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Conifer–Angiosperm Interactions: Physiological Ecology and Life History

Christopher H. Lusk

ABSTRACT. Worldwide, conifers are most successful on sites subject to chronic stresses that limit productivity (low temperatures, nutrient poverty, poor drainage). They are poorly represented in the lowland tropics but are often important in montane tropical forests. Here I explore some functional differences between leaf and xylem traits of conifer and angiosperm trees and their implications for the distributions of these two groups on environmental gradients. Analysis of a global data set shows that compared with angiosperm trees, conifers tend to have longer-lived leaves with greater mass per area (LMA) and lower mass-based photosynthetic capacity. As leaf life span is thought to be the main determinant of nutrient retention time, the prominence of conifers on infertile soils worldwide is at least partly attributable to thrifty use of nutrients through long leaf life spans. Furthermore, because leaf life span correlates with litter decomposition rates, these leaf trait differences could potentially influence the competitive balance between conifers and angiosperms via positive feedbacks on nutrient cycling. Although scaling of leaf life span with LMA is similar in the two groups, angiosperms achieve slightly longer leaf life spans than conifers of similar photosynthetic capacity. This might be caused by less-efficient leaf display in conifers, resulting in the useful life span of leaves being curtailed by self-shading. Representatives of both lineages have narrower conduits in the temperate zone than in the lowland tropics/subtropics, reflecting selection for resistance to freeze-thaw embolism in cold climates. However, conduit diameters of conifers and angiosperm trees differ more in tropical and subtropical forests than at higher latitudes. This probably reflects mechanical constraints on maximum tracheid diameters in the homoxylous wood of conifers, preventing this group from producing the highly conductive wood typical of fast-growing angiosperm pioneers in tropical forests. This pattern might explain why coexistence of conifers and angiosperms is more common in temperate forests and on tropical mountains than in the lowland tropics. Impairment of angiosperm carbon gain by freeze-thaw embolism during cold weather may further narrow performance differences between the two lineages on temperate sites. Differences in canopy residence time probably deserve more attention as a determinant of conifer-angiosperm coexistence in many temperate forests, the longer life span of conifers compensating for infrequent recruitment.

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INTRODUCTION

Conifers were dominant in forests worldwide during the Triassic and Jurassic (Florin, 1963; Miller, 1977) but have since been largely replaced by angiosperm trees in the lowland tropics, as well as losing much ground in temperate forests. Conifer dominance is now restricted mainly to cold or infertile sites (Bond, 1989), although they coexist with angiosperms in a variety of forest types (Enright and Hill, 1995; Becker, 2000). The advance of angiosperms at the expense of conifers and other lineages may have significantly altered ecosystem processes in forests. It has been suggested, controversially, that rainforests as we know them are a product of changes in ecosystem water fluxes resulting from angiosperm innovations in anatomy and physiology (Boyce et al., 2009). Accelerated nutrient cycling is another possible consequence of the angiosperm revolution at the end of the Cretaceous (Berendse and Scheffer, 2009).

Angiosperm success was initially attributed to reproductive innovations (Raven, 1977; Regal, 1977). Biotic pollination, used by many angiosperms, might require less investment in pollen than wind pollination and might be more effective at achieving sexual recombination in low-density populations. Vertebrate seed vectors might have dispersed seeds further and to safer sites. After reviewing fossil and contemporary evidence, Midgley and Bond (1991) concluded there was little support for the reproductive hypothesis. For example, isolated female trees of wind-pollinated *Podocarpus* in South African forests sometimes set appreciable quantities of seed (Midgley, 1989), calling into question the supposed inefficiency of wind pollination in dense, species-rich forests. Furthermore, vertebrate-dispersed fruits, far from being a uniquely angiosperm innovation, are also found in many conifers such as *Taxus, Podocarpus*, and *Dacrydium*.

