

# THE ECONOMICS OF Leaves

Plants build leaves as investments that vary in cost, revenue and lifespan, report Ian Wright and Mark Westoby.

Next time you go bushwalking, take some time to look at the amazing diversity of leaf types around you. One of the more obvious ways that leaves vary is in their size. Even among species growing in a single patch of vegetation, leaf sizes may differ 10,000-fold.

Leaves also vary in many less visual ways. Some of these have profound consequences for the core business of leaves, which is to harvest energy from the Sun for photosynthesis (see *The Core Business of Leaves*).

Plants are the driving force of terrestrial ecosystems, and variation in leaf structure and function flows on to every other level of organisation in nature.

- Biogeochemical cycles are driven by nitrogen uptake and CO<sub>2</sub> assimilation by plants.
- Nutrient recycling and accumulation of potential fuel for bushfires depend on how quickly or slowly leaves decompose after falling.
- Animals, fungi and many other organisms depend on plants as their food source.
- The physical structure of stems and foliage provides habitat for animals, both large and small, and moderates the microclimate they experience.

If we can quantify and understand the implications of leaf variation across the world's plant species, we will understand one of the most fundamental properties of all ecosystems.

## LEAF ECONOMICS

In the field of plant ecology, and particularly evolutionary ecology – where scientists are trying to understand how plants have evolved to be the way they are – economic analogies can be very useful. In fact, many economic concepts fit evolutionary patterns much better than they fit human behaviour because humans make all sorts of personal decisions that are not necessarily in their best economic interest.

Plants invest dry matter and mineral nutrients in building green leaves. During photosynthesis, carbon dioxide from the air is converted first to sugar molecules, then to carbohydrates such as cellulose and starch, using energy harnessed from the Sun. These carbohydrates are reinvested in the construction of leaves, in stems that support the leaves, and in other plant parts. They are also used to support metabolism and in the acquisition of mineral nutrients from the soil.

Across the world there are more than 250,000 vascular plant species, all engaging in these processes of investment and reinvestment of carbon and mineral nutrients. Plants inhabit a sharply competitive world, and all the species we see around us today are successful “businesses” that have been operating for thousands to tens of millions of years with proven profit strategies. The invisible hand of natural selection is much stronger than the forces operating in human economics.



Leaves vary in their size and shape, colour and texture, the way they are arranged on stems, and in their investment properties: their mass per area, lifespan, nutrient concentrations, photosynthetic capacity and respiration rate.

These six traits describe many of the important features of leaves: how much they cost to build, how fast carbon revenue can be potentially returned from this investment, the costs of metabolism and other processes inside the leaf, and the duration of the carbohydrate revenue stream from the investments of dry mass and nutrients. These are the same things you would want to know if you were investing in a business: what the potential rate of return would be and how long the revenue stream would be sustained before the machinery had to be replaced.

## THE LEAF ECONOMICS SPECTRUM

The GLOPNET collaboration demonstrated that these six leaf traits are correlated with one another in predictable ways across the world's plant species. Considered together, the traits form a “spectrum” of leaf economics consisting of these six key chemical, structural and physiological properties. The spectrum runs from species with potential for quick returns on investments of nutrients and dry mass in leaves, to species with a slower potential rate of return. At the quick-return end are species with high leaf nutrient concentrations, high rates of photosynthesis and respiration, short leaf lifespan and low dry-mass investment costs per unit of leaf area. At the slow-return end are species with long leaf lifespan, high leaf mass per area, low nutrient concentrations and slower photosynthesis and respiration.

Across all biomes worldwide, species have converged onto this leaf economics spectrum and also diverged along it (Fig. 1). In other words, whether you are looking at plants

Any plant business strategy defined by a given mix of DNA has to actually turn a profit in carbon terms every generation or its DNA will become extinct.

While all plants are looking to turn a profit, it is obvious that they do this with different business strategies. If they didn't do this, all plants would look the same.

