

Commentary

An evolving approach to understanding plant adaptation

The advent of genomics and other ‘omics’ has stimulated movement towards linking gene function and molecular mechanisms to whole-plant physiology, ecology and evolution. The impetus for this feature issue was the 12th *New Phytologist* Symposium, ‘Functional genomics of environmental adaptation in *Populus*’ (DiFazio, 2005); hence, most papers in this issue focus on poplars or other forest trees. Although studies on the molecular basis of adaptation are progressing in *Arabidopsis* (Stenøien *et al.*, 2002; McKay *et al.*, 2003), and in other plants that are long-standing models of adaptive evolution (e.g. *Mimulus*; Bradshaw & Schemske, 2003), studies on forest trees will have an important niche. Trees are good models for studying the genetics of adaptation because of their extensive natural populations with little confounding substructure, random mating, sufficient nucleotide diversity, rapid decay of linkage disequilibrium, economic importance and long history of ecological genetic research (Morgenstern, 1996; Neale & Savolainen, 2004). Although difficulties in genetic transformation will constrain research in most forest trees, transformation is relatively easy in *Populus*, allowing hypotheses to be tested using controlled experimentation with homologous or heterologous gene insertion (Busov *et al.*, pp. 9–18; Man *et al.*, pp. 31–39; both in this issue). Furthermore, the availability of the complete genome sequence in *Populus* (<http://genome.jgi-psf.org/Poptr1/Poptr1.home.html>) will unlock possibilities for ecological genetic research that were unforeseen just a few years ago. Despite this progress, a complete understanding of the molecular genetic basis of adaptation will require cross-disciplinary collaboration on a scale that has been rarely seen, including collaborations among experts in molecular biology, physiology, ecology, population biology, statistics and bioinformatics (Wright & Gaut, 2004; DiFazio, 2005). Fortunately, this area is beginning to form the dendritic connections between diverse disciplines that are needed to answer some of the most fundamental questions in biology.

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How do plants adapt?

The phenotypic changes we see over evolutionary time, across diverse environments and among taxa often reflect adaptive evolution (Orr, 1998; Kawecki & Ebert, 2004). In the broad sense, adaptations are phenotypic traits that have been favored by natural selection, and can be identified by being variable, heritable and responsible for variation in Darwinian fitness. Individual plants also adjust (acclimate) their physiology and development in response to changes in their environment. For example, the morphological and physiological changes that occur in temperate-zone trees from summer to winter are dramatic examples of adaptive phenotypic plasticity. The genetics, ecology and evolution of phenotypic plasticity was the focus of a recent issue of *New Phytologist* (Vol. 166, No. 1, April 2005) and new information on phenotypic plasticity is presented in this issue.

Local adaptation may occur in species exposed to diverse abiotic or biotic environments – and may contribute to speciation (Schluter, 2001; Kawecki & Ebert, 2004). Furthermore, an understanding of local adaptation is important for designing effective breeding programs and conserving genes (Aitken, 2000). In contrast to locally adapted phenotypes, characters that are unconditionally adaptive tend to become fixed within species (Kawecki & Ebert, 2004), and may distinguish closely related species. The best measure for judging the relative importance of an adaptive trait is its effect on fitness itself, or well-documented components of fitness such as seed production, germination, survival and vegetative biomass. Eventually, however, we would like to understand the multifaceted biochemical, physiological and

morphological bases of these adaptations, and their genetic control. For example, which component traits contribute to survival and vegetative biomass – and which genes are responsible for genetic variation in these traits? Studies of the biochemical and physiological bases of fitness components have a long history, which continues in this issue, including analyses of *Populus* productivity and architecture (Cooke *et al.*, pp. 41–52; Monclus *et al.*, pp. 53–62), survival and biomass of *Arabidopsis* on serpentine-like nutrient solutions (Bradshaw, pp. 81–88), *in situ* respiration of tree roots (Cheng *et al.*, pp. 297–307), and carbon transport and partitioning in *Populus* (Babst *et al.*, pp. 63–72). Furthermore, this issue addresses both adaptation and acclimation to a variety of environmental challenges, including edaphic factors such as soil moisture and nutrients (Bradshaw; Cooke *et al.*; Di Baccio *et al.*, pp. 73–80; Man *et al.*; Monclus *et al.*), competition (e.g. productivity, Monclus *et al.*; and tension wood formation; Paux *et al.*, pp. 89–100), and pathogens (Jorge *et al.*, pp. 113–127).

