

## Opinion

# Depolarizing the GM debate

*'Each GM case must be considered separately by plant scientists or opportunities for the wider use of new GM technologies could be permanently lost'*

Genetic modification (GM), the heritable alteration of genes, has come to apply specifically to newly developed recombinant DNA technologies, where the genome of an organism is modified using artificial techniques (here termed 'new GM'). The potential applications of the new technology in plants are currently set against widespread public concern. Even if particular concerns are valid when considered for particular applications of new GM, it is argued here that many are ultimately invalid because they are simplistically generalized to all cases of new GM, as if they were all the same. Equally, rebuttals of these anti-GM concerns should consider each type of GM separately. Concerns raised that are unique to new GM should be addressed scientifically to assess their validity. This should be for both scientific and political reasons. If politically pragmatic strategies are not taken more seriously, opportunities for the wider use of new GM technologies in plants could be permanently lost. Boxes 1 and 2 provide information on links and books that illustrate the contentious issues surrounding GM in the mind of the public.

### What is 'new GM'?

Genetic modification is the modification of genes so that the modification is passed on to the organism's descendants. Strictly, it is a general term that covers many processes, some of which have been used for 10 000 yrs, since agriculture began at the end of the last ice age. However, the term has come to be used for 'genetic engineering', where newly developed processes of molecular biotechnology are employed to insert relatively few genes into an organism's genome. Here, GM using the new technologies is termed 'new GM' to distinguish it from GM using traditional techniques.

There are at least three traditional methods of genetic modification: selecting for variability within existing populations; crossing closely related species; and isolating mutants. In addition to these traditional approaches, there is the new GM, involving the modification of specific genes in single cells using recently developed biotechnologies (Watson *et al.*, 1992; Alcamo, 1999). Traditional techniques for gene modification limited modifications to those occurring between

closely related organisms. New GM can be used for similar types of gene modifications, but it also enables the transfer of genes between any two organisms (including between a plant and an organism from another Kingdom – 'wide transfer' (Tester, 1999)). Thus, although new GM enables the addition to a crop's genome of just one gene, with a specific trait, the one gene could come from any organism, or even be created *de novo* in the laboratory. Overall, new GM tends to bring in fewer genes, but potentially from further away (evolutionarily), compared to 'old' GM.

This inclusion of traditional ('breeding') techniques as a type of GM has been misused by some in the 'pro-GM lobby' as an argument for claiming that there is no significant difference between traditional and modern approaches of crop improvement. This is fundamentally wrong. However, it is equally wrong to say that traditional approaches are not a type of GM. It is useful to show traditional breeding to be a type of GM, because it highlights the fact that most features of new GM are not significantly different to those of traditional techniques. Such features are thus not valid as arguments against new GM (unless, of course, the argument is also against traditional breeding). Equally, comparison of new and old GM enables the unique features of new GM to be highlighted and so seriously considered for risks and benefits.

### Applications of new GM

The first major product of new GM was developed in 1982, for the production of human insulin by bacteria for the treatment of diabetes. In 1990, the first GM food product was approved for use in the USA, an enzyme employed in cheese making. In 1994 the first food product was sold commercially, the so-called FlavrSavr™ tomato, which had reduced activity of 1-aminocyclopropane-1-carboxylate oxidase, a gene essential for ripening. The development of GM animals with the disruption of gene function is providing numerous insights into the molecular basis of disease, and there is the distinct possibility of modifying pigs to provide organs for human transplants. Opposition to these applications of new GM has been muted or nonexistent.

## Box 1 Links

These links are from a cross-section of sources, ranging from anti- to pro-GM, and show the contentious issues surrounding GM in the mind of the public:

