Opinion

When Short Stature Is an Asset in Trees

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With their imposing grandeur, the small number of very tall tree species attract a disproportionate amount of scientific study. We right this bias by focusing here on the shorter trees, which often grow in the shade of the giants and many other places besides. That tall trees are so restricted in distribution indicates that there are far more habitats available for small trees. We discuss some leading candidates for the mechanisms that limit maximum plant height in any given habitat, as well as why every habitat has a range of plant sizes. At least two attributes — greater adaptation capacity and higher drought resistance — suggest that the forests of the future belong to short trees.

Tall Trees Have Obscured Our Attention to Short Trees

Height is an essential characteristic of what gets called a tree, and although the tallest tree species get a lot of attention [1], the great majority of tree species are in fact short [2–5]. Here, we right this biased attention to the tallest individuals by focusing on short trees; these short trees often grow beneath the giants and in a lot of other places besides. We unify two ideas from recent ecological and evolutionary studies that make it likely that short-statured tree species will better withstand climate change effects compared to tall trees: (i) higher adaptation (see Glossary) capability and (ii) higher resistance to drought. In support of the first mechanism, short-statured trees appear to have, on average, a lower minimum reproductive threshold size than tall species [6], and short generation time gives more opportunity for recombination and more rounds of selection per time period [7,8]. All else being equal, one would expect more rapid adaptation in short-statured tree species. In support of the second mechanism, short-statured tree species have predictably narrower water-conducting conduits than taller species, which appears to make them less vulnerable to conduction-blocking cavitation [4]. One of global warming’s most alarming consequences is the downsizing effect, that is, a shrinkage in average body size over time [9,10]. We explore why trees are likely no exception, and explore the attributes that likely make the forests of the future shorter.

Where to Grow Tall?

Extant individuals of tree species such as Sequoiadendron giganteum, Sequoia sempervirens, Pseudotsuga menziesii (Pacific Coast, USA), and Eucalyptus regnans (southeastern Australia), can surpass 100 m in height. For instance, the tallest specimens of S. sempervirens grow in a small area of California where there is plentiful water and soil nitrogen concentrations can be very high [5]. These conditions are uncommon, and only a narrow combination of temperature and precipitation coincide with the occurrence of the tallest trees. The tallest specimens (>90 m) of the world’s nine tallest tree species grow in climates with an unusually narrow isotherm (with an average annual temperature of just 7.0–15.4°C), and, most conspicuously, with a very low seasonal temperature variation (7.0–19.7°C) [11]. Water availability, in the form of the difference between annual precipitation and annual potential evapotranspiration (P-PET), also appears to be a good predictor of the global tallest forest canopies, with a global quadratic optimum found at around 680 mm of P-PET [12]. This means that maximal height is only expressed in a very narrow combination of environmental conditions that, moreover, are

Highlights

Global warming threatens many tree species, particularly through drought.

We give reasons to think that short-statured tree species are best equipped to face drought and global warming in general because they have a high adaptation capacity and a high resistance to drought-induced cavitation.

Short trees are able to persist in a higher number of niches than tall species, which are much restricted to a narrow climatic belt.

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found only at a relatively short distance from the coast [11]. These conditions appear only in western North America from California to British Columbia and in southeastern Australia (Victoria and Tasmania).

Biologists are still elucidating the factors that limit tree height [5,11–13] (Box 1), but it seems likely that the maximum height of any given community is imposed by some combination of the scaling of plant carbon economy as well as hydraulic factors [4,14,15]. Carbon economy refers to how leaf area, the sites of production of photosynthates, scales with the metabolically active wood (‘sapwood’ plus other parts such as bark that consume the energy fixed by the leaves, but sapwood is by volume the greatest contributor). Given variation in a population, selection should favor a minimal increase or even constant sapwood volume per unit leaf area with height growth. This is because the metabolic demands of a given volume of sapwood are not expected to change with height. So, a cubic meter of living stem or root demands the same amount of photosynthates from the leaves in a tree 10 m tall as in a tree 100 m tall. But the biophysical challenges of providing leaves with water and in providing metabolically hungry tissues with photosynthates changes radically with height growth. As a result, although the details remain to be worked out, there should be a limit to what the productivity of a given habitat can sustain in terms of sapwood growth in a growing season, and, because the volume of a tree is directly proportional to its height, a limit to height. Any factor that limits productivity should limit the maximum height at any given site.