Other ways to judge adaptive traits include looking for evidence that they are under strong natural selection, including nonrandom interactions between genotypes and environments (Kawecki & Ebert, 2004) and nonrandom distributions of genotypes relative to important environmental variables (Howe *et al.*, 2003). Bradshaw, for example, chose to study tolerance to serpentine soils because reciprocal transplant studies demonstrate that plant adaptation to serpentine soils has a genetic basis. Furthermore, Bradshaw mimicked these transplant studies by growing wild-type and mutant *Arabidopsis* genotypes on normal and 'faux serpentine' nutrient solutions, and demonstrated that the *cax1* mutants have most of the phenotypes associated with tolerance to serpentine soils. In their review article, Cooke & Weih (pp. 19–30) noted the geneecological characteristics of seasonal nitrogen cycling, and how its timing is closely tied to the environmental cues that control the annual growth cycle in poplar trees.

Articles in this issue also shed light on both short-term and long-term acclimation to changing environmental conditions, including changes in poplar biomass accumulation, plant architecture and gene expression in response to nitrate levels (Cooke *et al.*), changes in carbon transport and partitioning in response to jasmonic acid (a signaling molecule that mimics the induction of plant resistance by herbivores; Babst *et al.*), and changes in gene expression in response to tree bending (Paux *et al.*) and elevated levels of CO₂ and O₃ (Gupta *et al.*, pp. 129–142; Taylor *et al.*, pp. 143–154). Although the extent and adaptive significance of phenotypic plasticity remains to be fully understood, it is clear that large-scale modifications in gene expression occur rapidly in response to many environmental changes. Gene expression profiling using microarrays not only provides a remarkably sensitive tool for studying phenotypic plasticity, but also

provides an entry into uncovering the actual genes responsible for natural variation in adaptive traits. Moreover, by revealing molecular genetic networks, microarrays also provide inroads into understanding how a gene's position within a pathway affects its potential to contribute to adaptation (Cork & Purugganan, 2004).

Genetics of adaptation

The prospects for understanding physiological, ecological and evolutionary genetics have changed dramatically in recent years – we now have the tools to identify the specific genes responsible for adaptive genetic variation in natural populations. Despite a rich literature describing empirical studies of quantitative genetic variation and expectations from theoretical treatments of adaptation and speciation (Orr, 1998, 2003; Mauricio, 2001), we still know little about the genetic basis of adaptation. Which classes of genes vary among ecotypes, ecoclines, varieties and species? Are the same classes of genes involved? Does adaptation and speciation involve few genes with large effects or many genes with small effects? In the near future, there will be a wealth of new information on each of these questions.

Although we have the tools in-hand, understanding the genetic basis of adaptation is still a daunting task. We only have a rudimentary understanding of which traits are most important, and the numbers of genes controlling each of these traits is large. Therefore, the most thorough (and objective) approach would be to associate genes with phenotypes by scanning the entire genome, presumably with single nucleotide polymorphism (SNP) markers. The practical difficulties of this approach, however, are enormous. Therefore, most researchers are focusing on a small to modest number of candidate genes – genes believed to be associated with particular phenotypes based on indirect or circumstantial evidence (Pot *et al.*, pp. 101–112). How are these candidates chosen? The most obvious approach is to choose genes based on their known function – either in the plant of interest or in other species. Of course, it is best if the candidates have been directly tested in the species of interest. The review by Busov *et al.* reveals that transgenic approaches have been widely used to demonstrate that individual genes can influence specific adaptive traits. Man *et al.*, for example, shows that a pine glutamine synthetase gene can enhance nitrogen assimilation efficiency in transgenic poplar, leading to increased leaf area, plant height and leaf dry weight. Traditional mutational approaches and activation-tagging may be even more valuable because they can be used to find 'new' genes that are associated with adaptive phenotypes (Busov *et al.*). Using activation-tagging in *Arabidopsis*, Bradshaw found that mutations in a gene that encodes a tonoplast calcium-proton antiporter (*CAX1*) results in plants that have most of the phenotypes that are associated with