Greenpeace <i>International environmental pressure group</i>	<a href="http://www.greenpeace.org.uk">http://www.greenpeace.org.uk</a>
Friends of the Earth <i>International network of environmental groups</i>	<a href="http://www.foe.co.uk">http://www.foe.co.uk</a>
Genewatch UK <i>Independent organization concerned with the ethics and risks of genetic engineering</i>	<a href="http://www.genewatch.org">http://www.genewatch.org</a>
Union of Concerned Scientists <i>Independent alliance of citizens and scientists in the USA</i>	<a href="http://www.ucsus.org">http://www.ucsus.org</a>
BBC Online – see GM links <i>UK national television</i>	<a href="http://www.news.bbc.co.uk">http://www.news.bbc.co.uk</a>
Agriculture and Environment Biotechnology Commission <i>UK government</i>	<a href="http://www.aebc.gov.uk/aebc/index.htm">http://www.aebc.gov.uk/aebc/index.htm</a>
American Phytopathology Society	<a href="http://www.scisoc.org">http://www.scisoc.org</a>
European Federation of Biotechnology (see the Task Group on Public Perceptions of Biotechnology) <i>Association of European scientific and technical societies</i>	<a href="http://www.efbweb.org">http://www.efbweb.org</a>
GM Issues <i>Compiled by The Genetic Modification and Biosafety Assessment Research Group of the John Innes Centre, Norwich, UK</i>	<a href="http://www.gmissues.org/frames.htm">http://www.gmissues.org/frames.htm</a>
National Agricultural Library <i>Biotechnology information site from the National Agricultural Library of the US Department of Agriculture – ARS</i>	<a href="http://www.nal.usda.gov/bic/">http://www.nal.usda.gov/bic/</a>
Department of the Environment, Transport and the Regions (see Environmental Protection – Advisory Committee on Releases to the Environment) <i>UK government</i>	<a href="http://www.detr.gov.uk">http://www.detr.gov.uk</a>
National Farmers Union (USA)	<a href="http://www.nfu.org">http://www.nfu.org</a>
AgBioWorld <i>GM discussion forum</i>	<a href="http://www.agbioworld.org">http://www.agbioworld.org</a>
Aventis <i>Multinational company</i>	<a href="http://www.aventis.com">http://www.aventis.com</a>
Monsanto <i>Multinational company</i>	<a href="http://www.monsanto.com">http://www.monsanto.com</a>

Recent commercial, plant-based applications of new GM, which have also been controversial with the public, include the introduction of herbicide tolerance into crops such as soybean and oilseed rape, and the ability to synthesize insecticidal proteins in cotton and maize. Many other applications of new GM are being developed, including conferral of the ability to make antibodies in fruits (Walmsley & Arntzen, 2000) and the ability to decontaminate polluted land by degrading organic pollution (French *et al.*, 1999). New GM also provides opportunities to alter the composition of food to increase its nutritive value, such as increasing the mineral and vitamin content of grain (e.g. 'golden rice':

Ye *et al.*, 2000). Increases in food production are also possible, by improving overall plant qualities (e.g. dwarfing rice: Peng *et al.*, 1999) and by increasing tolerance to biotic stresses (pests and diseases) and abiotic stresses (e.g. low temperature, drought and salinity). Indeed, for world stability, Conway (1997) argues persuasively that such increases are essential and that new GM technology is an essential tool for this to occur.

It is clear that there are many applications of new GM in plants, and that these involve a wide range of crops and many different types of gene transfer. Making generalizations about such a set of applications, as is made by both pro- and

**Box 2** Further reading

These books explore some of the issues that concern the public about GM:

Bruce D & Bruce A (eds). 1998. *Engineering genesis: the ethics of genetic engineering in non-human species*. London, UK: Earthscan.

Ho, M-W. 1999. *Genetic engineering – dream or nightmare?* Dublin, Ireland: Gill and Macmillan.

anti-GM campaigners, is clearly over-simplistic. In fact, it is dangerously over-simplistic: questions raised about some applications may have validity, but to argue against these in the context of all new GM crops could prove detrimental for other applications of new GM should such an argument be lost.

### Problems of application

Some current traits conferred on crops reduce application of insecticides and herbicides, and, although benefiting producers financially, offer no such tangible benefits to consumers. For those who experience no benefit, but sense a possible risk, the natural reaction is one of rejection. Furthermore, allowing patenting of the technological processes of GM (in contrast to plant variety rights that protect the output of traditional breeding) places new GM in a different position to traditional GM, a situation related to this second 'green revolution' being privately funded, in contrast to the publicly funded first 'green revolution'. This comes in the context of a general distrust of science, fed by historically recent misuse of science (e.g. for the development of biological weapons) and mistakes by scientists (e.g. over BSE in the UK).

GM plants have been subject to various types of objection. They have been pronounced unnatural, and held to pose an unjustifiable risk to the environment and to human health. The charge of being unnatural has been levelled at a host of targets. Those who bring it in this case still have to explain what is specifically unnatural about new GM that it does not share with many long accepted procedures (notably, of course, traditional breeding techniques).