Likewise, hydraulic factors, the mechanisms of conduction of water from roots to leaves, are also plausibly involved in imposing limits to height. Plant water-conducting conduits widen from the stem tip to the base in such a way that conductance per unit leaf area can remain constant with height growth (or at least that the drop in conductance with height growth is minimized [16–18]). This means that taller plants have predictably wider conduits [4,19]. If wider conduits are more vulnerable to embolism, all else being equal, taller individuals should be more vulnerable than shorter conspecifics. If height is associated with vulnerability, this would help explain why maximum height varies across climates. It would also explain why plants grow to different heights in different microsites and why so many plants remain at the same height for decades or centuries [1,20]. These phenomena are consistent with the idea that plants grow in height until they reach the maximum mean conduit diameter that is compatible with the embolism risk posed by the microsite they experience. So, selection should favor different

Box 1. Height Variance across Communities

Although maximum height varies across communities, maximum height of the shortest woody species does not, and virtually all communities have wide ranges of plant height at any given time. As maximum plant height changes across communities, so does variance. Why all communities have a range of heights would seem to posit a different question than what factors impose limits to maximum height across communities, but they are perhaps related in the following way. An examination of any plant community shows that there is an array of growth forms in plants, with most of them being shorter than the maximum possible height at the site. However, it seems possible that the factors that we identify here (shorter species with higher capacity for adaptation and higher resistance to drought than taller species) are operative across height ecological strategies, that is, the different height-related lifestyles found in each community, from understory shrubs to short trees to the tallest emergents. For example, maximum height in the tallest tree species in a given community might be taller by virtue of deeper roots tapping into more dependable water. With its shallower roots, an understory shrub in the same community might be exposed to more fluctuations in water availability, imposing a narrower maximum conduit diameter and shorter maximum height.

Whatever the exact causes of the limits of maximum height, and even the factors favoring ranges of heights across communities, it is clear that the tallest trees are highly restricted in where they can grow [11,12]. With such highly specific conditions only expected to become more narrowly distributed under changing climates, shorter trees will surely become even more common.

Glossary

Adaptation: differential survival and reproduction due to heritable within-species variation with fitness consequences, leading to a fit between organismal form and function. Also used to describe the traits resulting from this process.

Drought: a prolonged period of abnormally low rainfall, leading to a shortage of water with detrimental effects on organisms.

Embolism: xylem conduit blockage that commonly occurs under water stress conditions, caused by bubbles of air or other gasses.

Hydraulic failure: an event occurring when water transport is disrupted in a large number of embolized vessels, resulting in the desiccation of plant tissues. Hydraulic failure is an important cause of tree mortality under drought conditions.

P-PET: the difference between annual precipitation (P) and annual potential evapotranspiration (PET); a measurement of selective pressure an environment imposes from lack of water.

Phenotypic plasticity: the adaptive ability of one genotype to produce different and environmentally appropriate phenotypes when exposed to different environments, such that performance/fitness are higher in that environment than without the plastic adjustment.

West, Brown, and Enquist (WBE) model: an allometric model that, among other things, predicts the tip-to-base widening of plant (and animal) conduits along the vascular system. Named after the model developers Geoffrey B. West, James H. Brown, and Brian J. Enquist, University of New Mexico (USA).
maximum heights across communities, as well as the capacity for individual plants to detect the xylem tensions that they are exposed to and set their conduit diameters accordingly, via height [19]. Most importantly, the possible link between tree height and conduit diameter also suggests that as droughts become more frequent or severe, plants growing in formerly moist areas will be excessively vulnerable given novel dry conditions. All else being equal, the largest individuals of a species, with their vulnerable conduits, will be especially prone to mortality, just as is being observed worldwide [21–24].