In contrast, Bond (1989) argued that the outcome of competition between angiosperms and conifers could be determined during the juvenile phase, as a result of vegetative differences between these two groups. Tracheids, being limited to relatively small diameters, are usually less conductive than angiosperm vessels. This is likely to limit the ability of conifer seedlings to supply leaves with water and hence constrain carbon gain and growth. Bond (1989) further contended that very small initial leaf areas restrict the growth rates of young conifer seedlings; although some conifers can attain high productivity in later life by accumulating many leaf cohorts, their seedlings are likely to be outcompeted by angiosperms on productive sites that permit rapid growth. The more sophisticated vascularization of angiosperm leaves also enables them to produce a wider variety of leaf sizes and shapes (Bond, 1989), giving them advantages in light interception efficiency (C. H. Lusk, unpublished data). Bond (1989) famously applied the "tortoise and hare" metaphor to competition between conifers and angiosperms. In essence, conifers are relegated mainly to cold or infertile sites because these adverse environments nullify or reduce the potential growth advantages of the angiosperm "hares," preventing them from outpacing the "tortoises."

Bond's landmark paper is first and foremost a synthesis of ideas, and relatively few data were then available to test or explore the mechanisms involved. The intervening 20 years have witnessed tremendous growth of plant physiological ecology; although only a handful of empirical papers have directly addressed the issue of conifer-angiosperm interactions (e.g., Becker et al., 1999; Lusk et al., 2003; Brodribb et al., 2005), a good deal of relevant data and ideas have nevertheless been published. Although both lineages encompass a wide range of maximum growth rates, comparative studies of seedlings confirm that even relatively "harelike" conifers such as *Pinus* species are unable to match the performance of the fastest-growing early successional angiosperm trees (e.g., Cornelissen et al., 1996; Reich et al., 1998). Differences between maximum seedling growth rates of late successional conifers and angiosperms have also been reported in some studies (e.g., Hattenschwiler and Korner, 2000) but not in others (e.g., Shipley, 2002), suggesting that some angiosperms are also rather "tortoiselike."

Developments in plant physiological ecology have also given us a better understanding of the traits underlying variation in plant growth and survival in different habitats (e.g., Lambers et al., 1998). Of particular relevance here is our increased understanding of the traits that enable conifers to dominate many forests on cold or infertile sites despite slow seedling growth rates (Sperry et al., 2006). This chapter examines data on some stem and leaf traits relevant to carbon gain and growth of juvenile conifers and angiosperms and, therefore, likely to influence the outcome of competition between them. I also briefly consider evidence that differences in adult longevity contribute to the coexistence of conifers and angiosperms in some temperate forests.

CONDUIT DIAMETERS

It has long been recognized that vessels tend to be more conductive than tracheids, as their diameters are usually larger (Zimmerman and Brown, 1971). According to the Hagen-Poiseuille law, conductivity of a conduit is proportional to the fourth power of its diameter. All else being equal, a conduit with a diameter of 60 μm should thus conduct about 16 times more water than one with a 30 μm diameter.

More recently, there has been a better understanding of the trade-offs associated with variation in xylem anatomy and how small conduits can be advantageous in certain situations. Conduit diameter is strongly correlated with susceptibility to freeze-thaw embolism (Davis et al., 1999). When xylem sap freezes, air bubbles form inside conduits; when the ice thaws, these bubbles can either dissolve back into the sap solution or expand to fill the entire conduit, blocking water transport to the subtended leaves. There is less risk of freeze-thaw cavitation in small conduits because the bubbles formed therein are small and easily redissolved during thawing, unless xylem tensions are very high (Hammel, 1967; Feild and Brodribb, 2001). As a result, species with narrow conduits suffer much less loss of hydraulic conductivity after freeze-thaw events. This is probably one of the main factors underlying the prominence of conifers in cold climates worldwide.

Some angiosperms in tropical forests have very large vessel diameters (e.g., Ewers et al., 1990). This presumably reflects a lack of selection for resistance to freeze-thaw embolism in tropical climates and the advantages of heteroxylous wood: as fibers do most of the job of supporting the tree's weight, vessel diameters are not subject to strong mechanical constraints. On the other hand, the dual role of tracheids in homoxylous wood probably means that conifers are not as well placed to take advantage of the relaxed climatic constraints on conduit diameters in the tropics. Wood made up of very large diameter tracheids would have a very low density and so might be too weak to support a large tree. Tracheid dimensions may thus be limited more by unicellularity and their structural role than by the need to protect against cavitation (Sperry et al., 2006).