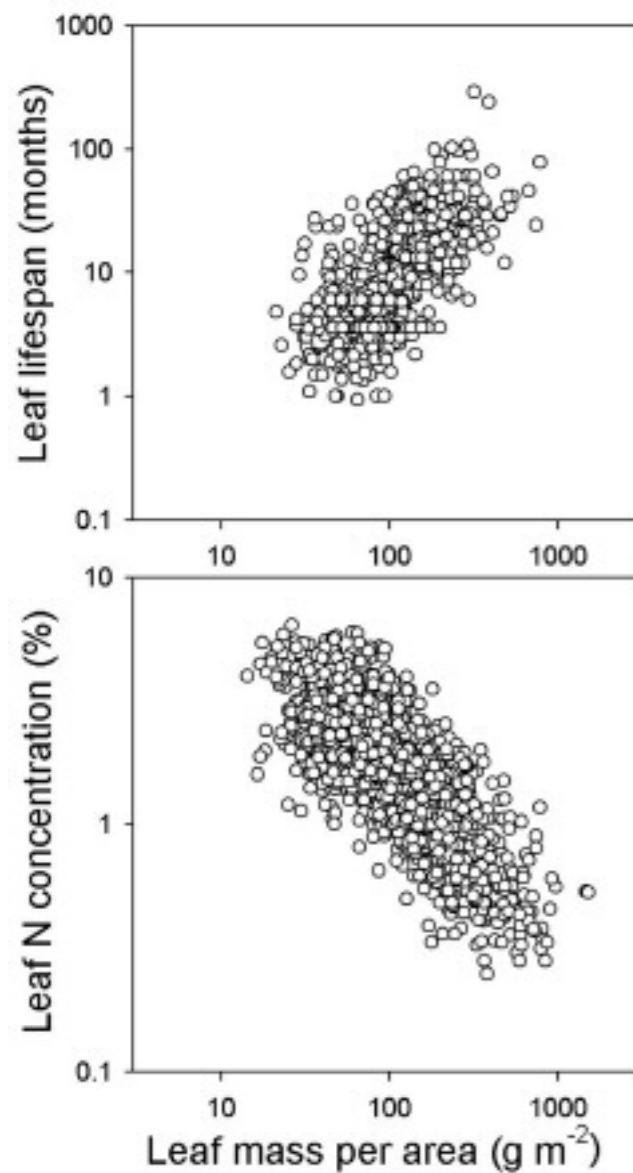
Researchers from 15 countries have formed a global plant trait network (GLOPNET) to quantify leaf economics across the world's plant species. The GLOPNET dataset covers 2548 species from 219 families at 175 sites from around the world, a dataset at least tenfold larger than has ever been drawn together before. The dataset extends

to all vegetated continents, from Arctic tundra to tropical rainforest, from hot to cold deserts, and from boreal forest to grasslands.

We have been leading this project with Peter Reich of the University of Minnesota, and have compiled data on six key leaf traits:

- leaf mass per area, which indicates the dry mass investment required to build a unit area of light-capturing leaf tissue;
- leaf nitrogen concentration, as nitrogen-rich proteins such as Rubisco are responsible for photosynthesis, and leaf nitrogen is one of the major costs involved in building a leaf;

- leaf phosphorus concentration, as phosphorus is found in nucleic acids such as RNA, the phospholipid outer membranes of cells, and bioenergetic molecules such as adenosine triphosphate (ATP);
- photosynthetic capacity, which is the maximum rate of carbon fixation that is possible under favourable conditions such as high light and abundant water supply;
- background respiration rate as a measure of how much energy is made available to the plant from the metabolism of carbohydrates; and
- leaf lifespan, which is the average time that a leaf is held on a plant before it is shed or eaten by herbivores.



**Figure 1.** Two of the pairwise trait relationships underlying the leaf economics spectrum. **Top:** Leaf lifespan versus leaf mass per area (678 species). **Bottom:** Leaf nitrogen concentration versus leaf mass per area (1958 species). Each data point represents a species. Plants with low leaf mass per area (LMA) have short leaf lifespans and high leaf nutrient concentrations. These plants occur at the “quick-return” end of the leaf economics spectrum. At the “slow-return” end of the spectrum are species with long leaf lifespan, expensive leaf construction (high LMA) and low nutrient concentrations.

the combination of leaf traits that have evolved in each and every species allows us to place them along this spectrum. In fact, the spectrum accounts for three-quarters of all variation worldwide in the six leaf economic traits. Some important features and implications of the leaf economics spectrum are that:

- species growing on very poor soils tend to occur towards the slow-return end of the spectrum, while species on very fertile soils occur towards the quick-return end;
- within any set of coexisting species there can be substantial variation in the combinations of leaf traits we observe; and
- there is patterning along the spectrum in terms of plant growth form, with herbaceous species occurring towards the quick-return end and woody plants towards the slow-return end. Still, there is substantial variation within trees, grasses, herbs or shrubs.

#### CLIMATE INFLUENCE ON LEAF INVESTMENT

Plant ecologists have emphasised broad relationships between leaf traits and climate for at least a century. In particular, a general tendency has been recognised for species inhabiting low rainfall regions to have leathery leaves with high leaf mass per area.