So, although the exact mechanisms leading to height limitation are still actively debated (see Outstanding Questions), there are good reasons to expect that future climates, with more climatic extremes including drought, will often kill large trees outright or lead to death of terminal branches. In their place will be shorter trees, and we turn to two likely reasons why this is so now.

High Adaptation Capability

Because of their shorter generation times, on average, small trees should have more opportunities for selection and thus a higher capacity for adaptation. In general, the crown volume in trees, in which propagules can be produced, scales approximately with the cube of canopy radius. Thus, individuals that attain a greater stature will have a disproportionally greater reproductive output compared with shorter individuals of the same species [25,26]. The cost of this greater fecundity, however, is that taller growing individuals usually need to grow to a larger threshold size to attain reproductive maturity [7,8,13,25]. So, there should in general be a trade-off between time to first reproduction and height [27] (but see [28]). On average, then, the tallest growing trees in the ‘tall tree’ climate are likely to have long generation times and fewer rounds of selection per unit time (centuries, say) [29,30]. In contrast, the greater number of generations for a given time period in short-statured trees would offer the possibility for relatively rapid local adaptation [7,8], and even speciation [29]. If heritable variants that arise in each generation are better suited to new climate conditions, then the means of these populations will shift along with the climate. So, if adaptation to novel climates is sufficiently fast with regard to the rate of climate change, small trees should survive best into novel climates. This capacity for adaptation might be one reason that some short-statured species have such wide ecological tolerances. To be sure, many small tree species have very narrow ecological tolerances and small ranges, but all of the trees that have very wide distributions are short (two remarkable examples are given in Box 2). Just as conspicuous is that tall trees are restricted in distribution,

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**Box 2. Short-Statured Tree Species Ranging across Very Wide Precipitation Gradients**

In southern South America, two tree species exemplify that short-statured trees can span vast environmental ranges, far wider than any even approached by tall tree species. Embobuthrum coccineum (Proteaceae) and Nothofagus antarctica (Nothofagaceae) are able to grow in contrasting environments including waterlogged soils in very moist rain forests (with up to 10,000 mm of annual precipitation; Isla Madre de Dios, 51° SL, Figure IA), in temperate forests (1100 mm), and in dry sites near the steppe along with xerophytic plant species, where precipitation barely reaches 400 mm [48] (Figure I, B and D), and from sea level to high elevation, where they can occasionally reach treeline [49]. Although they are not the dominant species, very wet locations do support *N. antarctica* and *E. coccineum* (Figure I, A and C, respectively). At the extreme of the precipitation gradient, xeric species characterize the steppe landscape with their small and tough leaves and high wood density, and yet *N. antarctica* and *E. coccineum* (Figure I, B and D, respectively) still thrive in these dry environments. Several functional traits of these two species (*E. coccineum* and *N. antarctica*, i.e., EcNa in red) do not appear to vary (climate does not elicit a plastic response in these traits) across a precipitation gradient that goes from 2100 mm (humid) to 1100 mm (mesic) to 500 mm (dry) of annual precipitation compared to local species (others in blue) (Figure I). Other species include *Weinmannia trichosperma* and *Calodexia paniculata* (Convolvulaceae) (wet), *Nothofagus dombeyi* and *Nothofagus pulmillo* (Nothofagaceae) (mesic), and *Maytenus boaria* (Celastraceae) and *Schinus patagonicus* (Anacardiaceae) (dry). *", **", **, and ns, indicate P values of <0.05, <0.01, <0.001, and >0.05, respectively. Photo credits: A, Alvaro Hammamé; B and C, Alex Fajardo; D, Fernán Silva.
Figure I. Two Short Stature Tree Species (Embothrium coccineum and Nothofagus antarctica) Thrive in Contrasting Environments.
even within species that range well beyond the ‘tall tree’ climate, for example, *P. menziesii* and *S. sempervirens*. In addition to being more adaptable, there are reasons to think that small trees are more resistant to a factor becoming ever more common: drought.