If constraints on conduit diameters differ between conifers and angiosperms, this points to one possible explanation for the scarcity of conifers in the lowland tropics. On sites subject to freezing temperatures during the growing season (e.g., temperate maritime climates, tropical mountains), angiosperm vessels will likely be constrained to relatively small diameters, not too different from those of tracheids. On frost-free sites, in contrast, angiosperms could potentially develop vessel diameters far in excess of anything achievable by plants with homoxylous wood, giving them a considerable advantage over conifers in terms of stem conductivity (Sperry et al., 2006). This will influence the economics of hydraulic supply to leaves: for a given investment in stem tissue, angiosperms will be able to irrigate a larger leaf area and/or develop higher leaf conductances, permitting higher potential carbon gain and growth.

Data collated from the literature support the proposal that conifer and angiosperm conduit diameters differ most at low latitudes (Figure 9.1). Reported conduit diameters of evergreen conifers and angiosperms were compared at high versus low latitudes. As data on lowland tropical conifers were scarce, the low-latitude category was broadened to include data from lowland subtropical sites (<30° latitude). Conifers growing at >2000 m elevation in the montane tropics were excluded, as were vesselless angiosperms. Conifer and angiosperm conduit diameters differed only about twofold on average at >30° latitude, and the range of diameters overlapped considerably between the two lineages. In the lowland tropics and subtropics, conifer and angiosperm conduits differed more than fourfold on average, and there was minimal overlap between the two lineages (Figure 9.1). In the tropics, conifers will therefore be at an overwhelming disadvantage in terms of maximum stem conductivity. This is one obstacle to the evolution of fast-growing early successional conifers capable of competing with tropical angiosperms such as *Cecropia* and *Macaranga* (Lusk, 2008). Most conifer species in the lowland tropics are shade-tolerant podocarps, which although never dominant on productive sites, are able to persist in competition with angiosperms by harvesting understory light efficiently (see Brodribb, this volume).

In temperate regions, any angiosperm advantage in stem conductivity will be reduced as the smaller difference in conduit diameters will be compensated to some extent by the high conduit density of homoxylous conifer wood (Sperry et al., 2006). This is one factor contributing to the frequent coexistence of conifers and angiosperms in temperate evergreen forests, although even within this biome, conifer distributions tend to favor relatively cold and/or infertile sites (Enright and Hill, 1995). Even though co-occurring evergreen conifers and angiosperms tend to differ in maximum hydraulic capacity (Feild and Brodribb, 2001; Lusk et al., 2007), this difference will not necessarily translate into higher net carbon gain under all conditions. Feild and Brodribb (2001) found that vessel-bearing angiosperms growing at the timberline in Tasmania were severely affected by freeze-thaw embolism, losing 17%–83% of stem conductivity after a single freeze-thaw cycle. In contrast, none of their coniferous associates lost more than 12% of stem conductivity, as was also true of the vesselless angiosperm *Tasmannia lanceolata*. Even if

