood anatomical evolution, and invert the correct structure of causal evolutionary explanation.

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Key words: adaptation, comparative wood anatomy, evolution, major trends of xylem evolution, natural selection, pattern and process, scalariform perforation plates, xylem hydraulics.

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