More serious is the contention that new GM threatens unintended, undesirable, and perhaps also unforeseeable environmental and medical consequences. It brings the potential risk of the escape of organisms, or at least their genes, into wild populations. For example, the spread of insecticidal proteins into wild plants could, in theory, confer a competitive advantage on those plants, disrupting semi-natural systems. Likewise, effects on insect populations could be significant. There are many arguments of detail in scientific research on this issue, and the outcome of these will be important for the use of these particular crops. However, because of the way these arguments are worded, the outcome of this debate will have implications for the wider applications of new GM. This is

fundamentally wrong, and I urge those engaged in the heart of this debate not to allow generalizations about new GM technology *per se* to be extrapolated from the details of the benefits and costs of a particular application of new GM.

Likewise, there is a current debate about the generation of herbicide-resistant crops. Although it seems most unlikely that having herbicide-resistant crops will increase herbicide use, there is little doubt that they will increase the effectiveness of applications, reducing weed densities and, thus continuing a decline of wildlife that has been going on since agriculture began.

Exposure of human populations to large amounts of novel proteins that have never previously been in the human food chain could have unpredictable effects. In particular, allergenicity could cause problems that would be difficult to detect, as symptoms can take a long time to develop. Previous low level exposure of human populations to such toxins is not an argument against this concern, as the quantitative differences between exposure to, for example, Bt toxins from soil-contamination of food and long-term ingestion of significant quantities of this protein in a range of foodstuffs could easily prove crucial. Current testing regimes are not adequate to screen for such responses, although it is hard to see, technically, how such screening could be done – the low quality (both scientifically and statistically) of the feeding experiments of Ewen & Pusztai (1999) provide an example of the difficulty of such work. Nevertheless, I think it is notable that extensive testing is required prior to the introduction of new drugs (that are usually not taken chronically, and whose benefits to the patient are usually clear). In contrast, new GM could lead to an increase by orders of magnitude in the quantity of a protein in the food chain, with this protein being ingested chronically (and with little, if any, benefit to the consumer) – yet this can be done with a testing regime that is much more modest than that required for new pharmaceuticals. The pro-GM lobby should take this concern on board more seriously, especially when considering the outputs from 'wide transfer', which is an important, novel power of new GM.

### Summary

In considering GM issues, scientists must beware the generalizations so apparent in the popular media. It is vital that those either pro- or anti-GM focus their attention on specific examples, otherwise crude generalizations from 'local' arguments may jeopardize important plant GM research of global value.

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## References

- Alcamo E. 1999. *DNA Technology*. London, UK: Academic.
- Conway G. 1997. *The doubly green revolution*. Ithaca, NY, USA: Cornell University Press.
- Ewen SWB, Pusztai A. 1999. Effect of diets containing genetically modified potatoes expressing *Galanthus nivalis* lectin on rat small intestine. *The Lancet* 354: 1353–1354.
- French CE, Rosser SJ, Davies GJ, Nicklin S, Bruce NC. 1999. Biodegradation of explosives by transgenic plants expressing pentaerythritol tetranitrate reductase. *Nature Biotechnology* 17: 491–494.
- Peng JR, Richards DE, Hartley NM, Murphy GP, Devos KM, Flintham JE, Beales J, Fish LJ, Worland AJ, Pelica F, Sudhakar D, Christou P, Snape JW, Gale MD, Harberd NP. 1999. 'Green revolution' genes encode mutant gibberellin response modulators. *Nature* 400: 256–261.
- Tester M. 1999. Seeking clarity in the debate over the safety of GM foods. *Nature* 402: 575.
- Walmsley AM, Arntzen CJ. 2000. Plants for delivery of edible vaccines. *Current Opinion in Biotechnology* 11: 126–129.
- Watson JD, Gilman M, Witkowski J, Zoller M. 1992. *Recombinant DNA, 2nd edn*. New York, USA: Freeman.
- Ye XD, Al-Babili S, Klott A, Zhang J, Lucca P, Beyer P, Potrykus I. 2000. Engineering the provitamin A (beta-carotene) biosynthetic pathway into (carotenoid-free) rice endosperm. *Science* 287: 303–305.

**Key words:** genetic modification (GM), plant breeding, recombinant DNA technologies, anti-GM, pro-GM, genetic engineering.

