

PLANT HYDRAULIC PROPERTIES LIMIT PHOTOSYNTHETIC CAPACITY AND REGENERATION POTENTIAL

GABRIEL KATUL, RAM OREN,
HEATHER McCARTHY, and KIMBERLY NOVICK

1. INTRODUCTION

The fossil spore record suggests that non-vascular plants appeared in wet tropical and temperate areas on the terrestrial surface some 450 million years ago [1-3]. Since that time, plants increased their efficiency of capturing sunlight and photosynthesizing by vertically distributing chlorophyll and photosynthetic machinery, packaged mostly in leaves, along crowns. More sparsely distributed foliage can utilize light more efficiently than compactly arranged foliage, an arrangement in which a small proportion of the foliage receives an oversupply of light while a large proportion of the foliage must do with very low light level. Moreover, in forest settings, positioning leaves above those of the neighbors' is a common strategy for increasing light harvesting and photosynthesis. Thus, since plants moved to land, some species developed crowns that attained great lengths and are positioned at great heights. For species that rely on wind dissemination of pollen and seed, attaining height increases the dispersal distance. Further increase in dispersal distance is gained when attaining height brings a plant crown above those of its neighbors, because of the effect of canopy leaf area on the flow of air. However, not all species rely on height to obtain sufficient photosynthates to grow and reproduce, and not all species rely on height to increase dispersal distance of wind disseminated pollen and seeds. Species that rely on height to support photosynthesis and dispersal must make adjustments to overcome the limitations to water flow between the soil and leaves, so leaves can keep stomata open enough to permit a reasonable rate of photosynthetic CO₂ uptake.

Operating in a desiccating atmosphere, terrestrial plants must maintain photosynthetic tissues at the proper state of hydration. As height increases, the delivery of water to leaves becomes more difficult because of the longer transport path and greater loss of energy for moving water. Thus, attaining height to support photosynthesis and dispersal requires a hydraulic transport system that can adjust as trees grow taller and deliver the necessary amount of water to leaves. Such adjustments do not come without costs, which may ultimately put a limit to height as a solution for increasing photosynthesis and dispersal distance. A trade-off must exist between carbon uptake and water loss, with direct implication to the potential distance of wind dispersal of pollen and seed. This study focuses on assessing the trade-off and its impact on pollen dispersal distance.

Great advances have been made over the past century in understanding of (i) radiation attenuation, scattering, and absorption by leaves within canopies, [4-8] (ii) the relationship between leaf photosynthesis and its inter-cellular CO₂ concentration, [9-15] (iii) delivery of water from the soil pores to the leaves or soil-plant hydrodynamics, [16-28] and (iv) dispersal of seed and pollen [29-36]. These four research thrusts each produced a set of radiative, physiological, hydraulic, and dispersal parameters that can be considered independent. Here we concentrate on hydraulic, biochemical, and dispersal attributes of forest trees. In particular, we analyze two inter-related questions: 1) whether hydraulic and biochemical properties of plants are independent of one another, or do they change in concert as tree height increases, and 2) whether the key attributes that describe the relationship between hydraulic and biochemical properties also explain seed and pollen dispersal. Preliminary experimental and theoretical work on the first question has received recent attention, [37,38] and we use these preliminary findings as a starting point.

2. THEORY

We first identify the plausible functional parameters that link hydraulic and biochemical properties of plants and then proceed to assess their significance on seed and pollen dispersal. To establish the interdependency between hydraulic and physiological properties, the leaf transpiration rate and leaf photosynthesis formulations are reviewed.

2.1. Plant Hydraulics

Within forested ecosystems, the transport of water (per unit leaf area) from the soil to the leaf may be described by Darcy's law, given as

$$E_l = \left(\frac{\psi_s - \psi_l - \rho g h_c}{h_c} \right) k_s \frac{A_s}{A_l}, \quad (2)$$

where E_l is the average transpiration rate per unit leaf area, ψ_l and ψ_s are the leaf and soil water potential, h_c is the canopy height and is used here as a surrogate for the hydraulic path length from the soil to the leaf, ρ is the density of water, g is the gravitational acceleration, k_s is the soil-to-leaf tissue specific hydraulic conductivity, A_s is the sapwood area, and A_l is the leaf area.

Since the interest is in deriving simplified expressions relating plant hydraulic to physiological attributes, we adopt two simplifications:

- 1) $|\psi_s| \ll |\psi_l|$;
- 2) $(-\psi_l - \rho g h_c) k_s \approx c$ where c is a constant.

The first simplification assumes that the soil system is sufficiently hydrated (typical values of $|\psi_l| \sim 1.5 \text{ MPa}$ while typical values for $|\psi_s| < 100 \text{ kPa}$ even at 50% the field capacity of the soil). [Care must be taken when extrapolating the low-dimensional model used in our analyses to cases when $|\psi_s|$ is not much smaller than $|\psi_l|$ (e.g. during drought conditions). During drought conditions, plant function and structure changes with the intensity and duration of water deficit]. The second simplification is approximate because it assumes that leaf pressure must adjust to counteract the extra weight of water that must be pulled up to the leaf surface (i.e., $\psi_l = \psi_r + \rho g h_c$ where ψ_r is a reference leaf pressure). Detailed xylem pressure measurements within redwood trees (*Sequoia sempervirens*), including the tallest known tree on Earth (=112.7 m), collected in the wet temperate forests of northern California supports the argument that $\partial \psi_l / \partial z = \rho g$ [39].