**High Resistance to Drought**

With ongoing climate change, recent work has shown that tall trees, contrary to expectations that they should have greater root reach and greater volume for stem water storage, tend to be especially vulnerable to drought [23,31,32]. Current evidence shows that taller individuals within a species have higher risk of decline and ultimately tree mortality due to drought than short-statured conspecifics [24,33]. Although factors such as insects, disease, and fire certainly intervene, hydraulic failure is the single common factor in vulnerability to more frequent, intense, and unpredictable drought events [34]. Plants conduct water in narrow xylem conduits under negative pressure. As trees grow taller, the distance over which water needs to be moved gets longer. With no change in conduit diameter, the amount of wall area, and therefore friction, per unit water volume would increase and conductive rate would drop as trees grow taller. Trees compensate for this increase in friction, however, with a precise widening of conduit diameter from the tip to the base of a tree, at exactly the rate predicted to maintain conductance constant per unit leaf area as a tree grows taller [4,17,18,35]. Conduit diameter appears to be strongly associated with vulnerability to embolism. Although the mechanism is still not clear as to why, narrow conduits appear to confer embolism resistance, with wider conduits embolizing more readily than narrow conduits, at least within individuals or species [36–39]. Although it is traditionally accepted that selection favors narrow conduits in environments with low water availability or cold temperatures [40–42], it is becoming clear that across biomes it is plant height, and not climate per se, that is the main driver of conduit diameter variation [4,43]. Importantly, conduit widening with height is in agreement with the rate predicted by the **West, Brown, and Enquist (WBE) model** of hydraulic optimality [44], confirming its adaptive role. Thus, climate and ecological strategy determine tree height, but tree height is the proximate driver of natural selection on conduit diameter. Therefore, the plastic ability of plants to grow to their maximum conduit diameters, and therefore height, permitted by microsite conditions appears plausibly involved in limiting plant height. Narrow conduits confer embolism resistance and shorter trees have relatively narrow conduits, making short-statured tree species less vulnerable to drought and freezing. This is consistent with the conspicuous dieback of taller specimens under climate change-induced drought in forests worldwide [21–23,33] and the maximum tree height at alpine treelines (3 m) and in dry biomes being very short. In summary, factors such as carbon economy and hydraulics mean that trees are participating in the global reduction in size observed in so many groups of organisms.

**The Downsizing Effect**

Discussion of the ongoing trend of average organismal size decreasing over time, dubbed the downsizing effect, has mainly focused on conspicuous ectotherm animals, leaving plants to only an anecdotal treatment. In addition, studies dealing with the downsizing effect of organisms due to global warming have mainly supported their claim on evidence showing a negative correlation between growth and temperature [9,10,26,45]. They state that a reduction in body size comes as a response to climate change and predict a higher rate of extinction in organisms, something that has already occurred during geological history [26].

The factors we have discussed here give reason to think that trees are proving no exception to the downsizing effect. For one, if maximum permitted mean conduit diameter is a function of the microsite in which a plant finds itself, and plants produce this diameter via height, changing climates will lead to changing heights. Increasing drought will, on average, permit narrower conduits, leading to apical dieback and **phenotypic plasticity** remodeling in a shorter form.
Or, it could kill taller trees outright, leaving shorter and more resistant conspecifics to carry on. If population sizes of the tallest species are sufficiently reduced, they could become extinct. If the tallest species in an area goes extinct, the forests that follow will be shorter. Either way, because of the plastic abilities of shorter trees to adjust height to drier climates, or because of the extinction of obligate tall-growing species, maximum plant size is likely to decrease globally. As part of this process, short-statured tree species will likely maintain or increase their distribution over the coming century. Thus, the predicted increases in extinction rates will act to thin the upper end of the distribution of tree heights. What we identify here are tree traits and thus mechanisms through which persistence or extinction will most likely occur.

