NEWS & VIEWS
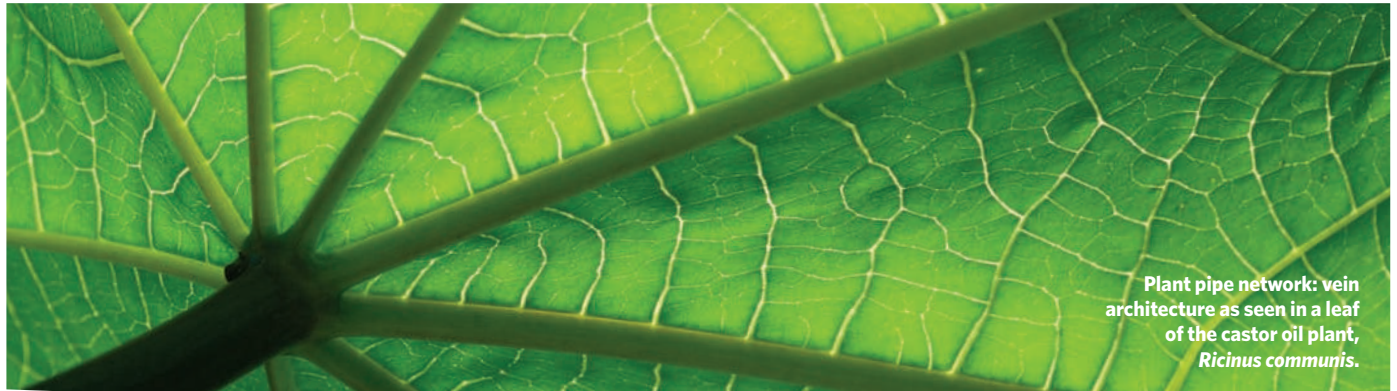

Plant pipe network: vein architecture as seen in a leaf of the castor oil plant, *Ricinus communis*.

PLANT SCIENCE

The hidden cost of transpiration

David J. Beerling and Peter J. Franks

Theoretical analyses reveal how plant investment in the architecture of leaf veins can be shuffled for different conditions, minimizing the construction costs associated with supplying water to leaves.

In the very first chapter of his magnificent 1727 book *Vegetable Staticks*, the pioneering English plant physiologist Stephen Hales observed[1] that plants lose water by "perspiration". He then went one better by conducting experiments to quantify the process. Today, through what we now know as Earth's 'transpiration engine', terrestrial plants add 32×10^3 billion tonnes of water vapour to the atmosphere annually — equivalent to about 30% of the precipitation that falls on land and double the total amount of water vapour in the atmosphere[2]. This huge global flux of water vapour passes through microscopic stomatal pores on the surface of leaves and represents a fundamental ecosystem service, contributing to the global water cycle and climate regulation by cloud formation. Writing in *The American Naturalist*, McKown *et al.*[3] provide a thought-provoking theoretical analysis that reveals how plants configure the internal pipe network (vasculature) of leaves to deliver more water for a given carbon investment in these specialized tissues.

The flowering plants (angiosperms) that dominate the tropical rainforests experience uniform year-round warmth and high irradiance, and with their sophisticated leaf vascular architecture have the greatest rates of transpiration on Earth[2]. To maintain such high rates of water loss, angiosperms have a relatively high density of veins (total vein length per unit leaf area) forming the pipe network that carries water from the leaf stem to the photosynthesizing tissues. This effectively brings the water source and the evaporating

sites within the leaf closer together to improve the leaf's overall hydraulic conductance. But a consequence, McKown *et al.*[3] show, is higher leaf-construction costs because it requires additional specialized water-conducting tissues rich in carbon-costly lignin.

Until now, these hidden carbon costs have tended to be overlooked, but McKown and colleagues' analysis reveals the strategies employed by angiosperms to help minimize them. The findings are particularly illuminating in an evolutionary context. A feature in the evolution of angiosperm leaves, and one that marks the final emergence of the terrestrial biosphere's transpiration engine, is the apparent surge in the density of veins during the angiosperms' rise to global dominance from the early Cretaceous (130 million years ago) onwards[4] that took place against a backdrop of falling atmospheric carbon dioxide concentrations[5] (Fig. 1a, overleaf). When considered alongside the findings of McKown *et al.*, this observation raises the question as to why evolution apparently drove the selection of leaves with a capacity for higher transpiration rates despite a rising carbon penalty for construction.