With these two simplifications, we find that:

$$E_l \approx c \frac{A_s}{A_l} \frac{1}{h_c}. \quad (3)$$

Several studies in forested canopies also reported that the ratio of the sapwood area to leaf area is approximately linear with h_c so that: [40,41]

$$A_s / A_l = A' + B'h_c, \quad (4)$$

although exceptions have been noted in some species [42]. The parameters A' and B' vary among species. *Mathematically*, for species that conform to eqn. (4) for a large portion of h_c , $A' \sim a_1 A_l$. Hence, the leaf transpiration rate is given by

$$E_t = (c a_1 A_l) \frac{1}{h_c} + (c B') \quad (5)$$

2.2. Photosynthesis

Leaf photosynthesis is given by the Farquhar *et al.* [11] model, which assumes that photosynthesis is either limited by light or enzymatic properties (i.e. Rubisco), and can be represented as:

$$A_n = \frac{\alpha_1 (C_i - \Gamma^*)}{C_i + \alpha_2} - R_d \quad (6)$$

where R_d is dark respiration, $\alpha_1 = \alpha_p Q_p e_m$ and $\alpha_2 = \Gamma^*$ for light-limited photosynthesis, and $\alpha_1 = V_{cmax}$ and

$$\alpha_2 = \kappa_c \left(1 + \frac{o_i}{\kappa_o} \right)$$

for Rubisco-limited photosynthesis. Here, α_p is the leaf absorptivity for photosynthetically active radiation (*PAR*), e_m is the maximum quantum efficiency for CO_2 uptake, Q_p is the *PAR* irradiance on the leaf, Γ^* is the CO_2 compensation point, V_{cmax} is the maximum catalytic capacity of Rubisco per unit leaf area ($\mu mol m^{-2} s^{-1}$), κ_c and κ_o are the constants for CO_2 fixation and O_2 inhibition with respect to CO_2 , respectively, and o_i is the oxygen concentration in air ($\sim 210 mmol mol^{-1}$).

2.3 Linking Hydraulics and Photosynthesis:

Noting that leaf-stomatal conductance is given by

$$g_s = \frac{E_t}{1.6VPD} = \frac{A_n}{C_a - C_i} \quad (7)$$

permits us to establish a relationship between α_1 and the plant hydraulic attributes:

$$\alpha_1 \approx \frac{C_a \left(1 - \frac{C_i}{C_a}\right)}{1.6VPD} \left[\frac{C_i + \alpha_2}{C_a - C_a} \right] \left[(c a_1 A_l) \frac{1}{h_c} + cB' \right]. \quad (8)$$

The ratio C_i/C_a varies by about 20% (between 0.65 and 0.90 for C3 plants), and may be treated as a constant [37,43] when compared to variations in h_c . In fact, a near-constant C_i/C_a approximation appears to be valid across a wide range of species as can be inferred from the linear relationship between maximum bulk conductance and maximum photosynthetic capacity per unit ground area [44] for tropical, temperate deciduous broadleaved forests, temperate evergreen broad-leaved forests, and herbaceous tundra with an approximate slope consistent with $C_i/C_a=0.82$. Hence, with a constant C_i/C_a , we find that in the case of Rubisco-limited photosynthesis, the maximum carboxylation capacity can be related to the canopy height via

$$V_{c\max} \approx R' \frac{C_a}{VPD} \left(A'' \frac{A_l}{h_c} + B'' \right) \quad (9)$$

where, R' , A'' , B'' can be readily computed from coefficients in equation (8). Having shown that the maximum leaf photosynthetic rate is controlled by A_l/h_c (for a given atmospheric dryness) the next logical question is whether A_l/h_c governs pollen spread.

2.4. Pollen Dispersal

To link the canopy attributes A_l and h_c to pollen dispersal, it becomes necessary to show how these two variables impact pollen trajectory inside and above canopies. These trajectories are difficult to describe because complex turbulent processes govern them. However, using a low-dimensional turbulent transport model, Katul *et al.* [35] showed that the canonical shape of the dispersal kernel is a Wald distribution, given by:

$$p(x_1) = \left(\frac{\lambda'}{2\pi x_1^3} \right)^{1/2} \text{Exp} \left[-\frac{\lambda'(x_1 - \mu')^2}{2\mu'^2 x_1} \right], \quad (10)$$

where

$$\mu' = \frac{x_{3,r} \bar{U}}{V_t} \quad \text{and} \quad \lambda' = \left(\frac{x_{3,r}}{\sigma} \right)^2, \quad x_{3,r},$$