plants adapted to serpentine soils. Bradshaw's data and physiological model suggest that mutations in this gene might be involved in the adaptation of a wide variety of natural plant populations to serpentine soils. Although physiological and biochemical studies can be used to test the functional relationships between specific genes and phenotypes (Bradshaw; Man *et al.*), these tests do not indicate whether these genes have any role in explaining adaptive genetic variation in nature. This requires a comparative analysis of naturally occurring alleles within a single species, or orthologous loci in sister taxa, perhaps using transgenic approaches (Bradshaw).

Candidate genes can also be identified based on their positions on quantitative trait locus (QTL) maps or patterns of gene expression. Jorge *et al.* mapped QTL for qualitative and quantitative resistance to leaf rust (*Melampsora*) in poplar hybrids and noted that analogs of NBS-LRR resistance genes have been found in the vicinity of *Melampsora* resistance loci in other hybrid poplar pedigrees (Zhang *et al.*, 2001). Paux *et al.* identified candidate genes for tension wood formation based on the differential and distinctive patterns of gene expression in bent vs unbent *Eucalyptus* trees. 'Reaction wood', which forms in leaning or bent trees, helps maintain upright growth of the main stem and adds support to large branches.

The approaches described above generally use 'forward genetics' to proceed from adaptive phenotype to adaptive genes. An alternative path toward uncovering the genetic basis of adaptation uses approaches more akin to 'reverse genetics'. In its purest form, the first step is to simply identify genes that have strong 'signatures' of natural selection (e.g. based on DNA sequence analysis and population differentiation), and then determine their phenotypes and specific roles in adaptation. Based on an exploratory study of nucleotide diversity in eight wood-related genes in pines, Pot *et al.* identified two genes with unusually high levels of population differentiation in *Pinus pinaster*, suggesting that artificial or natural selection was operating. *Pp1* encodes a glycine-rich protein thought to provide elasticity and tensile strength, whereas *KORRIGAN* is involved in cellulose-hemicellulose assembly. In contrast to approaches that incorporate careful physiological analyses, sequence-based approaches may use evidence of strong population differentiation or the distinctive characteristics of DNA sequences themselves as evidence for the important adaptive roles of these genes (Wright & Gaut, 2004). The effects of underlying population structure should be incorporated into these analyses to obtain valid conclusions about the role of natural selection on individual genes (Wright & Gaut, 2004). One way to do this is to characterize variation in neutral genetic markers. The microsatellite markers and sampling strategies described by Cole (pp. 155–164, this issue) may be suitable for these kinds of analyses.

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Genome evolution

Recent studies of plant genome sequences and large expressed sequence tag (EST) databases show that *Arabidopsis*, rice and several crop plants are paleopolyploids (Bowers *et al.*, 2003; Blanc & Wolfe, 2004a; Wang *et al.*, 2005). Although all angiosperms and most land plants may be polyploid, the number, antiquity and types of genome duplications and subsequent genome reorganizations vary among taxa (Soltis, 2005). The mechanisms that direct the evolutionary fate of duplicated genes are still unclear. For example, the duplication itself (or successive rearrangements) might make the duplicated gene immediately different from its parental copy by placing it under the influence of new *cis*-regulatory elements (Lynch & Katju, 2004). In a study of duplicated genes originating from the most recent genome duplication in *Arabidopsis*, Blanc & Wolfe (2004b) found that certain classes of regulatory genes (such as kinases) were preferentially retained, whereas others (such as those involved in DNA repair) were preferentially lost. Is this a common pattern in plants? Are there lineage-specific patterns of gene retention and loss that are indicative of specialized functions or adaptations? With the rice and poplar genome sequences in hand, and other plant genome sequences on the horizon, we can begin to answer these questions. By analyzing ESTs from several *Populus* species, Sterck *et al.* (pp. 165–170) showed that a genome duplication occurred early in the evolution of the genus, before the species diverged. Based on synonymous nucleotide substitution rates, the authors estimated that the duplication occurred 8–13 Myr ago, which conflicts with fossil evidence that suggests that the species diverged 18–58 Myr ago (Eckenwalder, 1996). While misinterpretation of the fossil record is one possible explanation, Sterck *et al.* also note the potential impact of generation interval on synonymous substitution rates, which have been mostly estimated from plants that flower and reproduce at very young ages compared with poplar trees. Although an individual poplar tree typically lives for around 100 years, poplar's propensity for clonal propagation allows a genotype to survive and sexually reproduce for millennia.