We characterised all the sites for which we had leaf data by climate variables such as annual means of temperature, humidity, solar radiation and annual total rainfall. We then quantified the extent to which the leaf economics spectrum

growing in deserts, rainforests, mountain tops or grassy prairies, the leaf traits are correlated in a similar way, and

## HOW LEAF TRAITS ARE MEASURED

**L**eamass per area (LMA) is calculated as the area of a leaf divided by its dry mass. This gives the dry mass cost per unit of leaf area available to capture sunlight. LMA is affected both by the thickness of leaves and by the density of the tissue, with thicker and denser leaves having a higher LMA. The surface area of leaves is normally measured from a digital image, although it can also be measured by tracing the outline of a leaf onto graph paper and counting the squares within the outline. Variation in LMA can also be felt with the fingertips – hard, leathery leaves have a high LMA,

whereas soft, flimsy leaves have a low LMA.

Photosynthetic and background respiration rates are measured with an infrared gas analyser. Leaves are held in a glass chamber with air flowing in and out at a known rate. The concentration of CO<sub>2</sub> is measured for the in-flowing and out-flowing air, allowing the amount of CO<sub>2</sub> taken up during photosynthesis or produced during respiration to be calculated. Photosynthesis is measured in bright sunlight or with an artificial light source. The rate of background respiration is measured in the dark so that the rate of

varied with climate.

There were indeed statistically significant effects of climate. For example, at a given leaf mass per area, species from drier sites had shorter leaf lifespans (Fig. 2) but higher leaf nitrogen concentrations. These sorts of differences indicate that the return on investments of dry mass and nutrients in leaves varies considerably depending on where plants grow, with differences shaped by millions of years of evolution.

Nevertheless, a major finding from this project is that the influence of climate is generally quite modest. This is because much of the total leaf economic variation occurs among coexisting species, and also because leaf traits tend to vary in concert, with the leaf economics spectrum operating similarly in different biomes.

This is not to say that climate does not exert important influences on trait relationships nor has it played an unimportant role in shaping plant evolution. Rather, it is an extension of the fact that so much of the total variation in leaf traits is captured by the primary axis of the leaf economics spectrum.

#### THE STATE OF KNOWLEDGE

Prior to the GLOPNET project, plant ecologists were already aware that some leaf traits tend to vary in a coordinated fashion, and leaf trait relationships can be modulated by climate. However, during this research we drew together data for hundreds to thousands of more species than had been included in previous data compilations, and thus were able to describe general patterns at a scale never previously possible, and across all the major biomes of the world.

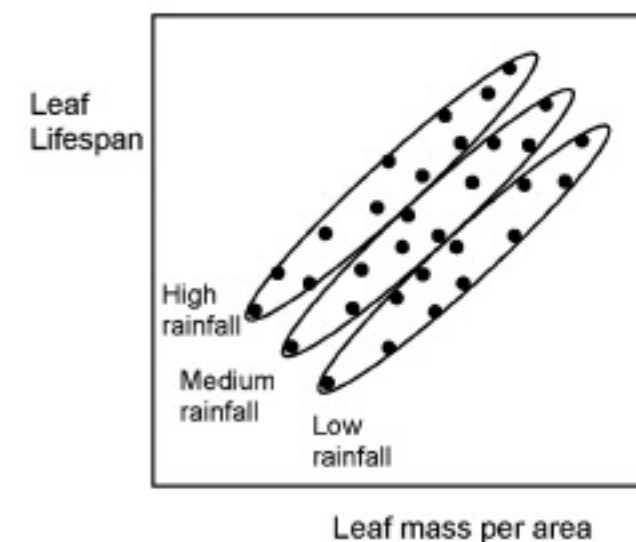
Reliable quantification of the global leaf economics spectrum and its relationship to climate will prove valuable in modelling how carbon and nitrogen are tied up and used in plant biomass, and how nutrient fluxes and vegetation boundaries will shift with land use and climate change.

At a more basic level it has given us greater understanding

CO<sub>2</sub> production is not masked by CO<sub>2</sub> uptake due to photosynthesis.

Leaf nitrogen and phosphorus concentrations can be measured by a variety of analytical techniques. Leaf tissue is collected, dried, finely ground and analysed.

Leaf lifespan can be measured by tagging leaves as they are produced and recording when they are eaten by herbivores or shed from the plant. However, like censuses of human lifespan, there are mathematical techniques for estimating leaf lifespan that do not require us to follow every leaf from birth to death. Populations of leaves are tagged and over time the numbers of births and deaths are recorded.



