Do tall trees scale physiological heights?

Does genotypic variation in leaf form and function among tree species reflect adult height or only the seedling regeneration niche? For trees in closed canopy forests, typical adult tree height directly indicates the position of the species in the light hierarchy of the canopy. However, it is unknown whether trees that characteristically differ in mature height have similar or different canopy attributes. Given that light levels decrease vertically in canopies[1,2], and that leaf form and function are linked with light availability as a result of adaptation[3–5] and acclimation[2–6], it is logical to hypothesize that trees that differ in adult height should vary systematically in leaf structure and function.

But do they? If so, how and why? This issue has received little attention in spite of the interest in whether species that regenerate and spend their lives in markedly differing light environments vary in leaf traits: this is the foundation for the classic contrast of sun versus shade plants[3–6]. However, a new paper[7] by Thomas and Bazzaz advances our understanding of trait variation in trees differing in typical adult height. They compared leaf traits of late-successional Malaysian rainforest species that regenerate in shaded-forest understories, but which occupy diverse canopy strata as mature individuals. They discovered that leaf traits of saplings growing in comparable light environments are correlated with adult tree height (i.e. the vertical position and light environment of the canopy of mature trees). Their study is the first to provide quantitative evidence of scaling of leaf traits with tree size and indicates that the mature-tree phase is an important evolutionary 'axis'.

Does tree height select for certain leaf traits?

Phenotypic variation in leaf traits across pronounced light gradients has been a major issue in plant ecology for a long time[5,6], as has genotypic variation that helps to explain species habitat distributions[3,4]. Thomas and Bazzaz note that most sun versus shade trade-offs have been interpreted in relation to successional status, with early-successional species tending to exhibit sun-plant characteristics, and late-successional species exhibiting shade-plant characteristics. The examination of genotypic adaptation among species that regenerate in shaded understories is less advanced[6,8]. Although phenotypic variation in leaf traits has been examined vertically within canopies[2,9], Thomas and Bazzaz provide the first test of whether photosynthetic characteristics have evolved in response to these vertical light gradients. They ask whether species that regenerate in shaded microhabitats, but inhabit different canopy positions as mature individuals, are characterized by innately different leaf attributes: they hypothesize that this should occur given the ubiquitous pattern of decreasing light availability from the top to the bottom of a forest canopy.

Thomas and Bazzaz point out the ecological axiom that photosynthetic physiology is linked to ambient light levels owing to the acclimation of individual leaves of all species to variation in light and to adaptive differences among species, which provide benefits in either high or low light. For instance, it is well known that 'sun plants' tend to have higher light-saturated photosynthetic rates on an area basis than 'shade plants'. Thomas and Bazzaz suggest that tree species differing in adult stature probably differ in realized leaf physiology as mature individuals, as a result of both acclimation to the vertical light gradient found through the forest canopy and intrinsic species differences. In essence, such a comparison would incorporate both genotypic differences and phenotypic responses to light gradients. Moreover, they argue that species of differing adult stature should also show systematic (innate) differences in physiological characteristics as saplings, even when growing under uniformly low light conditions.

They based this key hypothesis on three assumptions. First, photosynthetic characteristics are determined by genetic factors, as well as by acclimation to light conditions, which is clear in any broad species comparison[10]. Second, 'developmental processes determining adult-phase physiology also determine to at least some extent, the morphology and physiology of sapling leaves' (i.e. developmental processes determining adult-phase and juvenile-phase leaves are unlikely to be entirely independent). This suggests that a species is unlikely to be sufficiently plastic to produce leaves of a completely different form and function at the sapling versus adult tree stage (ignoring species that developmentally produce markedly different juvenile versus mature leaves). The third aspect involves the idea that trees attaining a larger size at maturity experience higher ambient light levels on average (i.e. throughout the life cycle). Thus, individuals of these species would be subject to a selective regime favoring the evolution of high light photosynthetic characteristics even if as small seedlings and saplings they occupy approximately comparable light environments as those individuals that do not attain as great a height at maturity.

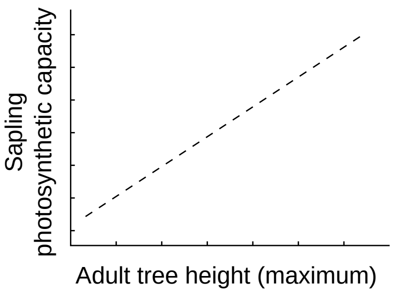
The alternative hypothesis is that a convergence in traits arises from an adaptation to the common understory-regeneration niche, and outweighs divergence arising from adaptations that are important to mature trees. Hence, genotypic differences might not exist for saplings of species that differ in adult height.

A test of tree height in relation to leaf traits

To address these issues, Thomas and Bazzaz implemented a study of 28 late-successional species in the Pasoh Forest Reserve, West Malaysia. To account for possible phylogenetic confounding, they selected species representing four genera, which each include taxa ranging in size from understory 'treelets' to canopy-level trees. For each of the 28 species, they estimated asymptotic height (an index of average maximum height) and measured leaf physiology for mature trees and saplings. To ensure a fair comparison in comparable light environments, they measured saplings of all species in the forest understory at locations where they were growing under similar light levels, thus eliminating acclimation by individuals as a potential explanation for species differences. They measured maximum rates of light-saturated photosynthesis (A_{max}) for all 28 species. For a subset of 12 intensively studied species (three from each of the four genera) photosynthetic light-response curves were also measured.