$x_{3,r}$ is the release height, V_t is the pollen terminal velocity, x_1 is the distance from the source, and \bar{U} and σ are the mean longitudinal velocity and the flow velocity standard deviation that can be linked to the vertical velocity standard deviation (σ_w) via

$$\sigma^2 = \kappa_d h_c \left(2 \frac{\sigma_w}{\bar{U}} \right) \quad (11)$$

where $\kappa_d \in [0.3, 0.4]$ is qualitatively connected to the structure of turbulence inside the vegetation (i.e. the mixing length) but must be considered as a semi-empirical parameter here because all the model assumptions (including vertically homogeneous and low intensity flows, instant attainment of terminal velocity upon pollen release, zero inertia of the pollen grain, and the negligible effects of vertical velocity correlation relative to pollen settling time) are lumped into its numerical value. Both \bar{U} and σ_w can be predicted from the leaf area density distribution and drag properties of the canopy using higher order closure principles [45-49]. Figure 1 (see over) illustrates how pollen disperses away from the source as a function of leaf area index (LAI) and release height (often proportional to tree height) for a typical above canopy friction velocity of $u_* = 0.5 \text{ m s}^{-1}$. It is clear that a finite number of pollen grains can travel up to 10 km, and with decreasing leaf area index the tails of the dispersal kernel become 'heavier'. That is, the extreme long-distance events become more probable with increasing height and decreasing LAI . We note that A_l and LAI are not the same quantity, but are directly related through the density of individual trees in a stand and are used interchangeably.

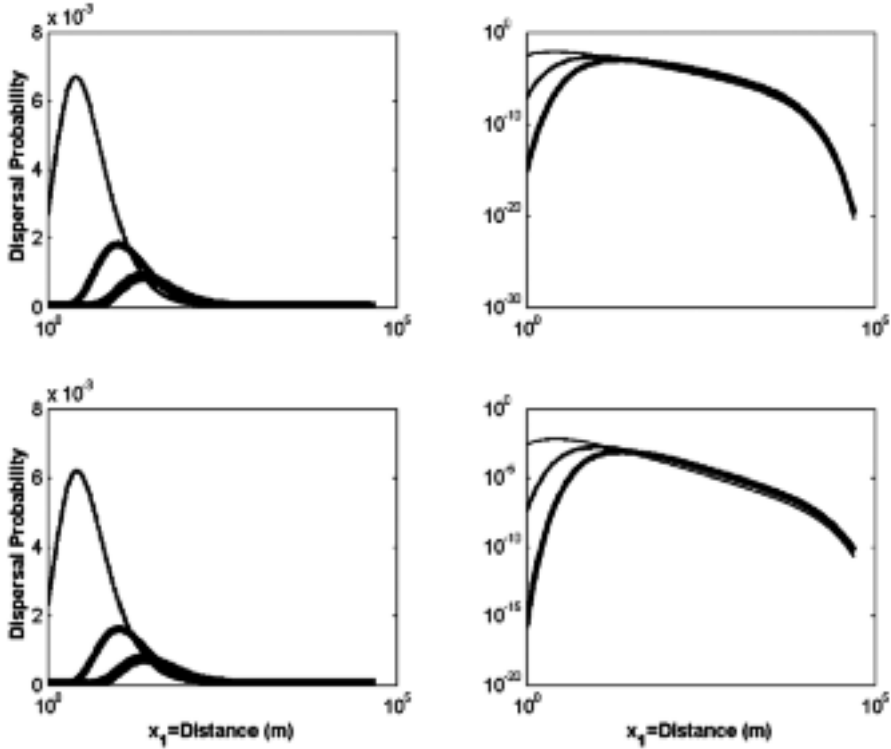


Figure 1. Computed dispersal kernels for a forest with $h_c=35\text{m}$, a typical friction velocity ($u_s=0.5\text{m s}^{-1}$), and $LAI=5\text{ m}^2\text{ m}^{-2}$ (top panels) and $LAI=2\text{m}^2\text{ m}^{-2}$ (bottom panels). The lines indicate different pollen release heights starting with $0.25 h_c$ (thinnest), $0.5 h_c$, and $0.75 h_c$ (thickest). The semi-logarithmic (left) and log-log (right) plots demonstrate the impact of variations in h_c and LAI on the mode and the tails. The assumed terminal velocity (V_t) is 0.05 m s^{-1} .

3. RESULTS AND DISCUSSION

3.1. Linking Plant Hydraulics and Photosynthetic Potential

To explore whether equation (9) correctly predicts the relationship between $V_{c\text{max}}$ and A_l/h_c , we used published data summarized in Table 1 (see over). As predicted, $V_{c\text{max}}$ varied linearly with LAI/h_c for a wide range of forest types (Figure 2, see over), including boreal conifers, temperate broad-leaf forests, maturing loblolly pine forests, and young southern

TABLE 1. Published values for canopy height (h_c), leaf area index (LAI), and maximum carboxylation capacity (V_{cmax}) at 25°C for a wide range of forested ecosystems.

