

# For richer, for poorer

Peter D. Moore

Is size a matter of importance among seeds? Maranon and Grubb<sup>1</sup> have looked into the question as it concerns Mediterranean annuals and have come up with an answer — their conclusion is that big seeds equip a plant for growth in rich environments.

Seed size is normally a remarkably consistent character within any given species of plant, meaning that this feature has probably evolved in response to strong and persistent environmental pressures. Yet the precise value and ecological advantage of a particular size of seed, be it large or small, is still a matter for conjecture. It is not even clear whether large-seeded species are better equipped for low- or high-resource habitats.

A wide range of factors needs to be taken into consideration when assessing the potential advantages of producing large seeds. Dispersal by wind is hampered, but dispersal by animals or water may not be (consider the coconut). Resources for seedling establishment are in rich supply, which could be advantageous if the plant has to cope with competition from other plants or with a lack of such requirements as water or minerals in the early stages of growth. If long-term dormancy is likely, a high seed weight is apparently distinctly disadvantageous, because most long-dormant weed seeds (such as those of poppies) are small. But protection from fire or insect predation could demand a thick seed coat. Put all this together, and it becomes evident why general principles relating to the adaptive value of particular seed sizes have been hard to find<sup>2,3</sup>.

With respect to the resource richness or poverty of the site in which germination and establishment are to take place, however, one might predict that a large-seeded species is at an advantage under conditions of low resource availability. In the fynbos heathlands of southern Africa<sup>4</sup>, for example, members of the Proteaceae bear few, large seeds, as they do in Australia where as much as 40 per cent of the annual uptake of phosphorus by the parental plant may be invested in seed production<sup>5</sup>. Presumably this high investment equips the seed with a valuable store of this vital element as it germinates and establishes itself in the phosphorus-poor soils of these areas.

On the other hand, it could be argued that environments rich in resources such as light, water and minerals are likely to be inhabited by robust, fast-growing, competitive species<sup>6</sup>. Under such conditions the extra start in life offered to a seedling by nutrient supplies in the seed could make a substantial difference to its estab-

lishment. But this view assumes that growth is faster in the seedlings that develop from big seeds. In fact, studies of various plant families have demonstrated that the reverse may be true, and that the relative growth rate (RGR, the rate of weight increase per unit of initial weight) has a negative relationship to seed weight. Maranon and Grubb have examined 27 species of annual Mediterranean plants, including grasses, composites and legumes, and have confirmed that, in these species, high RGR is associated with small seeds.

Plant growth can be considered in terms of two components — the unit leaf rate (ULR, the rate of weight increase per unit area of leaf), which is an expression of the photosynthetic efficiency of leaves; and specific leaf area (SLA, leaf area per unit weight of plant). When the two were examined separately in the test species, Maranon and Grubb found that ULR was greater in the large-seeded species, but that SLA was less. So the low RGR of large-seeded plants is a consequence of their poor rate of production of leaf tissue per unit initial weight. What seems to be happening is that the large seeds are producing thick leaves that are efficient at using light (hence their high ULR), but their rate of leaf production is relatively inefficient considering their initial weight advantages. Overall, small-seeded species are able to intercept more light per unit mass.

Relative growth rates can be misleading, however. Larger seeds do give rise to large seedlings but, on the basis of the observations described here, the greater RGR of the small-seeded species would

allow them to overtake their advantaged colleagues within six weeks, as long as competitive interactions had not interfered with the process. Understanding the precise effect of competition demands a knowledge of density as well as growth analysis, so it is a complication that Maranon and Grubb have not fully faced. They have, however, gone back to the field to check where the small- and large-seeded plant species mainly occur. In the richer, deeper soils with higher organic matter derived from tree leaf-litter, large-seeded species, such as the grass *Bromus diandrus* and the thistle *Carduus pycnocephalus*, were typical. In the shallow, resource-poor sites, small-seeded species, such as the smooth catsear *Hypochoeris glabra* and the grass *Agrostis pourretii*, predominated.

Maranon and Grubb believe that, as far as Mediterranean habitats are concerned, they have hit upon a reasonably robust generalization. Large-seeded plants are at their best in environments with rich resources and small-seeded ones have an advantage in poverty-stricken sites. It remains to be seen whether the generalization will hold good in other geographical areas and other ecological situations, when, for example, the limiting resource is not water or minerals but light. □

Peter D. Moore is in the Division of Life Sciences, King's College, Campden Hill Road, London W8 7AH, UK.

1. Maranon, T. & Grubb, P. J. *Funct. Ecol.* **7**, 591–599 (1993).
2. Fenner, M. *Seed Ecology* (Chapman & Hall, London, 1985).
3. Bazzaz, F. A. & Ackerly, D. D. in *Seeds: the Ecology of Regeneration in Plant Communities* (ed. Fenner, M.) 1–26 (CAB International, Wallingford, Oxfordshire, 1992).
4. le Maitre, D. C. & Midgley, J. J. in *The Ecology of Fynbos* (ed. Cowling, R.) 135–174 (Oxford University Press, 1992).
5. Kuo, J. *et al. Austral. J. Bot.* **30**, 231–249 (1982).
6. Grime, J. P. & Hunt, R. *J. Ecol.* **63**, 393–422 (1975).

## GREENHOUSE GASES

# The mutable carbon sink

John Taylor

OUR inability to balance the global carbon cycle has led to the widespread use of the term 'missing sink'<sup>1</sup> or 'missing carbon' to reflect the fact that our estimates of the sources of carbon dioxide to the atmosphere exceed our estimates of the sinks by about 2 gigatonnes of carbon per year. The latest review of the uptake of CO<sub>2</sub> by the oceans<sup>2</sup>, as derived from ocean modelling studies, concluded that it is the terrestrial biosphere which is taking up the excess carbon. The challenge is to identify the location of this sink and describe the processes by which it is operating.

Two papers<sup>3,4</sup> in *Global Biogeochemical Cycles* consider this question and arrive

at very different conclusions. Richard Houghton<sup>3</sup> finds that data available from forest surveys do not support the hypothesis that the temperate regions of the Northern Hemisphere are a significant sink for atmospheric CO<sub>2</sub>. Aiguo Dai and Inez Fung<sup>4</sup>, in contrast, report that climate changes over the past 60 years have produced a CO<sub>2</sub> sink of about half of what is required to balance the carbon budget, and that this sink does lie predominantly in mid-latitudes in the Northern Hemisphere.

Houghton<sup>3</sup>, in a paper that seems sure to be controversial, argues that the search for the missing carbon may be "getting out