THE COST OF LEAFING

J. PARDOE/ALAMY

Understanding the trade-offs involved for plants making leaves promises fresh insights on every scale from the plant to the planet, finds **John Whitfield**.

There are about 250,000 different types of plant — and almost as many types of leaf, from blades of grass through downy beech leaves to the needles of cedars or the fronds of palms. But the differences hide a basic similarity, says ecologist Ian Wright of Macquarie University in Sydney, Australia. "Within any habitat, you'll find that each square centimetre of leaf will process a roughly similar amount of carbon per unit area over its lifespan."

Wright and his colleagues have discovered that most of the variation in the physical and biochemical properties of leaves can be represented on a single axis running, to put it crudely, from quick and juicy to slow and tough. They call the axis the 'worldwide leaf economics spectrum'[1], and it embodies many of the trade-offs that govern how plants deploy their resources within the limits that physics places on biological possibility.

According to the Thomson in-cites website, the work is the second-most cited paper on ecology and the environment published in the past two years. It has attracted the attention of everyone, from plant physiologists studying how leaves work to biogeochemists looking at the cycling of nutrients on a global scale. In part, the paper is so popular because of the size and scope of the database that underlies the work; but the popularity also reflects the intellectual excitement that surrounds the discovery that so much can be explained by so little. This has given some ecologists hope that by looking at the large-scale patterns in how organisms work, they can gain a general understanding of why species live where they do, and why some are common and others are rare. Such findings are not of purely academic interest: climate researchers are using them to improve their models of the consequences of global warming.

From rainforest to tundra

The spectrum was discovered by compiling and analysing a database of the leaf biology of 2,548 species from 175 locations, ranging from tropical rainforests to the Arctic tundra. For every species, six key traits were recorded: leaf mass per unit area (affected by a leaf's thickness and tissue density); nitrogen and phosphorus content; the lifespan of the leaves; and the rates of photosynthesis and respiration. Wright and his colleagues compiled the data from their own and other people's studies — "much of it was languishing in bottom drawers", he says.

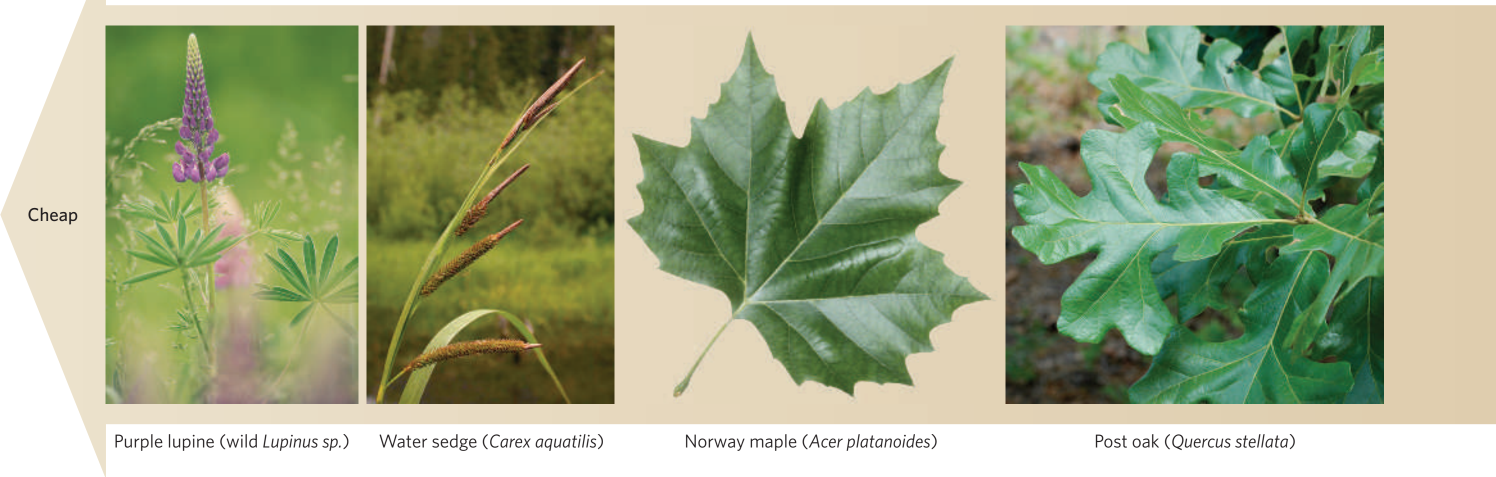
When the database was analysed statistically, its first principal component — the most informative way of looking at all the traits using a single axis — turned out to account for 74% of all the variation in all six traits. This principal component is the worldwide leaf economics spectrum. It ranges from leaves that are cheap to manufacture, highly active (ie, they have a high nitrogen content and photosynthetic rate) and short-lived, to those that are expensive and less active but make up for that in durability. In terms of an English woodland, think of going from flimsy short-lived beech leaves to tough old holly.