Ecosystem	h_c (m)	V_{cmax} ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	LAI (m^2m^{-2})
Boreal Conifers [73]	14	46	2.04
Temperate Broadleaf Forest [73]	24	40	4.70
Maturing pine plantation [74]	16	59	3.80
6-year-old pine plantation, control [75]	4.1	85	1.65
6-year-old pine plantation, fertilized [75]	6.8	100	3.51

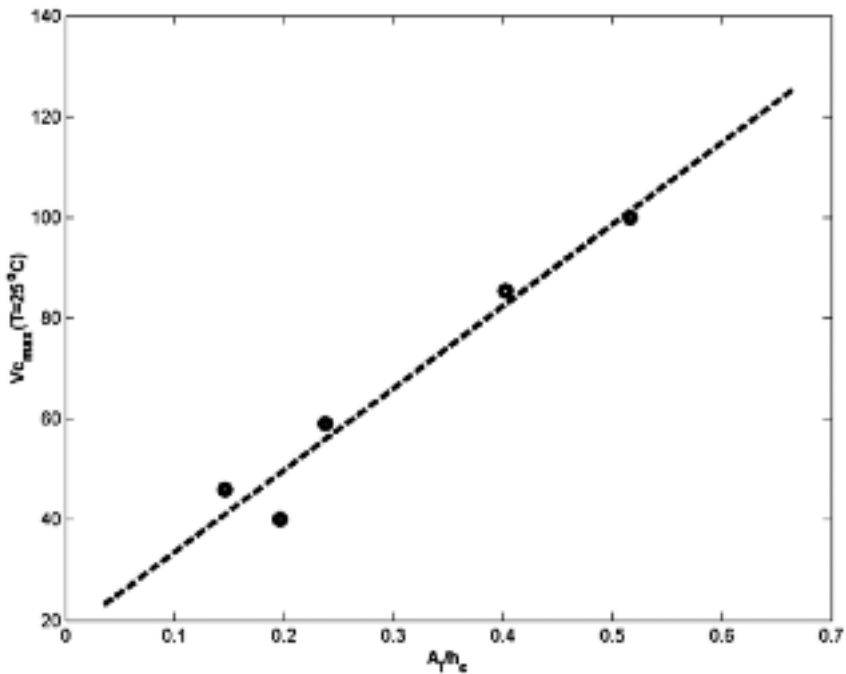


Figure 2. Testing the predicted linearity in V_{cmax} with LAI/h_c from equation (9) for the forest canopies in Table 1.

pine plantations (unfertilized and fertilized with nitrogen). Hence, based on this finding, it is safe to state that canopy height and leaf area can explain variations in the maximum carboxylation capacity (at a reference temperature of 25°C), which is the upper limit for leaf photosynthesis.

Equation (9) is consistent with the linear relationship between photosynthetic capacity and plant hydraulic conductivity reported by Brodrigg and Feild [38] (their Fig. 2) who used a combination of chlorophyll fluorescence and hydraulic analysis on seven conifers and 16 angiosperm rainforest species in New Caledonia and Tasmania (Australia). We are unable to directly employ equation (9) with their results because they reported the mean quantum yield of photo-system II electron transport and provided no information about the other requisite variables. Equation (9) is also consistent with the field observations that photosynthetic rates tends to decline with age even after stands reach a stage of approximately constant LAI [40,50-54].

3.2. Linking Plant Hydraulics and Dispersal Potential

It is difficult to test whether equation (10) correctly predicts the entire dispersal kernel, including long-distance dispersal tails. Katul *et al.* [35] tested the Wald predictions against seed dispersal data for a wide range of species, release heights, terminal velocity, leaf area density, and u_* conditions and noted good agreement ($r^2=0.89$) between predictions and measurements. However, the furthest seed distance reported in their comparison did not exceed 100m.

It is possible to use the Wald model in equation (10) to predict the probability of seed uplifting above the canopy, a necessary condition for long-distance seed dispersal [33,35,36,55]. As shown in Katul *et al.*, [35] the probability of seed or pollen uplifting by the Wald model is given by

$$\Pr(x_{3,r} > h_c) = \frac{\exp\left(2\frac{V_t}{U}\frac{x_{3,r}}{\sigma^2}\right) - 1}{\exp\left(2\frac{V_t}{U}\frac{h_c}{\sigma^2}\right) - 1} \quad (12)$$

Predictions from equation (12) can be compared with uplifting probability estimates determined from vertically arrayed seed traps within and above the canopy. Using the seed release height and terminal velocity data reported in Nathan *et al.*, [33] Figure 3 (see over) shows the comparison between predictions from equation (12) and uplifting probability measure-