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## Meetings

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### Plant physiological ecology: linking the organism to scales above and below

#### Ecological Society of America Meeting Snowbird, UT, USA, August 2000

From its origins as a small subdiscipline of ecology, plant physiological ecology has become a dynamic, highly experimental field focusing on questions of both basic scientific importance and deep social concern. A comprehensive understanding of organismal function remains central, but physiological ecology now provides the underpinnings for the emerging field of ecosystem physiology (Mooney *et al.*, 2000) on the one hand and organismal adaptation on the other (Ackerly *et al.*, 2000). Moreover, physiological ecology is embracing advances in molecular biology, providing new insight into the adaptive significance of physiological and morphological traits, thus strengthening its connection to population genetics and evolutionary biology. A symposium at the 2000 meeting of the Ecological Society of America provided an opportunity for introspection and the expression of a new vision for the discipline. Here we report some emerging themes from this symposium.

#### Physiological ecology – the foundation

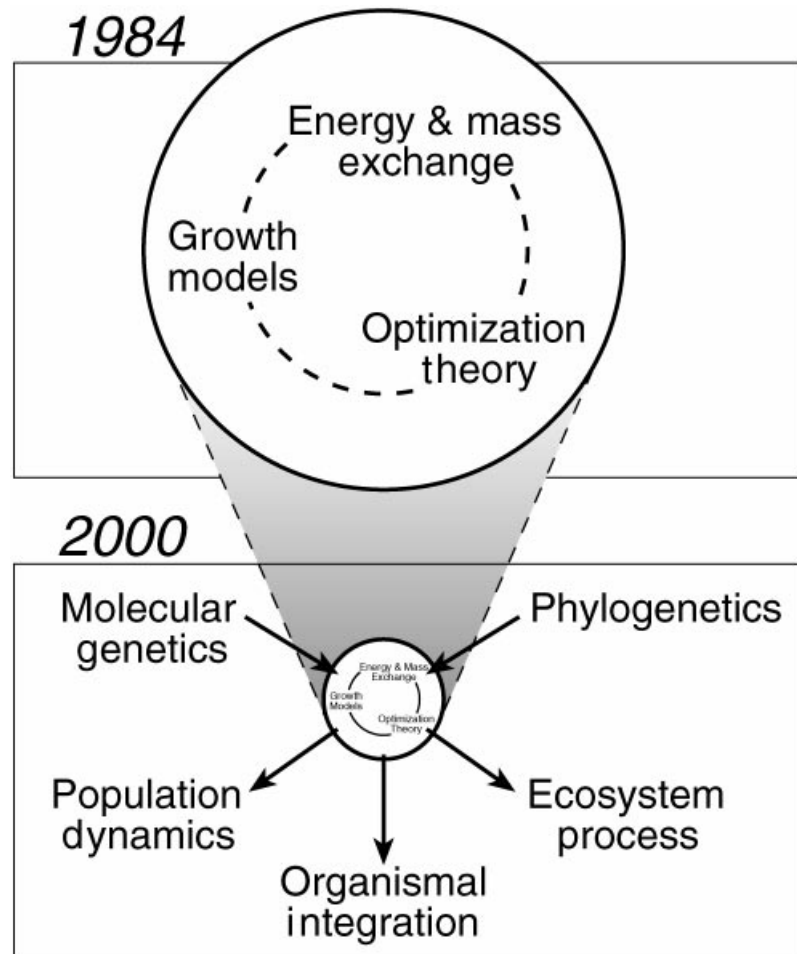
A solid foundation for physiological ecology took shape in 1987 with the publication of a seminal series of articles, leading with 'Plant physiological ecology today' (Mooney *et al.*, 1987). These articles defined the core of physiological

ecology and brought integration to its various avenues of inquiry. The study of physiological and morphological responses of plants to variation in the physical world, the 'adaptive value' of these responses, and their contribution to our understanding of the factors defining the distribution of individual species were the central themes of the discipline. Theories of resource optimization, matter and energy exchange, and mathematical growth modelling provided a conceptual framework (Fig. 1); evolutionary inferences were drawn largely from comparative measurements. Thirteen years later, new methodologies are bringing a renewed experimental approach to organismal research and entirely new avenues of inquiry have opened at the molecular and ecosystem scales.