One definition of economics is the study choice under the constraint of scarcity, and the narrow range of choices in the leaf economics spectrum provides a vivid illustration of the various scarcities that dominate plants' lives. The fact that all leaves lie fairly close to the axis of the spectrum shows that, despite the vast diversity of foliage produced over hundreds of millions of years of evolution, plants have little room for manoeuvre in how they build their leaves. "Most textbooks of ecology project the idea that there's an almost infinite diversity of organisms," says plant ecologist Philip Grime of the University of Sheffield, UK. "But if you look at the core biology of what organisms do with resources, you find severe constraints and trade-offs."

> **"By looking at plant traits, you can go from physiology up to ecosystem functioning."** — Bill Shipley

One tack taken in following up on this ground-breaking work has been to ask what the constraining trade-offs are. When Wright and ecologist Bill Shipley of Sherbrooke University

SOME OF THE 250,000 LEAF OPTIONS AVAILABLE



Purple lupine (wild *Lupinus sp.*) Water sedge (*Carex aquatilis*) Norway maple (*Acer platanoides*) Post oak (*Quercus stellata*)

L. KENNEDY/CORBIS; B. LEGLER; J. PEACH/IMAGEQUESTMARINE.COM

in Quebec, Canada, used a mathematical technique that can find the direction of causality in the correlations[2], they found that "there was no way to explain the correlations based only on the measurements in the data set", says Shipley. Some not yet measured factor was at work.

The missing link

Shipley thinks that the missing fundamental trade-off is between the volume of a leaf's cell and the thickness of its cell wall. Leaves at the tough end of the spectrum have cells like — well, like cells: small spaces surrounded by thick, solid walls. Cell walls require a lot of materials to make and do not photosynthesize. Sturdier cell walls make the leaves more opaque and less permeable to gases, hindering the capture of light and carbon dioxide. But these leaves also live longer, and the investment in the cell wall is thus paid off with a low rate of photosynthesis that can be maintained for a very long time.

Another way to take the work forward is to include some aspects of a leaf's size and shape. The factors measured in the spectrum are usually expressed per unit mass. But Charles Price of the University of Arizona, Tucson thinks that a leaf's absolute size is also important. He has sought to explain how a leaf's surface area and mass are linked in terms of the geometry of the vein network that carries resources to, and away from, its cells[3]. Large networks supply cells more slowly: this, he predicts, will cause large leaves to photosynthesize more slowly, per unit area, than small ones, and might be another reason why leaves with a large mass per area photosynthesize more slowly.

Perhaps the most striking aspect of the trade-offs to be investigated further, though, is that different plants in the same places make very different 'decisions'. "The dogma was that plants differed between places that are dry and wet, and those that have low and high levels of nutrients," says Wright. "But frequently, the range of trait values within any one habitat is as large or larger than that seen between sites." This illustrates, he says, that the various ways of making a leaf are equally good routes to the same place. Variation within sites will also result from small-scale changes in soil, shade and moisture, and from the fact that a plant's best strategy depends on what everything else is doing — in a wood full of fast-growers, tolerating shade might be better than trying to compete directly.

Climate, though, does play a part in the shape of the spectrum. In the coldest places, doubling the leaf mass per area lengthens the lifespan by five times, whereas for the hottest sites, the same doubling lengthens lifespan by only 2.5 times. About 20% of the variance not captured in the basic leaf economics index is explained once climate is added to the equation[4].

D. VILE/CN

Vintage years: the same vineyard after 44 (top) and 42 (middle) years of abandonment, and another (bottom) after just five years.

Onwards and upwards

The implications of a leaf's-eye view go beyond the plants themselves. Leaves are the gateways through which energy enters ecosystems, and choices made on the leaf economics spectrum affect detritivores, herbivores and, indirectly, carnivores. Plants with short-lived, rapidly photosynthesizing leaves are less tolerant of self-shading, and so have broader, flatter canopies than those with tougher, slow-growing leaves, such as conifers, which tend to grow more compactly. And the litter from plants that are fast-living decomposes more quickly than the tough foliage of the slow-coaches, controlling the speed at which nutrients cycle through the ecosystem. This sort of thinking is bolstering some ecologists in their belief that the study of traits is central to many aspects of their discipline[5].

To try to understand things such as what determines the number of species that can coexist in a place, how numerous each species is, and how productive the system as a whole is, ecologists have traditionally looked at what species are present, how they interact, and how their abundance affects that of the others. Such an approach is an extension of ecology's roots in natural history, says Brian McGill of McGill University in Montreal, Canada. "People become ecologists because they love to go outdoors and look at the woods. They get attached to putting names on things, and get focused on knowing lots about particular organisms."

But this approach soon becomes intractably knotty, as the number of possible interactions between species rises geometrically with the number of species. "We don't have the capacity to learn as much as we need to know by studying one species at a time. Studying interactions between species, and then trying to build that up, hasn't panned out. It's too complicated," explains McGill.