The answer emerges with the realization that the processes of transpiration and CO_2 uptake for photosynthesis are tightly coupled. Under recent relatively low CO_2 concentrations, leaves capable of fast rates of photosynthesis require large numbers of small stomatal pores, which creates a high stomatal conductance to CO_2 but inevitably permits the escape of more water as transpiration. The whole process proceeds providing plants maintain the hydraulic

pathway of water from the soil to leaves.

Now consider the situation early in the Cretaceous, when a CO_2-rich atmosphere fertilized photosynthesis in leaves constructed with fewer stomatal pores and lower transpiration rates. In these circumstances, a modestly engineered leaf vascular system, with low vein density, was perfectly adequate. The long, slow decline in the concentration of atmospheric CO_2 over the next 130 million years forced plants to increase leaf stomatal conductance to CO_2 (Fig. 1), leading to higher rates of transpirational water loss[6]. Plants supported this additional water loss with improved vascular systems that could outcompete their predecessors, effectively a 'hydraulic arms race' amongst species (Fig. 1b). This CO_2-driven selection of leaves with a greater capacity to exchange gases with the atmosphere had to be coordinated with greater hydraulic flow, as provided by additional vein infrastructure but with a steadily increasing construction cost — particularly when expressed relative to photosynthetic rates (Fig. 1, vein density/photosynthesis rate). Relative construction costs escalated dramatically over the past 50 million years, as photosynthetic rates declined with falling CO_2.

McKown *et al.*[3] show that the angiosperm solution to this evolutionary problem involved more than greater vein density. Like reticulated water supplies to towns, leaf veins are configured in a hierarchical order, branching from larger, 'low-order' conduits to ever smaller, 'higher-order' conduits. Depending on how a plant shuffles its investment into these different vein categories, the cost of increased

hydraulic conductance can vary enormously. Theoretically, increasing the density of the highest-order, or 'minor veins', together with vein tapering, is by far the most cost-effective strategy[3], and indeed both were evolutionary innovations in angiosperms. These innovations allowed higher leaf hydraulic conductances and faster rates of photosynthesis for a given carbon investment in lignified tissues.

Theoretical cost–benefit models such as that used by McKown et al.[3] are valuable, but are still in their infancy. They require improvement to facilitate rigorous evaluation against observations, and representation of a broader range of transpiration functions[7]. Vascular tissues of leaves and stems, for example, provide mechanical support and, because they are lignin-rich, they contain less nitrogen and phosphorus than actively photosynthesizing tissues. Modification of the ecological stoichiometry of nutrient use during photosynthesis and transpiration[7] is, then, one possible

consequence of the Cretaceous evolution of angiosperms that have higher vein densities.

For all his pioneering studies on plant–water relations, Hales didn't discover that plants transpire water from leaves or that this flux of water is regulated by stomatal pores studding the epidermis. Inspired by Isaac Newton and Robert Boyle to bring precision to his "natural philosophizing", he did calculate the burden of "perspiration" to plants as they grow[1]. But the hidden additional costs and functions of this process are only now being unveiled. ■

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1. Ayres, P. The Aliveness of Plants: The Darwins at the Dawn of Plant Science (Pickering & Chatto, 2008).
2. Hetherington, A. M. & Woodward, F. I. Nature 424, 901–908 (2003).
3. McKown, A. D., Cochard, H. & Sack, L. Am. Nat. 175, 447–460 (2010).
4. Brodribb, T. J. & Feild, T. S. Ecol. Lett. 13, 175–183 (2010).
5. Fletcher, B. J., Brentnall, S. J., Anderson, C. W., Berner, R. A. & Beerling, D. J. Nature Geosci. 1, 43–48 (2008).
6. Franks, P. J. & Beerling, D. J. Geobiology 7, 227–236 (2009).
7. Raven, J. A. New Phytol. 179, 905–907 (2008).

Figure 1 | The hydraulic 'arms race' in plants. a, The decline in atmospheric CO_2 concentration over the past 200 million years[5]; the shaded envelope represents uncertainties due to the weathering rates of basalt rocks. **b**, Maximum photosynthesis rates are estimated to have fallen over the past 50 million years[6] (red line), mainly due to declining CO_2. That decline led to increases in maximum stomatal conductance[6], requiring more investment in carbon-costly leaf vascular tissue, indicated by increased maximum vein density[4]. This investment in hydraulic capacity, relative to photosynthesis rate, has increased with the rise of the angiosperms (arrow). But the analyses of McKown et al.[3] show that design features such as hierarchical vein organization, conduit taper and relatively higher density of the highest-order (smallest) veins made the investment highly cost-efficient.