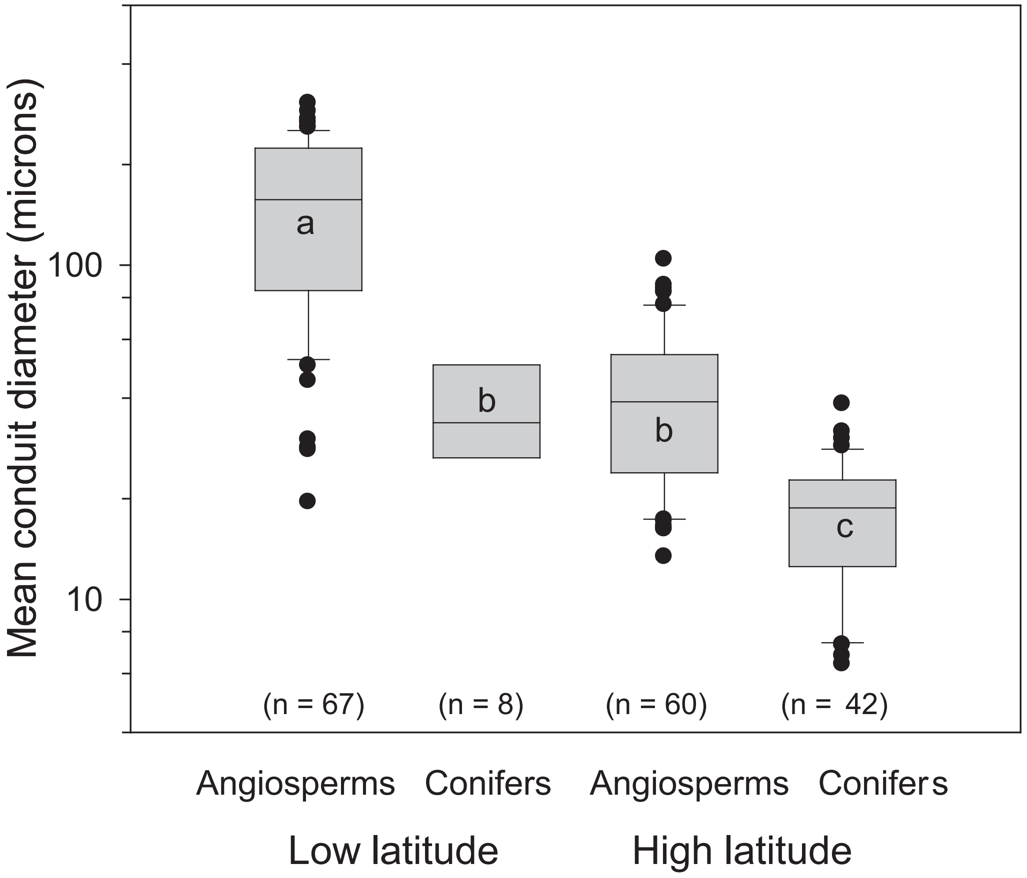

FIGURE 9.1. Conduit diameters of aboveground material from evergreen angiosperms and conifers growing at low latitude (<30°) and high latitude (>30°). Data are taken from sources in the appendix. Box plots show the 10th, 25th, 50th, 75th, and 90th percentiles. Species growing at high elevations (>2,000 m above sea level) were excluded from the low-latitude categories. Values in parentheses show the number of species in each category. Means of categories sharing the same letter do not differ significantly at $p = 0.05$ (Tukey–Kramer honestly significant difference tests). Diameter data were collated by searching BIOSIS previews, obtaining a total of 233 entries from 54 references, representing 166 species. Multiple entries for a species were averaged. Stem diameters in which conduits were measured ranged from 1 to >1,000 mm, indicating that the means presented above include unquantified effects of stem diameter on conduit taper.

temperate evergreen angiosperms gain much more carbon than their coniferous associates during frost-free periods, this could conceivably be reversed during winter, when vessel-bearing angiosperms are likely to be partly embolized much of the time.

LEAF TRAITS

Recent reviews have highlighted coordinated scaling of a suite of structural and functional traits of leaves across species and ecosystems (Reich et al., 1999; Wright et al., 2004). Most leaves worldwide can be ordinated on a single axis of trait variation, reflecting a trade-off between persistence and performance. It must be stressed that this "leaf economics spectrum" represents a general principle of leaf evolution, not a unique law, because the exact nature of bivariate relationships among the traits involved varies geographically (Wright et al., 2005), depending on climate, soils, and which resources are most limiting to plants. It might be asked whether habitat partitioning between conifers and angiosperms reflects different trait-scaling relationships in these two groups (Lusk et al., 2003). For example, conifer leaves have a reputation for longevity (Chabot and Hicks, 1982; Lusk, 2001): does this reflect an ability to achieve longer life spans for a given investment in leaf mass per area (LMA), and might this explain the success of conifers on nutrient-poor soils? Or does the slope of the relationship between LMA and leaf life span differ between conifers and angiosperms?