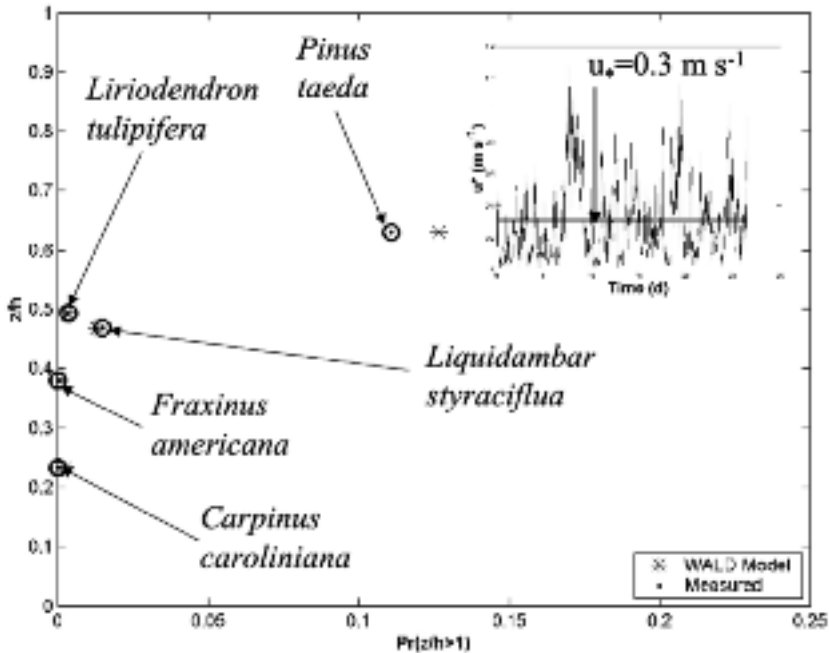


Figure 3. Comparison between measured and modeled uplifting probability for 5 species co-occurring in one 80-100 year-old second-growth mixed Oak-Hickory forest in the Blackwood Division of Duke Forest, near Durham, North Carolina, USA. The ordinate is the seed release height of the species normalized by the mean canopy height (data taken from Nathan *et al.*, 2002, their Table 1). *Inset*: The time series of the friction velocity and its mean value used in the model calculations.

ments (also in Table 1 in Nathan *et al.* [33]). The good agreement between measurements and predictions, despite the uncertainty in the data, lends confidence in the capability of the Wald model to reproduce the necessary conditions leading to long-distance dispersal (LDD, the minimum distance which 99% of the particles do not exceed).

The effect of variations in pollen release height (which is often proportional to tree height [56]) and *LAI* can be combined via simulations to describe the LDD of pollen (Figure 4, see over). We use LDD as a ‘surrogate measure’ for the dispersal potential most relevant to rapid colonization. The analysis in Figure 4 clearly demonstrates that LDD dramatically decreases with decreasing release height and increasing *LAI*. That is, the attributes that regulate maximum photosynthesis also regulate LDD.

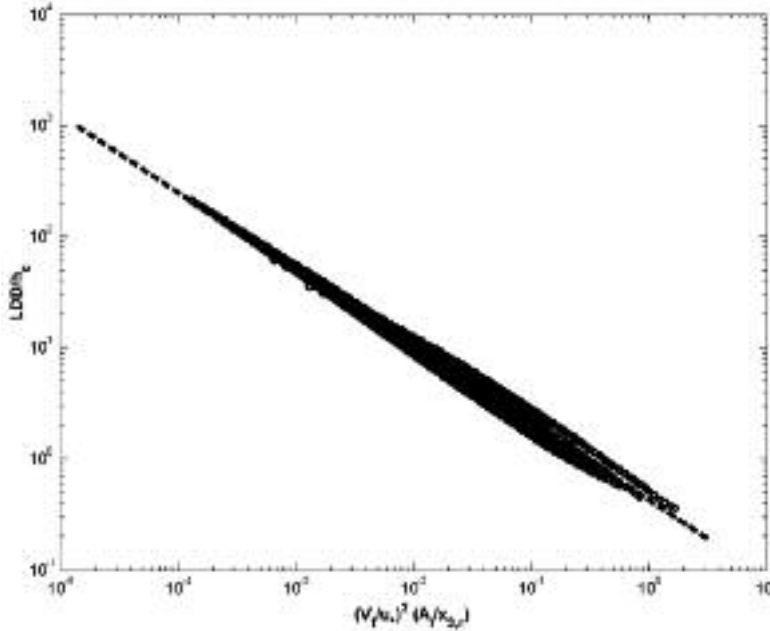


Figure 4. The dependence of normalized long-distance pollen dispersal (LDD) on leaf area index (LAI) and pollen release height ($x_{3,r}$). LDD is normalized by the overall mean canopy height (h_c). LDD is defined as the minimum distance for which 99% of the pollen did not reach. In the simulations, the maximum $A_l=5\text{ m}^2\text{ m}^{-2}$, and $h_c=35\text{ m}$ (typical for a southern hardwood forest).

The dashed line is the regression $\frac{LDD}{h_c} = 0.43 \frac{V_t^2}{u_*^2} \left(\frac{A_l}{x_{3,r}} \right)^{-0.69}$ with $r^2=0.97$.

The model calculations were conducted for $V_t=0.01-0.2\text{ m s}^{-1}$ (typical for pollen) and $u_*=0.1-0.9\text{ m s}^{-1}$.

When combining Figures 2 and 4, we find that for a given LAI , as h_c increases, $V_{c\max}$ decreases (and hence the ability of trees to accrue more height diminishes) in proportion to h_c^{-1} but the dispersal potential (measured via LDD) increases in proportion to $h_c^{0.69}$ (see caption of Figure 4). It is clear from the height exponents that for tall trees, the tradeoff between increasing dispersal potential and reductions in photosynthetic capacity favors the latter. That is, photosynthesis is more sensitive to plant hydraulics than dispersal.