Because of its status as a model plant species (Busov *et al.*), poplar research could provide a more direct means to assess the influence of generation interval, longevity, organism size and effective population size on genome evolution and adaptation (Lynch & Conery, 2003).

In addition to genome duplication and restructuring, a recent study revealed a previously unknown process for genome-wide sequence changes. Lolle *et al.* (2005) found that *Arabidopsis* plants carrying mutations in the *HOT-HEAD* gene can inherit allele-specific DNA sequences at multiple loci that were not present in the genomes of their parents, but were present in an earlier ancestor. The authors propose that a cache of stable RNA serves as the template for this extra-genomic mechanism of DNA sequence reversion, and may provide a way for self-fertilizing species to circumvent the negative consequences of inbreeding or recover from the effects of a genotype that is maladapted to its present environment. As described by Chen *et al.* (pp. 171–180), flax exhibits phenotypic and genomic changes associated with environmental factors. When an inbred variety of flax (P1) is grown in an inducing environment, it gives rise to progeny called genotrophs that exhibit stable changes in size, branching, seed hairs, isozymes, hormone levels, nuclear DNA contents, number of ribosomal genes and number of other repetitive sequences. Although the parents remain phenotypically plastic when grown in different environments, the altered phenotypes of the genotrophs are stable. Building on previous work that showed that the flax genome undergoes highly specific DNA changes at multiple loci from parents to progeny, they identified a site-specific insertion sequence (LS-1) in the genotrophs that is also found in natural populations of flax. Reminiscent of the changes associated with the *HOTHEAD* mutants, an intact LS-1 is not present in the genome of the progenitor, P1. These studies suggest the possibility that an extra-chromosomal, RNA-based mechanism of inheritance might be operating in flax as well.

Perspectives

This feature issue illustrates that we are at an exciting and challenging crossroads in the study of plant adaptation. A powerful suite of tools is now available for *Arabidopsis*, and other taxa that are highly divergent with respect to evolutionary distance (rice) and perennial growth habit (poplar). Moreover, genomic resources are becoming increasingly available for other tree species and plants that are models of adaptive evolution. Because EST databases and high-throughput techniques for assessing both molecular and phenotypic variation are becoming widely available, progress will not be limited to model plants. Perhaps the most difficult challenge is not the development of tools and resources, but the complete merging of genomic, ecological and evolutionary perspectives.

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Meetings

Challenges to plant mega-diversity: how environmental physiology can help

Environmental Physiology and Plant Diversity in Mexico: From Molecules to Ecosystems. A symposium within the XVI National Botanical Congress, Sociedad Botánica de México, Oaxaca, Mexico, October 2004

Mexico is one of the 12 megadiverse countries that together contain about half of the world's biodiversity. Specifically,

nearly 10% of known vascular plant species can be found in Mexico, owing to its intricate topography that leads to numerous microenvironments, and to the convergence of Nearctic and Neotropical biotas in this country (Neyra González & Durand Smith, 1998). A corresponding botanical knowledge has also emerged in Mexico throughout its history, contributing with the domestication of universally important plants such as bean, cacao, maize and tomato. Unfortunately, the southern Mexican states, which are the most biodiverse, are the ones facing the nation's highest rates of deforestation and the gravest hindering of socio-economic development. Thus, a pressing need for understanding the mechanisms leading to species persistence emerges simultaneously with an urgency to implement management

practices that make conservation compatible with development. In this context, the XVI National Botanical Congress considered the 'scientific and conservation challenges in a megadiverse country'. Some examples of how environmental physiology can address such challenges were discussed during the symposium.