#### Organismal biology and evolution

Fuelled by the arrival of the complete sequence of the *Arabidopsis* genome, momentum is building among physiological ecologists to employ molecular methods in their research (Purrlington & Bergelson, 1999). Documenting genetic variance and heritability are mainstays of the population approach to establishing the adaptive significance of traits, or at least their capacity to respond to selection (Geber & Dawson, 1997; Ackerly *et al.*, 2000). This approach is, at times, problematic because environmental variance for most physiological traits is large and measurements are time-consuming. Ecological genetic approaches have advanced our understanding of what leads to trait variation and how it evolves (Schmitt *et al.*, 1999). In addition, molecular transformation, either to introduce new genes or to silence existing ones, and the use of single-gene mutations (Baldwin & Schmelz, 1996; Arntz *et al.*, 2000) are powerful new tools for examining microevolutionary processes.

**Fig. 1** In the early 1980s plant physiological ecology focused on organismal physiology and ecology; theories of energy and mass exchange, mathematical growth models and optimization theory were central to the discipline. In 2000, phylogenetic and molecular analyses are providing new tools for examining the adaptive significance of physiological and morphological traits and the bridges between physiological, population and community ecology are being strengthened. Because many of the processes within plant organs scale to the ecosystem level, physiological ecology is playing an important role in understanding biotic and environmental control of ecosystem fluxes.



Using molecular transformation, physiological ecologists can obtain a greater understanding of the fitness consequences of important ecophysiological traits such as variation in photosynthetic rates, biomass allocation, plant size and flowering time.

Genomics and other molecular approaches present tremendous opportunities for physiological ecologists to increase our understanding of organismal function and the evolution of physiological traits (Coleman *et al.*, 1995). Because of the focus on the organism and interactions with other organisms and the environment, physiological ecologists are well positioned to use molecular tools such as DNA microarray technology to advance our understanding of organismal function and evolutionary processes.

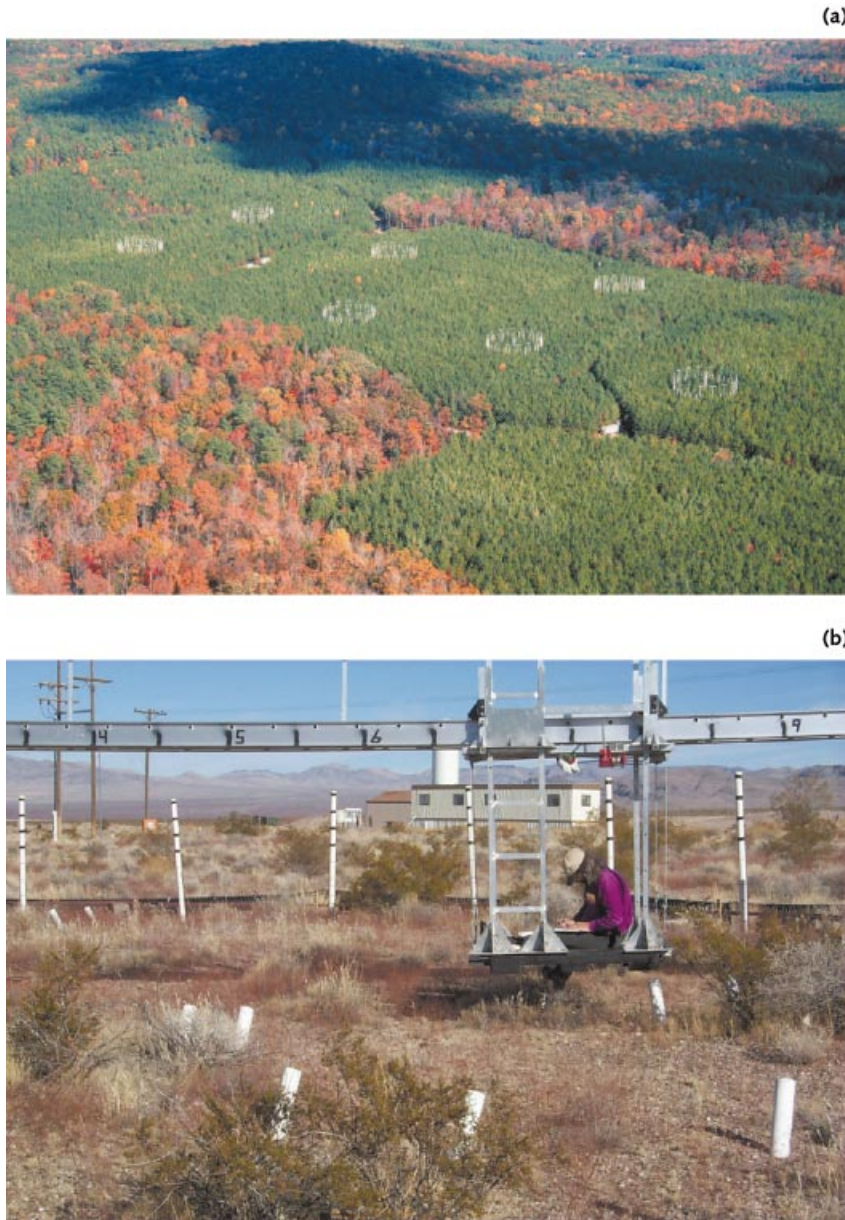
Traditionally, physiological ecologists have relied on comparative studies to document evolutionary convergence as a method to understand the adaptive value of traits, like leaf size and shape or the pattern of biomass allocation. A limitation of this approach has been the inability to isolate the potential influence of phylogeny. For example, have members of the genus *Pinus* evolved a low leaf area-to-stem area ratio (DeLucia *et al.*, 2000) as an adaptation to drought or is this feature a vestige from the shared evolutionary history of the