A global data set (Wright et al., 2004) was used to compare scaling of leaf life span with LMA in conifers and angiosperm trees. The two groups showed no significant difference in the slope of this relationship or in its elevation (Figure 9.2). Despite differences in leaf anatomy, the two groups achieved similar leaf life spans for a given investment of dry matter in leaf tissue per unit area. However, there was a significant shift along the common slope of this relationship: notwithstanding considerable overlap, extant conifer and angiosperm trees are essentially specialized on different regions of the continuum of leaf life spans. Conifers live up to their "tortoise" epithet by mainly occupying the "slow" end, with most having leaf life spans of >2 years. As leaf life span is the strongest influence on variation in nutrient residence time in woody plants (Escudero et al., 1992), the prominence of conifers on poor soils in many regions (Escudero et al., 1992; Read, 1995; Burns and Leathwick, 1996; Lusk and Matus, 2000) is therefore at least partly attributable to thrifty use of nutrients through long leaf life spans. Angiosperm trees are concentrated in the middle region of the spectrum, with most, but by no means all, species holding their leaves for between 4 months and 2 years. The "fast" end of the spectrum is dominated by herbaceous plants.

It was also found that the relationship between photosynthetic capacity and leaf life span differs significantly between angiosperms and conifers (Figure 9.3). The slope was very similar in the two groups, although angiosperms leaves achieved slightly longer life spans at a given photosynthetic capacity. One possible explanation lies in the

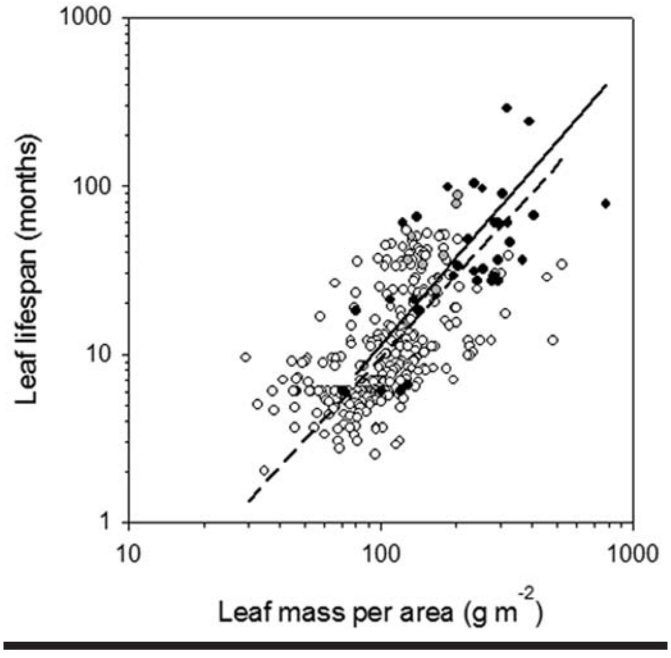

FIGURE 9.2. Relationships of leaf life span with leaf mass per area of evergreen angiosperms (white circles, dashed line) and conifers (solid line; gray circles show podocarps, and black circles represent all other conifers). Major axis tests (Falster et al., 2006) showed no difference in slope or elevation but showed a shift along a common slope ($p < 0.0001$). Data are from Wright et al. (2004).