'Because environmental productivity indices can help predict plant responses in productivity to different environmental factors, they can be utilized to evaluate different scenarios of global climate change'

From seedlings of endemic cacti to global environmental change

Cacti are emblematic of Mexico. This is reflected in many cultural aspects including the national seal, depicting an eagle perched on an opuntia, and even those stereotypical Hollywood allegories featuring a columnar cactus as a source for shade. In fact, Mexico is the center of origin and diversification for many cactus genera. Particularly, Oaxaca, the state where the meeting was held, contains the highest cactus diversity within the country. Also, perhaps most readers will not be familiar with the fact that opuntias, another contribution of the Mexican flora, are the most extensively cultivated crassulacean acid metabolism (CAM) plant worldwide, greatly exceeding the area dedicated to the better-known pineapple (Nobel, 2000).

Some cacti have C_3 metabolism after germinating and acquire CAM later during their development (Altesor *et al.*, 1992). For over a decade it has been thought that this could be the case for most cactus species, but recent studies have revealed a somewhat different story (Olivia Hernández-González & Oscar Briones, Instituto de Ecología, Xalapa, Ver., Mexico). It turns out that some columnar cacti from the tribe Pachycereeae and at least one barrel cactus from the tribe Echinocacteeae are CAM obligates; their seedlings always present a nocturnal build-up of organic acids following germination, although the amount accumulated does respond to light and water.

Approximately 700 out of *c.* 2000 known species of cacti occur in Mexico, 40% of which have government protection (NOM-ECOL-059-2001; <http://www.ine.gob.mx/ueajei/norma59a.html>). Because most of these cacti are endemic, they are especially threatened by changes in land use. This is the case for *Mammillaria gaumeri* (Britton & Rose), a small globose cactus restricted to coastal sand dunes (very valuable beach-front land) and tropical dry forests from

the northern Yucatan peninsula (Leirana-Alcocer & Parra-Tabla, 1999). Conservation efforts regarding *M. gaumeri* include the identification of favorable sites for its reintroduction following *ex situ* propagation. In particular, the responses in productivity to various microenvironmental factors, such as air temperature, photosynthetic photon flux and soil water potential, are being characterized for this species (Carlos Cervera, Centro de Investigación Científica de Yucatán, Mérida, Yuc., Mexico) to generate an environmental productivity index (EPI; Nobel, 1988). This is the first time that an EPI has been created for use in conservation.

Because EPIs can help predict plant responses in productivity to different environmental factors, they can be utilized to evaluate different scenarios of global climate change. For instance, plant responses to increasing air temperature could be estimated and areas most vulnerable to invasion by exotic species could be identified. One cause of global warming is the postindustrial increase in atmospheric CO_2 concentration. In general, higher CO_2 concentrations lead to higher plant productivities. An important caveat is that not all plants have the same response. Rapid-growth species are likely to be more sensitive than slow-growth species. This could result in shorter residence time for carbon in tropical forests because fast growing species also tend to be short-lived (Körner, 2003). For instance, lianas from the tropical forests of Yucatan show a considerably enhanced productivity under elevated CO_2 (Granados & Körner, 2002). Because lianas can affect the productivity of trees (Granados & Körner, 2002; Schnitzer & Bongers, 2002), which are the actual carbon sinks of forests (Körner, 2003), a net effect of increased atmospheric CO_2 is that tropical forests may eventually become carbon sources rather than sinks (Julián Granados, Centro de Investigación Científica de Yucatán, Mérida, Yuc., Mexico). Thus, the responses to elevated CO_2 by various functional types need to be considered when making estimates of carbon cycles at large scales. Furthermore, lianas play an integral role in several aspects of tropical forest dynamics, including a contribution to whole-plant transpiration (Schnitzer & Bongers, 2002; Andrade *et al.*, 2005). However, studies about the physiology of lianas and co-occurring trees are uncommon.