The results were straightforward: in all genera, sapling A_{max} increased linearly with mature adult height (Fig. 1). This trend was of substantial magnitude (a 2.5-fold variation) and explained much of the variation in A_{max} for both leaf area ($r^2=0.56$) and leaf nitrogen (N) ($r^2=0.75$) bases (i.e. net CO_2 uptake per unit leaf area or leaf N). The pattern was significant for A_{max} on a leaf mass basis, although the relationship explained less of the variance ($r^2=0.23$). The photosynthetic light-saturation point was also greater in trees that attain taller mature stature. Thus, taller trees, whose crowns spend proportionally more time under high light intensity, did have higher sapling photosynthetic capacity than shorter species, supporting the idea that

0169-5347/00/$ – see front matter © 2000 Elsevier Science Ltd. All rights reserved. PII: S0169-5347(99)01734-6



Trends in Ecology & Evolution

Fig. 1. A conceptual view of the interspecific relationship between sapling net photosynthetic capacity and adult tree height for 28 Malaysian rainforest tree species (from Thomas and Bazzaz[7]). Rates of net photosynthesis were measured in the field for saplings growing in comparably shaded-forest understory positions and were related to the typical maximum tree height (the asymptotic height) of conspecific adults in the same forest. The relationship was similar for net photosynthetic capacity expressed on a leaf area (mmol m^{-2} s^{-1}), a leaf mass (nmol g^{-1} s^{-1}), and a leaf nitrogen (mmol CO_2 gN^{-1} s^{-1}) basis.

leaf traits evolve in response to selection at various life stages.

It is worthwhile considering both proximate physiological explanations and the evolutionary explanations for these patterns. The relationships were similar in all four genera, supporting the generality of the finding and supporting the hypothesis that variation in photosynthetic characteristics represents an evolutionary response to the vertical gradient in light availability through the canopy. In spite of regenerating in relatively shaded positions, it is also possible that the 28 rainforest species might differentiate as saplings along light microhabitats within this dark end of the spectrum, in which case, differences in leaf traits among saplings could reflect both the regeneration niche[11] and the adult niche. Data are unavailable to answer this question.

Given the understanding of factors contributing to interspecific variation in A_{max}, how can we functionally explain these findings? Recent analyses indicate that variation in specific leaf area (SLA) and %leaf nitrogen (N) collectively explain most of the variation in A_{max} among terrestrial C_3 species[10]. Therefore, perhaps sapling A_{max} varies with mature tree height following height-related patterns in SLA or %N? It is plausible that species that occupy shadier habitats as adults might have evolved 'thinner' (higher SLA) leaves (the ubiquitous phenotypic acclimation response of tree species). However, this hypothesis is incorrect[7], because sapling SLA was not significantly correlated with average mature tree height, although the correlation was negative as predicted. What about variation in leaf %N or its allocation? For the 12 species sampled, sapling leaf %N was significantly lower (not higher) in species with greater adult tree height[7]. Given that terrestrial species with higher %N generally tend to have higher A_{max} on all three (mass, area and N) bases[10], higher sapling A_{max} in taller species cannot be explained by differences in %N. Because shaded plants allocate N differentially to biochemical versus photochemical constituents of the photosynthetic process[2,12], it is possible that saplings of taller adult tree species might allocate proportionally less N to compounds involved in photochemistry (e.g. chlorophyll), and more to those involved in CO_2 fixation (e.g. Rubisco), than the saplings of the shorter adult species. This would result in higher A_{max} on all three bases and likely influence realized photosynthesis in the low light conditions of the understory – although data are unavailable to address these points.

In summary, although the reasons why sapling A_{max} varies with adult height might have largely evolutionary roots, it should also be manifest in leaf features that are responsible for determining A_{max}. This should be a fruitful area for further research.

Conclusions

The research by Thomas and Bazzaz is important in two main respects. First, it suggests that the evolution of tree foliage traits is probably sensitive to all stages of the life history, rather than just the early-regeneration niche. The much greater mortality rates of trees at the early seedling, rather than adult, stage has led researchers to focus on the early-establishment period as a critical time for selection of plant traits. The Thomas and Bazzaz data suggest that other stages are also important. Second, these findings are important because for the first time there is quantitative evidence about the interspecific scaling of physiology with tree size: this might help us understand variation among species and also has potential utility for modeling. As with all new findings, it remains to be seen whether patterns in other forests will closely or distantly mimic those seen in Malaysia, and if taller trees routinely scale physiological heights.

Peter B. Reich

Dept of Forest Resources,
University of Minnesota,
St Paul, MN 55108, USA
(preich@forestry.umn.edu)

References

1 Yoda, K. (1974) Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. *Jpn J. Ecol.* 24, 247–254

2 Ellsworth, D.S. and Reich, P.B. (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* 96, 169–178

3 Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annu. Rev. Ecol. Syst.* 10, 351–371

4 Givnish, T.J. (1988) Adaptation to sun and shade: a whole plant perspective. *Aust. J. Plant Physiol.* 15, 63–92

5 Bjorkman, O. and Holmgren, P. (1963) Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. *Physiol. Plant.* 16, 889–914

6 Boardman, N.K. (1977) Comparative photosynthesis of sun and shade plants. *Annu. Rev. Plant Physiol.* 28, 155–177

7 Thomas, S.C. and Bazzaz, F.A. (1999) Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. *Ecology* 80, 1607–1622

8 Walters, M.B. and Reich, P.B. (1999) Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? *New Phytol.* 143, 143–154

9 Jurik, T.W. (1986) Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. *Am. J. Bot.* 73, 1083–1092

10 Reich, P.B. *et al.* (1997) From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci. U. S. A.* 94, 13730–13734

11 Grubb, P.J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52, 107–145

12 Evans, J.R. (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* 78, 9–19