members of this genus? A new synthesis of physiological ecology and phylogenetics will help resolve this issue.

Recent attempts to unravel the evolution of physiological and morphological traits using a phylogenetic approach are very promising. A study of variation in leaf size in maples, for example, established a relationship between leaf, twig and fruit size (Ackerly & Donoghue, 1998). This observation raises the possibility that selection pressures operating on dispersal biology may confound our interpretation of the relationship between leaf properties and the environment. Framing ecophysiological questions in a phylogenetic context is helping physiological ecologists crack the nut of seemingly intractable questions such as the number of times that  $C_4$  photosynthesis (Monson, 1996) or N fixation have evolved, or the adaptive value of water-use efficiency. This new union between physiological ecology and phylogenetics promises to uncover exciting new perspectives to organismal ecology and the evolution of physiological traits.

### Physiological mechanisms and ecosystem processes

Changes to global biogeochemical cycles and worldwide



**Fig. 2** Plant physiological ecologists measure fluxes of carbon, water, and nitrogen from the leaf to ecosystem scale in large manipulative experiments such as the North Carolina (a) and Nevada (b) free-air CO<sub>2</sub> enrichment (FACE) experiments. These experiments involve many investigators from several different Institutions. Large collaborative research projects provide another way to approach important questions such as how ecosystems will respond to rapid global change. In North Carolina, circular plots in a 17-yr-old loblolly pine forest are exposed to ambient or ambient plus 200  $\mu\text{l l}^{-1}$  CO<sub>2</sub>, simulating the atmospheric composition expected in the year 2050 (DeLucia *et al.*, 1999). A similar experimental treatment is applied in Nevada to a Mohave Desert scrub community, dominated by *Larrea tridentata* and *Ambrosia dumosa* (Smith *et al.*, 2000). In the Nevada experiment, researchers are suspended above the plot to avoid trampling delicate desert crusts. The North Carolina and Nevada photographs are courtesy of Will Owens and Lynn K. Fenstermaker, respectively.

reductions of biological diversity have fostered intense interest in the processes regulating productivity and other aspects of ecosystem function (Eviner & Chapin, 1997; Chapin *et al.*, 2000). Many of these processes scale directly from leaf to canopy function. The carbon and water cycles, for example, are directly regulated by physiological processes operating at the scale of individual leaves, creating a direct feedback from leaf physiology to canopy fluxes to regional climate. Because many of the characteristics that determine the success of individuals in stressful environments are also the processes driving ecosystem-level fluxes, it has been argued that '[e]cophysiology is ... preadapted for large scale problems' (Field & Ehleringer, 1993). By providing the

conceptual and analytical bases for scaling physiological processes to the ecosystem level, physiological ecology is helping to accelerate our understanding of the responses of ecosystems to global change.

Physiological ecologists have shortened the traditional measurement cycle of ecosystem processes from an annual time step to seconds or below, and by doing so have revealed new understanding of mechanisms regulating carbon and water fluxes. Beginning in the 1960s, and coinciding with the rise of ecosystem ecology and the International Biosphere Program, ecologists estimated net primary production of different ecosystems by harvest methods. Though useful for comparing ecosystems under different climatic regimes, this approach

could not assess the effect of seasonal variation in climate on productivity. Instantaneous measurements of net ecosystem exchange with rapid-response gas analysers and advanced data management methods are extending these early studies by allowing, for the first time, an examination of fine-scale environmental control of ecosystem carbon fluxes (Goulden *et al.*, 1996). Such advances have also been driven by interactions with micrometeorologists and scientists in disciplines outside ecology.