Stable 'iso-tropical' ecology

Over the last three decades, stable isotope studies have become a common part of physiological ecology in order to gain insight about various functional aspects of plant biology, including photosynthetic metabolism and water use by individual plants and by whole ecosystems (Dawson *et al.*, 2002). An area of current vigorous research using stable isotopes in plant ecophysiology is that of tracing the movement and utilization of water at various scales. For instance, variation of the natural isotopic composition of the various water compartments for an ecosystem can help

identify various ecological processes by separating the different water sources for plants in space and time. One difficulty for such studies is the procurement of water samples from the deeper layers of the soil. In most cases, such a sampling requires the efforts of a very strong graduate student using a soil borer. This task becomes even more complicated at places where, like in Yucatan, a calcareous hardpan occurs rather superficially. Nevertheless, the Yucatan peninsula also has numerous *cenotes* (singular, *cenote*), subterranean water deposits that had religious significance for the Maya. By using stable isotope tracers, *cenotes* provide a unique system for detailed accounting of potential water sources for tropical trees. In particular, preliminary work from a tropical dry forest of northern Yucatan revealed that perennial trees have access to *cenote* water, whereas deciduous trees do not (Paula C. Jackson, Kennesaw State University, Kennesaw, GA, USA). Proximity to caves has also allowed very detailed studies of water use for trees from North American temperate forests (McElrone *et al.*, 2004).

Legumes, especially shrubs and trees, tend to dominate the vegetation in tropical arid and semiarid regions of America and Africa. It is not surprising, then, that about 10% of the 20 000 known species in the Fabaceae are found in Mexico (again, Oaxaca, along with Chiapas, has the greatest legume diversity in Mexico; Sousa & Delgado, 1993; Doyle & Luckow, 2003), where just over half of the territory is arid or semiarid (Neyra González & Durand Smith, 1998). Soils from arid lands tend to be nutrient-poor, hinting that the success of legumes may be a result of the symbiotic association with nitrogen-fixing bacteria found for most species in the family (Doyle & Luckow, 2003). For tropical dry forests in the Yucatan, 21 out of 23 legume trees were nitrogen fixers, as indicated by the presence of root nodules (Louis Santiago & Todd Dawson, University of California, Berkeley, CA, USA). The contribution of biologically fixed nitrogen to the nitrogen budget of legumes can be evaluated with the nitrogen isotopic composition of leaf tissue. Indeed, biologically fixed nitrogen in trees from tropical dry forests of Yucatan tended to increase with the age of tree stands. It ranged from about 10% for 5- to 10-yr-old stands to twice as much for 20- to 30-yr-old stands. It became apparent that availability of biologically fixed nitrogen favors the higher photosynthetic rates observed for nitrogen-fixing species compared to those observed for nonfixing species.

Conclusions and Perspectives

Physiological research aims to explain the mechanisms by which plants adapt and persist in a given environment within an ecosystem. Questions of interest occur at various scales, from the spontaneous diffusion of solutes at the subcellular level (De la Barrera, 2005), to whole plant processes (Jackson *et al.*, 1999), and to ecosystem and global scales (Körner, 2003). Technological advances

leading to portable instruments have greatly contributed to the advance of ecophysiological knowledge. Nevertheless, despite the great diversity of plants and ecosystems in Mexico, studies about physiological ecology are relatively incipient in this country. Participants and attendants to the symposium committed to encourage the organization of at least three environmental physiology symposia for the next National Botanical Congress (in 2007) about CAM, stable isotopes and biological interactions. A considerably sized cohort of graduate students is nearing the completion of their PhD in several ecophysiological laboratories in Mexico. Their professional careers will surely improve our understanding of the mechanisms responsible for the impressively diverse Mexican flora.

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- Key words:** conservation, crassulacean acid metabolism (CAM), ecophysiology, environmental productivity index (EPI), global change, nitrogen fixation, plant megadiversity, stable isotope.



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