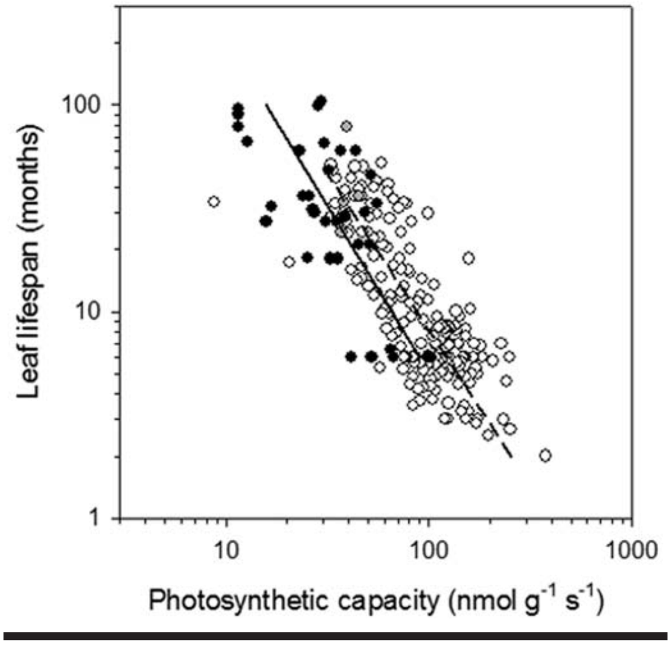

FIGURE 9.3. Relationships of leaf life span with photosynthetic capacity of evergreen angiosperms (white circles, dashed line) and conifers (solid line; gray circles show podocarps, and black circles represent all other conifers). Major axis tests (Falster et al., 2006) showed no difference in slope but showed a significant difference in elevation ($p = 0.003$) as well as a shift along a common slope ($p < 0.0001$). Angiosperm leaves therefore had significantly higher photosynthetic capacity, on average, than conifers, as well as living longer than conifer leaves of comparable photosynthetic capacity. Data are from Wright et al. (2004).

fact that large-leaved angiosperms often have more efficient leaf display than conifers (C. H. Lusk, unpublished data); the resulting differences in self-shading may influence the useful life span of leaves.

In view of the subject of this book, an analysis focused specifically on podocarp leaf traits would be advantageous. However, podocarps are not well represented in the global data set. The few data that are available suggest that leaf mass per area, leaf life spans, and photosynthetic capacity of podocarps are unremarkable, falling toward the middle of the range of values encompassed by conifers as a whole (Figures 9.2 and 9.3).

CANOPY RESIDENCE TIME AND COEXISTENCE OF ANGIOSPERMS AND CONIFERS

Bond's (1989) paper focused mainly on the likely impact of leaf and stem traits on relative performance of juvenile conifers and angiosperms, in an attempt to explain past and present habitat partitioning. One point not covered in his synthesis was the likely role of longevity differences in the coexistence of conifers and angiosperms in some forests. Chesson and Warner (1981) proposed that differences in adult longevity underlie persistence mixtures in many communities, including forests. The essence of this general hypothesis is that mixtures can persist if environmental fluctuation permits periodic recruitment of weak competitors that usually survive poorly as juveniles and if their adults are able to survive over long periods of poor recruitment. This "storage effect" is embodied by the dynamics of temperate conifer-angiosperm mixtures. Long canopy residence times enable conifers to coexist with angiosperms in many temperate forests, despite infrequent recruitment (Read and Hill, 1988; Lusk and Ogden, 1992; Carleton et al., 1996; Lusk and Smith, 1998). Data reviews have confirmed that conifers are appreciably longer-lived, on average, than angiosperm canopy trees in temperate forests of both Northern and Southern hemispheres (Loehle, 1988; Enright and Ogden, 1995). These poorly understood differences in longevity might ultimately prove at least as important as light environment partitioning (Lusk et al., 2009) in explaining the dynamics of tree species coexistence in these communities. Much less information on tree longevities is available from tropical forests, although radiocarbon dates suggest that some tropical *Agathis* species can attain ages of up to 1,000 years (Ogden, 1981). The role of longevity differences in explaining the dynamics of tropical forest communities is therefore unclear.

CONCLUSIONS

Developments during the last two decades shed light on several aspects of habitat partitioning between conifer and angiosperm trees. Bond's (1989) emphasis on vegetative traits and competitive ability of juveniles is largely vindicated by evidence of the constraints imposed by xylem and leaf traits on the performance of conifer seedlings. The present state of knowledge permits the generalization that conifers do best in habitats where fitness is more a function of nutrient conservation or cold resistance than of juvenile carbon gain potential and enables us to specify some of the mechanisms involved. More attention could be paid to the mechanisms underlying coexistence of conifer and angiosperm trees in some forests, despite the apparent competitive advantages of angiosperm juveniles. Likely mechanisms include differences in canopy residence time and impairment of angiosperm carbon gain by freeze-thaw embolism during cold weather.

APPENDIX: SOURCES OF CONDUIT DIAMETER DATA IN FIGURE 9.1

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