

PREFACE

Genes in evolution: the control of diversity and speciation

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This special Highlight section of *Annals of Botany* contains seven papers that show the rapid progress in understanding the genetics related to plant evolution – identifying genes that have immediate effects on reproductive behaviour and diversity, and that directly lead to further diversification and eventually speciation. Understanding the genetic effects and genes that enable these processes is critical for both wild ecosystems and crop species. The study of plant genetics is moving forward at an unprecedented rate: for most of the last century geneticists had a few phenotypes to work with, but by the early 1990s there were hundreds of isozyme and then DNA markers allowing fine mapping of plant genomes in carefully constructed crosses. By the year 2000, with the results from DNA sequencing, there were hundreds of genes known from their DNA and research could move from marker discovery to functional genomics, relating these gene sequences to single-gene, Mendelian phenotypes, some of which have surprising consequences.

For some years now, both simple characters and groups of genes have been related to complex phenotypes through QTL (quantitative trait locus) analysis, and mutation or transgenic approaches. Taxonomy has continued its development from a descriptive aspect of botanical research to having a strong phylogenetic and evolutionary basis, including DNA sequences to complement morphological analysis. The interpretation of the results from experimental hybridization has also been helpful in defining species and their relationships. However, results from hybridization can be misleading, with many exceptions in both directions to the simplistic concept that two plants that hybridize are the same species. Many characters, ranging from polyploidy to sexual incompatibility, prevent hybrids being made within a species, while otherwise well-defined species form hybrids that are among the most successful and dominant genotypes in many environments, and in some cases become species themselves. As our understanding of genetics has increased, ever more features of plant behaviour have been shown to be under close genetic control; this Highlight brings together seven outstanding articles showing the nature – and range – of genetic effects on speciation and domestication. While most Highlight issues featuring manuscripts on a particular important topic are planned a year or more in advance, these papers were submitted by chance around the same time, and have been published together in this issue to show the rapid advances in the area of understanding genetic effects on divergence and speciation.

The review by [Rieseberg and Blackman \(2010\)](#) identifies no less than 41 genes that have been considered to lead to reproductive isolation of populations. Interestingly, the genes are

very diverse, and include those which have prezygotic and postzygotic effects. Simple geographical isolation is not seen as the only widespread cause of speciation and the cessation of gene flow between populations; nevertheless, both larger and smaller features of geography lead to isolation of populations, and [He et al. \(2010\)](#) are able to show an example where the genetic structure of a species, *Banksia hookeriana*, is not solely dependent on the structure of a landscape, in this case where the population is located on sand dune crests physically separated by uninhabitable hollows. Occasional long-distance dispersal of seeds or movement of individuals from one population to another maintains connectivity within the species and prevents isolation. In contrast, [Nomura et al. \(2010\)](#) provide insight into the phylogeny and implications of habitat diversity. *Farfugium* (Asteraceae) is a monophyletic group associated with a wide range of habitats, including forest understorey (sciophytes), coastal crags (heliophytes) and riverbeds (rheophytes) in an archipelago in east Asia. They conclude that isolation on islands and subsequent parallel adaptation events followed migration over Quaternary land-bridges along the distribution range. Uninformative DNA sequence variation coupled with highly divergent morphologies suggest that adaptive diversification was rapid.

The other four papers make conclusions related to the genetic diversification and selection seen in crop plants. The Tehuacán Valley in Mexico provides a remarkable ‘natural laboratory’ for study of human selection effects on plants, because there are well over 100 native plant species where artificial selection is being practiced and these silvicultural and cultivated populations co-exist with wild populations. [Parra et al. \(2010\)](#) study the cactus *Stenocereus puiñosus* and find that despite selection for larger and sweeter fruit, there are high levels of gene flow that have promoted morphological divergence and moderate genetic structure between wild and managed populations, while conserving genetic diversity. Hence, despite strong selection, there is no evident genetic bottleneck that might limit breeders of the fruit in future, unlike that seen in many other domesticated species.

As noted above, hybridization or polyploidy – speciation by whole-genome duplication – can lead to new, and reproductively isolated, species in a single event. Evidence of evolutionarily recent polyploidy events is seen in half of all plants, and contributes significantly to plant biodiversity. [Shi et al. \(2010\)](#) look at ancient events, or paleopolyploidy, that may be inferred from genomic data and their analysis of the nuclear genomes of kiwi fruit (*Actinidia*) and related Ericales shows evidence for at least two paleopolyploidy events. Their results provide

evidence that gene-family methods are able to reliably uncover ancient polyploid speciation events.

Soybean, *Glycine max*, is an important tetraploid crop, but there are still gaps in its domestication history. Guo *et al.* (2010) carry out an extensive study of the diversity of soybean from its South China centre of origin using molecular markers, and propose a single origin with a moderately severe genetic bottleneck during domestication. Wild soybeans in this region have an unexploited and valuable gene pool for future breeding, but, unlike the situation in *Stenocereus*, it will require careful study and extensive crossing with selection to introduce this diversity into the germplasm pool available to plant breeders. The final paper in the Highlight presents an important example of how diversity from a wild species can be used in one of the world's three most important grain crops. Rice, *Oryza sativa*, requires fertilization to set seed, but the temperatures experienced during hot weather (over 32–36 °C) induce sterility. Considering that such temperatures are rarely reached in the early morning, Ishimaru *et al.* (2010) introgressed an early-morning flowering (EMF) trait from wild rice, *O. officinalis*, where anthesis occurs soon after sunrise. Although the temperature effect on sterility itself was similar in the two rice species, the avoidance of high temperatures by a few hours caused by the early-morning flowering trait leads to significantly increased fertility in the line with introgression of the EMF trait.

Together, these seven papers add considerably to our understanding of genetics in a broad evolutionary context. The results are of significance for wild species, with implications

for whole ecosystems, and indeed the species used as examples in these papers are those of coastal, island and duneland systems that are particularly threatened by changes including urban 'development', sea-level alterations, storm frequencies and temperature. The crop papers show how knowledge of the mechanisms of evolution and associated genes can impact on our exploitation of biodiversity in crops and their wild relatives.

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