From the inception of physiological ecology, conceptual advances and technological breakthroughs have come hand-in-hand. New molecular tools can help physiological ecologists better understand the genetic controls and environmental interactions that affect above- and below-ground plant functioning and their ecosystem links (Zhang & Forde, 1998; Jackson *et al.*, 1999). This progression is also readily apparent from carbon budget studies.

The earliest field infra-red gas analysis systems were housed in bulky 'portable' laboratories and making field measurements was a challenge. Today's miniaturized portable gas-exchange systems control the environment of the leaf precisely and reproducibly, permit rapid measurement and are readily carried to a mountain top or the depths of a tropical forest. Open-path analysers have revolutionized and dramatically reduced the cost of measuring ecosystem carbon fluxes. Rapid advances in our ability to measure and understand the factors regulating the distribution and fractionation of stable isotopes are helping to resolve previously intractable questions, like the proportion of soil CO<sub>2</sub> efflux from plant roots vs soil microbes (Norby & Jackson, 1999; Ehleringer *et al.*, 2000). The next generation of physiological ecologists will probably incorporate new and advancing technologies to help resolve longstanding ecological questions.

### Physiological ecology in practice

Large, collaborative experiments are playing a more prominent role in physiological ecology than ever before (Fig. 2). Though single-investigator research remains strong, the solution to many global ecological questions also requires large-scale collective research efforts. The effect of elevated CO<sub>2</sub> or variation in species composition on the biogeochemical cycling of carbon and nitrogen, for example, is being addressed in expansive, highly collaborative experiments (DeLucia *et al.*, 1999; Smith *et al.*, 2000). And, policy-driven question about the capacity of ecosystems to store atmospheric carbon have spawned international research programs using coordinated methodologies and analytical tools (e.g. see [www-eosdis.ornl.gov/FLUXNET/index.html](http://www-eosdis.ornl.gov/FLUXNET/index.html)). This new model for physiological ecology research is opening exciting opportunities for collaboration. Funding, however, has not kept pace with this new research model; the cultivation of new revenue sources will be essential for maintaining a healthy balance between creative single-investigator research and larger collaborative projects.

### Summary

Molecular genetics and the broader evolutionary view made possible by phylogenetic analyses, particularly when combined with the next generation of growth models (Pearcy & Yang, 1996), is bringing a new focus to organismal biology. With these tools in hand, physiological ecology is well positioned for further advances in the future. Genome sequences and other new molecular tools can be used to improve the understanding of plant biochemistry and physiology, and physiological ecologists could build many productive collaborations with molecular biologists to examine single and multiple gene responses and their interactions with the environment. Working up from the organism, physiological ecology now provides the mechanistic understanding of ecosystem fluxes. It is likely that plant physiological ecology will continue to grow along this axis, incorporating new molecular and biochemical tools and extending the physiology of the organism to larger scales of the community (Bazzaz, 1996), the ecosystem and beyond (Fig. 1).

### Acknowledgements

The authors regret not having space to cover the ecophysiological literature broadly, emphasizing instead participants in the Snowbird conference. E. H. D. gratefully acknowledges assistance preparing this article provided the Program in Ecology and Evolutionary Biology, University of Illinois, <http://www.life.uiuc.edu/programs/PEEB/>.

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### References

- Ackerly DD, Donoghue MJ. 1998. Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). *American Naturalist* 152: 767–791.
- Ackerly DD, Dudley SA, Sultan SE, Schmitt J, Coleman JS, Linder R, Sandquist DR, Geber MA, Evans AS, Dawson TE, Lechowicz MJ. 2000. The evolution of plant ecophysiological traits: Recent advances and future directions. *Bioscience* 50: 979–995.
- Arntz AM, DeLucia EH, Jordan N. 2000. From fluorescence to