**Figure 2.** Stylised representation showing how leaf economics is patterned by climate, using the relationship between leaf lifespan and leaf mass per area as an example. Each ellipse contains species from a different rainfall zone. This diagram shows how the leaf lifespan associated with a given leaf mass per area decreases with decreasing annual rainfall.

of the diversity of plants we see around us. Nothing can be more fundamental for vegetation management and for understanding and appreciating biodiversity than a deep understanding of the main dimensions of variation among plants in how and where they make a living, and how plant traits shape the properties of ecosystems.

The GLOPNET project can be seen as part of a new phase in ecology, where the importance of looking for consistent, worldwide patterns is becoming more recognised. By illustrating that plant evolution leads to powerful global patterns we are able to understand the world in a simplified way, while at the same time recognising that every species is unique and to be valued in its own right.

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From these data the average leaf lifespan can be calculated. Across the world's plant species, average leaf lifespan varies from a few weeks to several years.

All of these traits vary within species as well as among species, particularly between leaves growing in sunny and shady parts of the canopy. For example, leaves that develop in the shade often have lower LMA, longer lifespan, lower nitrogen and phosphorus concentrations, and slower photosynthetic and respiration rates. However, the variation among species in these traits tends to be much larger (20–50-fold) than the variation within a given species (less than tenfold).

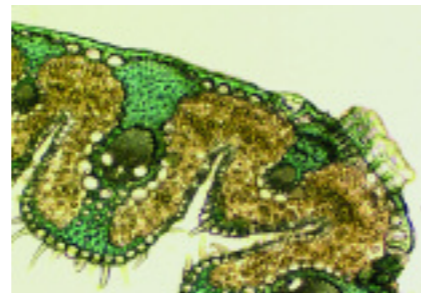
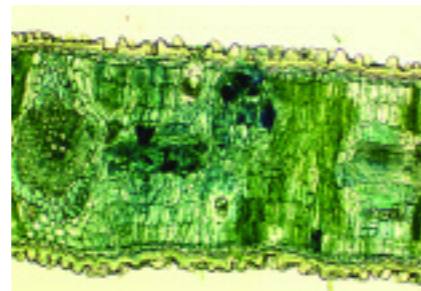
## THE CORE BUSINESS OF LEAVES

The basic features of leaves are similar in most plants. In between the epidermal cells and waxy cuticle that make up the outer skin of a leaf are various types of cells and structures.

- Mesophyll cells are the site of photosynthesis. Inside the mesophyll cells are chloroplasts, which harvest light as an energy source for photosynthesis. Their green pigments give leaves their colour. Other intercellular components include Rubisco, the major leaf protein involved in CO<sub>2</sub> fixation, and organelles such as ribosomes, the RNA-rich bodies where proteins are synthesised.
- Veins deliver nutrients and water into the leaf. Veins also carry the carbohydrate products of photosynthesis away from the mesophyll to the roots, stems, leaves, fruits and seeds, where they are required for construction of new tissue and for various cellular processes. In some species the veins also provide the main structural strength of the leaf.
- Various types of non-photosynthetic cells provide additional strength.

- A network of intercellular air spaces allows CO<sub>2</sub> to diffuse to the mesophyll cells.
- In the epidermis are large numbers of guard cells that, by swelling and shrinking, open and close pores called stomata. CO<sub>2</sub> molecules entering the leaf through the stomata are quickly captured and dissolved, lowering the CO<sub>2</sub> concentration in the intercellular spaces. This forms a CO<sub>2</sub> concentration gradient between the inside and outside of a leaf, so that more CO<sub>2</sub> diffuses into the leaf through the stomata.

The living activities of the cells are carried on in solution. Moist cell surfaces have to be exposed to absorb CO<sub>2</sub> into solution, so the process of taking up carbon from the atmosphere unavoidably goes hand-in-hand with the evaporation of water from the plant and into the atmosphere. The stomata shut when the rate of water loss exceeds the ability of the root system to supply water to the leaves. When this happens the rate of water loss is dramatically reduced, but at the same time the inward diffusion of CO<sub>2</sub> stops. The loss of water through stomata is



Photograph of a leaf cross-section.

an unavoidable cost at the expense of photosynthesis.

Sugar molecules produced during photosynthesis are converted into carbohydrates such as cellulose and starch. Cellulose is the major component of plant cell walls, and is the major component of plant dry matter. Starch is the major storage carbohydrate in plants. Plant carbohydrates are the main energy source for many fungi, bacteria and animals, including humans.

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