4. BROADER IMPACT

The origin and early evolution of land plants was a significant event in the history of life, with far-reaching consequences for the evolution of terrestrial organisms and global environments. By exploring the engineering solutions that permitted plants to function in a dry atmosphere and, thus, exist on land, we can begin asking about their adaptation and colonization potential in future climates – likely to be warmer, enriched with CO₂, and experiencing higher stochasticity in rainfall. Advances in systematics of living plants, when coupled with low-dimensional ecological theories, may hint at plausible future evolutionary strategies (or extinction).

It is well-worth quoting Lumley's statement [57] about low-dimensional models in the context of turbulent flows: 'in our present state of understanding, these simple models will always be based in part on good physics, in part, on bad physics, and in part, on shameless phenomenology'. Exploring the relationship between the photosynthetic, hydraulic, and dispersal strategies is fundamentally more challenging than turbulence; indeed, turbulence is only one element of the problem. However, recent advances in theory and measurements make it a topic ripe for progress. Perhaps, the recent advances in remotely sensed measurements of canopy vegetation structure and function [58], the estimates of past vegetation spread from the pollen record [59-67], and the advances in measurements and modeling of photosynthesis and plant hydrodynamics [21,41,68-72] will allow us to sieve out the bad physics and shameless phenomenology.

Acknowledgements

This study was supported, in part, by the United States Department of Energy (DOE) through both the Office of Biological and Environmental Research (BER) and the National Institute of Global Environmental Change (NIGEC) Southeastern Regional Center at the University of Alabama (Cooperative Agreement DE-FC02-03ER63613) and by the National Science Foundation (NSF-EAR and NSF-DMS).

REFERENCES

- 1 Heckman, D.S. *et al.*, Molecular evidence for the early colonization of land by fungi and plants. *Science* 293, 1129-1133 (2001).
- 2 Kenrick, P. & Crane, P.R., The origin and early evolution of plants on land. *Nature* 389, 33-39 (1997).

- 3 Wellman, C.H., Osterloff, P.L. & Mohiuddin, U., Fragments of the earliest land plants. *Nature* 425, 282-285 (2003).
- 4 Cescatti, A., Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. 1. Model structure and algorithms. *Ecological Modelling* 101, 263-274 (1997).
- 5 Cescatti, A., Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. 2. Model testing and application in a Norway spruce stand. *Ecological Modelling* 101, 275-284 (1997).
- 6 Smolander, H., Stenberg, P. & Linder, S., Dependence of light interception efficiency of scots pine shoots on structural parameters. *Tree Physiology* 14, 971-980 (1994).
- 7 Stenberg, P., Penumbra in within-shoot and between-shoot shading in conifers and its significance for photosynthesis. *Ecological Modelling* 77, 215-231 (1995).
- 8 Stenberg, P., Implications of shoot structure on the rate of photosynthesis at different levels in a coniferous canopy using a model incorporating grouping and penumbra. *Functional Ecology* 12, 82-91 (1998).
- 9 Farquhar, G.D., Feedforward responses of stomata to humidity. *Australian Journal of Plant Physiology* 5, 787-800 (1978).
- 10 Farquhar, G.D., Dubbe, D.R. & Raschke, K., Gain of feedback loop involving carbon-dioxide and stomata – theory and measurement. *Plant Physiology* 62, 406-412 (1978).
- 11 Farquhar, G.D., Caemmerer, S.V. & Berry, J.A., A biochemical-model of photosynthetic CO₂ assimilation in leaves of c-3 species. *Planta* 149, 78-90 (1980).
- 12 Farquhar, G.D. & Sharkey, T.D., Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 33, 317-345 (1982).
- 13 Farquhar, G.D. & Wong, S.C., An empirical-model of stomatal conductance. *Australian Journal of Plant Physiology* 11, 191-209 (1984).
- 14 dePury, D.G.G. & Farquhar, G.D., Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell, and Environment* 20, 537-557 (1997).
- 15 Farquhar, G.D., von Caemmerer, S. & Berry, J.A., Models of photosynthesis. *Plant Physiology* 125, 42-45 (2001).
- 16 Sperry, J.S., The form and function of the xylem. *Biorheology* 23, 198-198 (1986).
- 17 Sperry, J.S., Relationship of xylem embolism to xylem pressure potential, stomatal closure, and shoot morphology in the palm *rhaps excelsa*. *Plant Physiology* 80, 110-116 (1986).