- fitness: variation in photosynthetic rate affects fecundity and survivorship. *Ecology* 8: 2567–2576.
- Baldwin IT, Schmelz EA. 1996. Production and accumulation of an inducible defense after multiple inductions: do plants have memory? *Ecology* 77: 236–246.
- Bazzaz FA. 1996. *Plants in a changing environment: linking physiological, population and community ecology*. Cambridge, UK: Cambridge University Press.
- Chapin FS III, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S. 2000. Consequences of changing biodiversity. *Nature* 405: 234–242.
- Coleman JS, Heckathorn SA, Hallberg RL. 1995. Heat shock proteins and thermotolerance: linking ecological and molecular perspectives. *Trends in Ecology and Evolution* 10: 305–306.
- DeLucia EH, Hamilton JG, Naidu SL, Thomas RB, Andrews JA, Finzi A, Lavine M, Matamala R, Mohan JE, Hendry GR, Schlesinger WH. 1999. Net primary production of a forest ecosystem under experimental CO<sub>2</sub> enrichment. *Science* 284: 1177–1179.
- DeLucia EH, Maherali H, Carey EV. 2000. Climate-driven changes in biomass allocation compromise the ability of pines to store atmospheric carbon. *Global Change Biology* 6: 587–593.
- Ehleringer JR, Buchmann N, Flanagan LB. 2000. Carbon isotope ratios in belowground carbon cycle processes. *Ecological Applications* 10: 412–422.
- Eviner VT, Chapin FS III. 1997. Plant–microbial interactions. *Nature* 385: 26–27.
- Field CB, Ehleringer JR. 1993. Introduction: questions of scale. In: Ehleringer JR, Field CB, eds. *Scaling physiological processes: leaf to globe*. New York, NY, USA, Academic Press, 1–6.
- Geber MA, Dawson TE. 1997. Genetic variation in stomatal and biochemical limitations to photosynthesis in the annual plant, *Polygonum arenastrum*. *Oecologia* 109: 535–546.
- Goulden ML, Munger JW, Fan S-M, Daube BC, Wofsy SC. 1996. Exchange of carbon dioxide by a deciduous forest: responses to interannual climate variability. *Science* 271: 1576–1578.
- Jackson RB, Moore IA, Hoffmann WA, Pockman WT, Linder CR. 1999. Ecosystem rooting depth determined with caves and DNA. *Proceedings of the National Academy of Sciences, USA* 96: 1387–1392.
- Monson RK. 1996. The use of phylogenetic perspectives in comparative plant physiology and developmental biology. *Annals of the Missouri Botanical Garden* 83: 3–16.
- Mooney HA, Canadell J, Chapin III FS, Ehleringer J, Körner CH, McMurtrie R, Parton WJ, Pitelka L, Schulze E-D. 2000. Ecosystem physiology responses to global change. In: Walker BH, Steffen WL, Canadell J, Ingram JSI, eds. *Implications of global change for natural and managed ecosystems: a synthesis of GCTE and related research*. Cambridge, UK: Cambridge University Press.
- Mooney HA, Percy RW, Ehleringer J. 1987. Plant physiological ecology today. *Bioscience* 37: 18–20.
- Norby RJ, Jackson RB. 1999. Root dynamics and global change: seeking an ecosystem perspective. *New Phytologist* 147: 3–12.
- Percy RW, Yang W. 1996. A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. *Oecologia* 108: 1–12.
- Purrington CB, Bergelson J. 1999. Exploring the physiological basis of costs of herbicide resistance in *Arabidopsis thaliana*. *American Naturalist* 154: S82–S91.
- Schmitt J, Dudley SA, Pigliucci M. 1999. Manipulative approaches to testing adaptive plasticity: phytochrome mediated shade avoidance responses in plants. *American Naturalist* 154: S43–S54.
- Smith SD, Huxman TE, Zitzer SF, Charlet TN, Housman DC, Coleman JS, Fenstermaker LK, Seemann JR, Nowak RS. 2000. Elevated CO<sub>2</sub> increases productivity and invasive species success in an arid ecosystem. *Nature* 408: 79–82.
- Zhang H, Forde BG. 1998. An *Arabidopsis* MADS box gene that controls nutrient-induced changes in root structure. *Science* 279: 407–409.

**Key words:** plant physiological ecology, ecosystem physiology, organismal adaptation, ecosystem processes, global biogeochemical cycles.



## Tansleys – in-depth reviews from a personal perspective

The *New Phytologist* 'Tansleys' are commissioned in-depth reviews written from a personal perspective by leading international researchers in plant science. These reflect our commitment to easy communication and discussion, an ethos established when this journal was founded, by Sir Arthur Tansley, some 100 years ago. Tansleys are always peer-reviewed.

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