Red bloodwood (*Corymbia gummifera*)

Woollybush (*Adenanthos cygnorum*)

Scots pine (*Pinus sylvestris*)

Monkey-puzzle tree (*Araucaria araucana*)

I. WRIGHT; E. VENEKLAAS; J. C. REVY/SPL; P. HARCOURT/IMAGEQUESTMARINE.COM

Seeing ecological communities in terms of their constituent traits, rather than their species, might be less intuitive. But it makes measuring and comparing places a lot easier, says McGill. The trick is to find traits that are closely related to evolutionary fitness. The leaf economics spectrum is a prime example of this. Another example is the spectrum between plants that make a lot of small seeds and those that make a few big ones. Wright is now looking for other important axes, such as between plants that use water profligately to grow quickly, and those that are slow-growing but intolerant to drought.

Once researchers think they have identified an axis of variation, they can see, for example, whether plants cluster tightly at one point on the axis, suggesting that they have evolved similar responses to a common environmental challenge, or whether they spread out along its length as they do on the leaf economics spectrum, suggesting that they have adopted strategies to avoid competing with one another.

In October, Shipley and his colleagues published a study that tested how predictive such an approach might be[6]. Working in 12 French vineyards abandoned 2–42 years ago, they looked at the ways the traits of the plants change as the vineyards revert to an uncultivated state. As perennials replaced weedy species, the height and mass of the plants increased, and the number of seeds per plant dropped. The leaves of the perennials also had a greater mass per area, in a shift towards the slow/tough end of the economic spectrum that seemed to go along with the community's ageing.

From a knowledge of the average trait values for all 30 species looked at in the study and the age of each field, the researchers then predicted the abundance of each species in each vineyard by borrowing a technique from statistical mechanics and assuming that resources were spread between the species as randomly as possible. They predicted their number of species in each plot and their abundance with 94% accuracy. "By looking at plant traits, you can go from physiology all the way up to ecosystem functioning," says Shipley. "The potential that I see is in finally being able to integrate different levels of plant ecology together."

A species'-eye view might still reveal things about ecosystems that looking at traits cannot, says David Tilman of the University of Minnesota in St Paul. Plots with more species, for example, are more productive, and recover more quickly from perturbation than less diverse places[7]. Part of this trend is that more species mean a greater diversity of traits, Tilman says, but interactions between species are also important. "Looking at traits won't let us ignore the number of species. Both are equally important determinants of how an ecosystem functions."

"Either we watch the world change, or we gain a truly predictive knowledge of nature." — David Tilman

Predicting the future

But the role a trait-based approach could play in prediction is exciting some of the scientists studying the greatest environmental problem of the age at the largest possible scale—the planet-wide effects of global warming. A wide array of feedbacks ties the terrestrial biosphere into the changes in the atmosphere's carbon dioxide content. Making sense of these relationships requires models that predict what plants to expect where, on the basis of environmental factors such as temperature and water availability.

Today's models typically classify vegetation as belonging to one of 5–20 groups — evergreen, deciduous, woody, herbaceous and so on. Trait values, such as leaf longevity and photosynthetic rate, are then assigned to this group as a whole. This summer, researchers working on plant traits and those working on the interaction between plants and climate met in Sydney to try to see how a 'trait-first' approach to modelling might improve things.

It turns out that models that replace a fixed trait value assigned to each vegetation type with a spread of values taken from the leaf economics spectrum give values of plant productivity closer to those seen on the ground. They should thus yield more accurate predictions of future change, particularly at a regional or continental scale, says modeller Ian Woodward of the University of Sheffield. "Looking at Amazonia, we tend to find that incorporating these data into our models leads to changes in leaf longevity and primary productivity of about 10–15%. That's a significant difference, and an exciting eye-opener," he says.

In general, says Tilman, if we are to understand and mitigate the effects of processes such as climate change, nitrogen deposition, species introductions and habitat loss, ecology needs to home in on the most important ways in which species differ. "These broad global patterns greatly simplify what we need to understand about species. They let us sort through a hopeless morass of information, and go from conceptual models to real models that say how ecosystems will respond to environmental change," he says.

"If we can't be mechanistic and predictive, we'll be unable to provide society with explanations of the impacts of our actions. Either we watch the world change, and explain it in retrospect, or we gain a truly predictive knowledge of nature." ■

John Whitfield is a freelance writer based in London, UK.

1. Wright, I. J. *et al. Nature* **428,** 821–827 (2004).
2. Shipley, B., Lechowicz, M. J., Wright, I. & Reich, P. B. *Ecology* **87,** 535–541 (2006).
3. Price, C. A. & Enquist, B. J. *Ecology* (in the press).
4. Wright, I. J. *et al. Glob. Ecol. Biogeogr.* **14,** 411–421 (2005).
5. McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. *Trends Ecol. Evol.* **21,** 178–185 (2006).
6. Shipley, B., Vile, D. & Garnier, É. *Science* **314,** 812–814 (2006).
7. Tilman, D., Reich, P. B. & Knops, J. M. *Nature* **441,** 629–632 (2006).