- 18 Tyree, M.T. & Sperry, J.S., Do woody-plants operate near the point of catastrophic xylem dysfunction caused by dynamic water-stress – answers from a model. *Plant Physiology* 88, 574-580 (1988).
- 19 Sperry, J.S. & Tyree, M.T., Mechanism of water stress-induced xylem embolism. *Plant Physiology* 88, 581-587 (1988).
- 20 Sperry, J.S., Donnelly, J.R. & Tyree, M.T., A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell and Environment* 11, 35-40 (1988).
- 21 Hacke, U.G. *et al.*, Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124, 495-505 (2000).
- 22 Jackson, R.B., Sperry, J.S. & Dawson, T.E., Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science* 5, 482-488 (2000).
- 23 Sperry, J.S., Hydraulic constraints on plant gas exchange. *Agricultural and Forest Meteorology* 104, 13-23 (2000).
- 24 Hacke, U.G. & Sperry, J.S., Functional and ecological xylem anatomy. *Perspectives in Plant Ecology Evolution and Systematics* 4, 97-115 (2001).
- 25 Hacke, U.G., Stiller, V., Sperry, J.S., Pittermann, J. & McCulloh, K.A., Cavitation fatigue. Embolism and refilling cycles can weaken the cavitation resistance of xylem. *Plant Physiology* 125, 779-786 (2001).
- 26 Sperry, J.S., Hacke, U.G., Oren, R. & Comstock, J.P., Water deficits and hydraulic limits to leaf water supply. *Plant Cell and Environment* 25, 251-263 (2002).
- 27 Sperry, J.S., Evolution of water transport and xylem structure. *International Journal of Plant Sciences* 164, S115-S127 (2003).
- 28 McCulloh, K.A., Sperry, J.S. & Adler, F.R., Water transport in plants obeys Murray's law. *Nature* 421, 939-942 (2003).
- 29 Aylor, D.E. & Flesch, T.K., Estimating spore release rates using a Lagrangian stochastic simulation model. *Journal of Applied Meteorology* 40, 1196-1208 (2001).
- 30 Porporato, A., Laio, F., Ridolfi, L., Caylor, K.K. & Rodríguez-Iturbe, I., Soil moisture and plant stress dynamics along the Kalahari precipitation gradient. *Journal of Geophysical Research-Atmospheres* 108 (2003).
- 31 Okubo, A. & Levin, S.A., A theoretical framework for data-analysis of wind dispersal of seeds and pollen. *Ecology* 70, 329-338 (1989).
- 32 Levin, S.A., Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* 1, 431-436 (1998).
- 33 Nathan, R. *et al.*, Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418, 409-413 (2002).

- 34 Cain, M.L., Nathan, R. & Levin, S.A., Long-distance dispersal. *Ecology* 84, 1943-1944 (2003).
- 35 Katul, G.G. *et al.*, Mechanistic analytical models for long-distance seed dispersal by wind. *American Naturalist* 166, 368-381 (2005).
- 36 Nathan, R. *et al.*, Long-distance biological transport processes through the air: can nature's complexity be unfolded in silico? *Diversity and Distributions* 11, 131-137 (2005).
- 37 Katul, G., Leuning, R. & Oren, R., Relationship between plant hydraulic and biochemical properties derived from a steady-state coupled water and carbon transport model. *Plant Cell and Environment* 26, 339-350 (2003).
- 38 Brodribb, T.J. & Feild, T.S., Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant Cell and Environment* 23, 1381-1388 (2000).
- 39 Koch, G.W., Sillett, S.C., Jennings, G.M. & Davis, S.D., The limits to tree height. *Nature* 428, 851-854 (2004).
- 40 Schafer, K.V.R., Oren, R. & Tenhunen, J.D., The effect of tree height on crown level stomatal conductance. *Plant Cell and Environment* 23, 365-375 (2000).
- 41 Addington, R.N., Mitchell, R.J., Oren, R. & Donovan, L.A., Stomatal sensitivity to vapor pressure deficit and its relationship to hydraulic conductance in *Pinus palustris*. *Tree Physiology* 24, 561-569 (2004).
- 42 Ryan, M.G., Phillips, N. & Bond, B.J., The hydraulic limitation hypothesis revisited. *Plant Cell and Environment* 29, 367-381 (2006).
- 43 Katul, G.G., Ellsworth, D.S. & Lai, C.T., Modelling assimilation and intercellular CO₂ from measured conductance: a synthesis of approaches. *Plant Cell and Environment* 23, 1313-1328 (2000).
- 44 Schulze, E.D., Kelliher, F.M., Korner, C., Lloyd, J. & Leuning, R., Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition – a global ecology scaling exercise. *Annual Review of Ecology and Systematics* 25, 629-& (1994).
- 45 Massman, W.J. & Weil, J.C., An analytical one-dimensional second-order closure model of turbulence statistics and the Lagrangian time scale within and above plant canopies of arbitrary structure. *Boundary-Layer Meteorology* 91, 81-107 (1999).
- 46 Katul, G.G. & Albertson, J.D., An investigation of higher-order closure models for a forested canopy. *Boundary-Layer Meteorology* 89, 47-74 (1998).