**Concluding Remarks**

Many factors contribute to tree mortality with the increasingly severe droughts that accompany climate change [34,46]. Although a great deal remains to be elucidated regarding the link between plant height and climate, enough information is available to predict that short-statured trees will persist under future climate change conditions, and we touch here on two mechanisms. First, short-statured tree species are, on average, able to reach a reproductive threshold before taller species, potentially allowing them to adapt more rapidly to shifts in climate; second, thanks to their narrower conduits, shorter individual trees are likely more tolerant to drought than taller conspecifics.

Although there is every reason to expect forest cover to persist into a warmer and more extreme future, the shorter forests of the future will differ functionally from their taller forbears. Because the largest individuals contribute disproportionately to propagate banks, population demographics could shift seems inevitable. With their lower surface area for a given wood volume, larger individuals usually decay more slowly so the carbon they store is returned more slowly to the atmosphere than small individuals storing an equivalent amount of carbon, necessarily affecting carbon cycling. The capacity of forests to absorb heat appears to be positively related to plant height [47], potentially making future forests even warmer. Smaller crowns have narrower branches and narrower surfaces for epiphytes and the multitude of other organisms that depend on them. All of these factors predict differing forest functions in the short forests of the future.

Based on what is already known, the good news is that there appears to be likely mechanisms for forests to react to climate change-induced drought and even for designing strategies for preparing individual trees for drought. It seems likely that selection on standing variation could favor shorter individuals because of their greater drought resistance capacity, thus leading to shorter forests over time. Even individual plants could react via plastic responses, shedding high branches and resprouting shorter, with shorter conductive paths and narrower, more embolism-resistant conduits. To similar ends, plants could even in principle be proactively pruned in anticipation of drought. Re-growth at a shorter stature should be associated with narrower, more drought-resistant conduits. So, although tall trees are rightly celebrated, our warmer and drier future clearly belongs to the shorter trees.

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**References**


**Outstanding Questions**

Just what factors do limit maximum plant height? Plant biologists have examined everything from hydraulic resistance, gravity’s effects on conduction or even cell turgor, the mechanical support limits of wood, plant photosynthetic productivity, metabolic scaling between photosynthetic source (leaves) and sink (stem and root) tissues, and other factors as limiting plant height, but a firm consensus has yet to emerge. Source-to-sink scaling and hydraulics are the soldest candidates.

Is there evidence of fossil records of losses of the largest trees during climate shifts? The mechanisms we outline predict that tall trees should be rarest during periods of rapid climate oscillation and most abundant during long periods of climate stability. This prediction could be tested by seeing whether the largest fossil stumps known correspond to periods of climate stasis.

What factors lead to diversity in height ecological strategy? Virtually all communities have a range of plant sizes, from understorey to emergent, and only a few species reach the maximum height for any given site. Why such wide ranges coexist at a given site, and what limits the maximum height of each species at a given site, are important topics for research.

Is conduit diameter the cause of hydraulic vulnerability to drought? Many biologists find evidence for a link between conduit diameter and hydraulic vulnerability to drought. Indeed, it is the only current hypothesis that explains many observations, including variation in conduit diameter and plant height across climates, but then why annual growth rings always

How does sapwood volume scale with leaf area? The living tissue of the stem and root (broadly ‘sapwood’ but includes other tissues) consume the photosynthates produced by the leaves. As plants grow there is no reason to expect the metabolic demand of sapwood to change, so there should be an isometric relationship between sapwood and leaf area. If true, this scaling would establish a major pole of selection around which virtually all others would pivot, including the hydraulic system. Moreover, productivity could contribute to limiting height via the sapwood volume that can be supported in any given growing season. Because it requires measuring metabolically active sapwood volume and total leaf area across many individuals, testing such a relationship is empirically daunting.