MATERIALS SCIENCE

Reconfigurable colloids

Michael J. Solomon

Colloid particles that form bonds to each other at specific orientations might self-assemble into all sorts of useful materials. The key — and the lock — to such binding has been discovered.

On page 575 of this issue, Sacanna et al.[1] report a simple, scalable method for controlling the orientations of interactions between colloidal particles. Their technique can immediately be applied to existing processes for the self-assembly of colloidal particles. Moreover, because the resulting directional bonds are both switchable and mechanically flexible, previously inaccessible colloidal structures can now be imagined as targets for self-assembly, potentially allowing access to advanced, optically active materials.

Colloidal particles that are between roughly 100 nanometres and 1 micrometre in diameter make excellent building blocks for materials that interact strongly with light, because their size is about the same as the wavelengths of the visible spectrum. Everyone is familiar with the optical properties of colloids — the turbidity of milk and of silt-laden rivers is a consequence of the strong light scattering effected by dispersed colloid particles. If such particles self-assemble into colloidal crystals (three-dimensional arrays that have long-range order), then their turbidity is transformed into iridescence. Opals are naturally occurring examples. The optical properties of colloidal crystals can be tuned by changing their unit cells or inter-particle spacing, allowing useful materials to be made that have applications in processes such as chemical sensing[2,3].

But progress towards building high-quality colloidal crystals has been slow. Although crystals in which particles are closely packed can be made, more complex arrangements, such as the tetrahedral lattice found in diamond, have proved elusive. Simulations of colloids that assume directional interactions between particles have identified pathways for assembling

complex crystal structures[4]. However, these simulations are far ahead of reality because effective tools for controlling the direction of colloidal–particle interactions have been lacking. Currently, the best approaches are to use Janus spheres[5] (microscopic particles that have two chemically or physically different hemispheres) or mixtures of oppositely charged colloids[6].

Sacanna and colleagues' approach[1] to directional bonds involves the use of 'lock' and 'key' particles. Their lock particles contain a dimple that can accept spherical key colloids of matching size (Fig. 1a). Generating the dimple on the lock colloid was no mean feat, and required the authors to develop some clever colloid chemistry. The yield and selectivity of the synthesis are particularly good, which is essential for future applications of the technique.

To bind the lock and key particles together, the authors exploit a force known as the depletion interaction that is unique to the colloidal scale. Depletion interactions arise when nanometre-sized polymers or particles (known as depletants) are added to colloidal solutions. Because colloidal particles are in constant random motion, they occasionally come into close proximity. When this happens, depletants are excluded from the gap between the larger colloid particles (Fig. 1b). The imbalance in depletant density inside and outside the gap sets up a difference in osmotic pressure that leads to a pairwise attraction between the colloid particles[7,8].

The interaction can also be understood in terms of the volume of the colloidal system that is available to be occupied by the additives (the free volume). Depletants can't get any nearer to c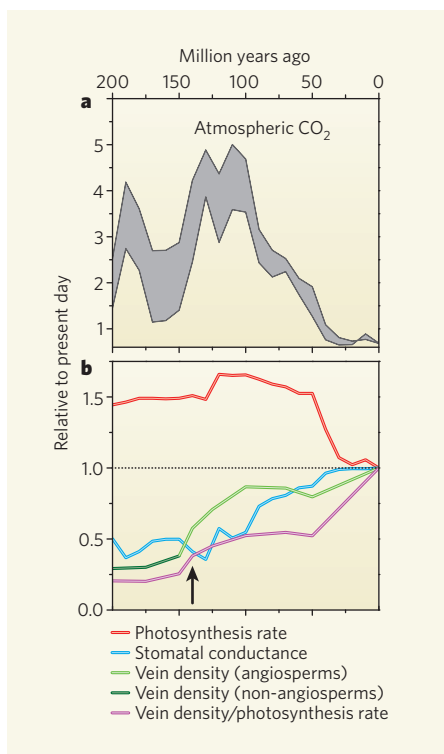olloid particles than the distance of their