- 47 Katul, G.G. & Chang, W.H., Principal length scales in second-order closure models for canopy turbulence. *Journal of Applied Meteorology* 38, 1631-1643 (1999).
- 48 Katul, G.G., Mahrt, L., Poggi, D. & Sanz, C., One and two equation models for canopy turbulence. *Boundary-Layer Meteorology* 113, 81-109 (2004).
- 49 Poggi, D., Katul, G.G. & Albertson, J.D., Momentum transfer and turbulent kinetic energy budgets within a dense model canopy. *Boundary-Layer Meteorology* 111, 589-614 (2004).
- 50 Ryan, M.G. & Yoder, B.J., Hydraulic limits to tree height and tree growth. *Bioscience* 47, 235-242 (1997).
- 51 Ryan, M.G. *et al.*, Transpiration and whole-tree conductance in ponderosa pine trees of different heights. *Oecologia* 124, 553-560 (2000).
- 52 Hubbard, R.M., Ryan, M.G., Stiller, V. & Sperry, J.S., Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant Cell and Environment* 24, 113-121 (2001).
- 53 Williams, M., Bond, B.J. & Ryan, M.G., Evaluating different soil and plant hydraulic constraints on tree function using a model and sap flow data from ponderosa pine. *Plant Cell and Environment* 24, 679-690 (2001).
- 54 Ryan, M., Binkley, D., Fownes, J.H., Giardina, C. & Senock, R.S., An experimental test of the causes of forest growth decline with stand age. *Ecological Monographs* 74, 393-414 (2004).
- 55 Soons, M.B., Heil, G.W., Nathan, R. & Katul, G.G., Determinants of long-distance seed dispersal by wind in grasslands. *Ecology* 85, 3056-3068 (2004).
- 56 Williams, C., LaDeau, S.L., Oren, R., Katul, G.G., 2006. Modeling seed dispersal distances: implications for transgenic *Pinus taeda*. *Ecological Applications* 16(1), 117-124 (2006).
- 57 Lumley, J.L., Some comments on turbulence. *Physics of Fluids A (Fluid Dynamics)* 4, 203-211 (1992).
- 58 Lefsky, M.A. *et al.*, Lidar remote sensing of above-ground biomass in three biomes. *Bioscience* 11, 393-399 (2002).
- 59 Clark, J.S. & Ji, Y., Fecundity and dispersal in plant-populations – implications for structure and diversity. *American Naturalist* 146, 72-111 (1995).
- 60 Pitelka, L. F. *et al.*, Plant migration and climate change. *American Naturalist* 85, 464-473 (1997).
- 61 Clark, J.S. *et al.*, Reid's paradox of rapid plant migration – Dispersal theory and interpretation of paleoecological records. *Bioscience* 48, 13-24 (1998).

- 62 Clark, J.S., Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *American Naturalist* 152, 204-224 (1998).
- 63 Clark, J.S., Silman, M., Kern, R., Macklin, E. & HilleRisLambers, J., Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* 80, 1475-1494 (1999).
- 64 Clark, J.S., Lewis, M. & Horvath, L., Invasion by extremes: Population spread with variation in dispersal and reproduction. 157, 537-554 (2001).
- 65 Higgins, S.I. *et al.*, Forecasting plant migration rates: managing uncertainty for risk assessment. *American Naturalist* 91, 341-347 (2003).
- 66 Clark, J.S., Lewis, M., McLachlan, J.S. & HilleRisLambers, J., Estimating population spread: What can we forecast and how well? *Ecology* 84, 1979-1988 (2003).
- 67 McLachlan, J.S. & Clark, J.S., Reconstructing historical ranges with fossil data at continental scales. *Forest Ecology and Management* 197, 139-147 (2004).
- 68 Schafer, K.V.R., Oren, R. & Tenhunen, J.D., The effect of tree height on crown level stomatal conductance. *Plant Cell and Environment* 23, 365-375 (2000).
- 69 Katul, G., Leuning, R. & Oren, R., Relationship between plant hydraulic and biochemical properties derived from a steady-state coupled water and carbon transport model. *Plant Cell and Environment* 26, 339-350 (2003).
- 70 Phillips, N.G., Oren, R., Licata, J. & Linder, S., Time series diagnosis of tree hydraulic characteristics. *Tree Physiology* 24, 879-890 (2004).
- 71 Bohrer, G. *et al.*, Finite element tree crown hydrodynamics model (FETCH) using porous media flow within branching elements: A new representation of tree hydrodynamics. *Water Resources Research* 41 Art. No. W11404 (2005).
- 72 Chuang, Y.L., Oren, R., Bertozzi, A.L., Phillips, N. & Katul, G.G., The porous media model for the hydraulic system of a conifer tree: Linking sap flux data to transpiration rate. *Ecological Modelling* 191, 447-468 (2006).
- 73 Baldocchi, D. & Meyers, T., On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and trace gas fluxes over vegetation: a perspective. *Agricultural and Forest Meteorology* 90, 1-25 (1998).
- 74 Lai, C.T., Katul, G., Oren, R., Ellsworth, D. & Schafer, K., Modeling CO₂ and water vapor turbulent flux distributions within a forest canopy. *Journal of Geophysical Research-Atmospheres* 105, 26333-26351 (2000).
- 75 Lai, C.T. *et al.*, Modelling the limits on the response of net carbon exchange to fertilization in a south-eastern pine forest. *Plant Cell and Environment* 25, 1095-1119 (2002).