

properties and the atmospheric water-vapor demand (Siqueira *et al.*, 2008).

To conclude, Bonner (1959) stated that some of the problems pertaining to water movement in plant physiology are becoming increasingly amenable to mathematical analysis and called for the creation of a branch in plant physiology titled 'Phytobiophysics'. This call was made in 1959 – and the occurrence of phenomena such as HL and HR simply reinforce this call today.

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**Key words:** carbon–water cycling models, drought, hydraulic redistribution, soil moisture, transpiration.

## What's good for you may be good for me: evidence for adaptive introgression of multiple traits in wild sunflower

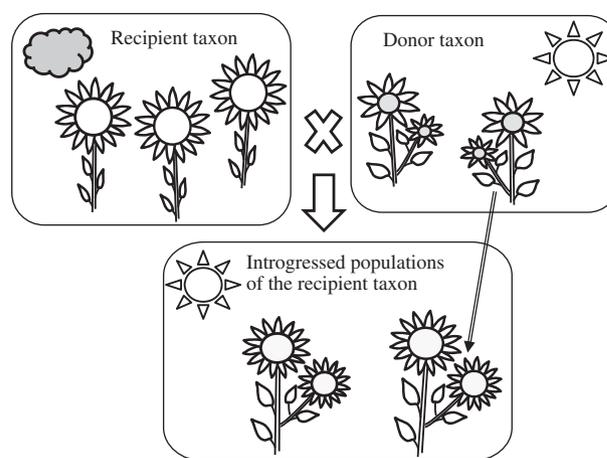
Interspecific hybridization has long been considered an important evolutionary mechanism in plants (Arnold, 2004). In particular, the transfer of adaptations among related taxa mediated by interspecific hybridization has received considerable attention from theoretical and empirical points of views. This process, often called 'adaptive introgression', involves the transfer of fitness-increasing alleles and their phenotypic effects from one taxon to another (Whitney *et al.*, 2006; Fig. 1). Although many empirical examples of this process have been proposed (Rieseberg & Wendel, 1993; Table 1), and some of them convincingly demonstrated using appropriate empirical approaches (e.g. Martin *et al.*, 2006; Whitney *et al.*, 2006), it remains difficult to evaluate the overall importance of this process between related taxa. Moreover, even in documented cases, it is typically unknown whether multiple traits are involved in adaptive introgression, and which traits are more likely to introgress. Theoretical studies indicate that under heterogeneous environments, a single allele that is at an advantage in the alternative environment and genetic background is expected to introgress readily (Barton, 2001). However the transfer of multiple traits in introgressed populations, possibly with complex epistatic interactions, is not straightforward and depends heavily on conditions such as the rate and duration of hybridization and the detailed genetics of hybrid fitness (Barton, 2001). In this issue of *New Phytologist*, Whitney *et al.* (pp. 230–239) specifically address the issue of adaptive introgression of multiple traits by comparing phenotypes and fitness of natural and synthetic hybrids of two wild sunflower species, *Helianthus annuus* and *Helianthus debilis*. Together with the results obtained in a previous investigation (Whitney *et al.*,

2006), they provide experimental evidence that introgression has modified several aspects of the recipient taxon's phenotype in an adaptive manner, including traits associated with adaptation to both abiotic (drought tolerance) and biotic (herbivore resistance) features of the environment.

'... adaptive introgression, coupled with some form of balancing selection, might constitute a recurrent evolutionary scenario.'

### Methodological approaches to demonstrate adaptive introgression

The ultimate demonstration of adaptive trait introgression would be based on evidence that a given haplotype originating from the donor parental species, and with a well-defined phenotypic effect, is subject to positive selection in a hybrid lineage (Martin *et al.*, 2006; Whitney *et al.*, 2006). A recent study by Kim *et al.* (2008) approached this standard, reporting the transfer of a cluster of regulatory genes (the RAY locus) from an introduced species *Senecio squalidus* to the UK-native species *Senecio vulgaris*. This study provided molecular evidence for introgression of this gene cluster into *S. vulgaris*, and showed that this event was associated with major changes in inflorescence morphology (introducing peripheral flowers with large conspicuous petals), possibly increasing outcrossing rates in this self-compatible species. Precise identification of the molecular basis of the adaptive trait allowed alternative processes, such as incomplete lineage sorting (ancestral origin of the trait maintained in both species since speciation) or parallel evolution (convergent evolution of the same trait), to be ruled out. However, in this case evidence for positive selection on the introgressed haplotype in *S. vulgaris* was missing.



**Fig. 1** Adaptive introgression under positive selection for drought tolerance. The recipient taxon has a wide distribution and comes into secondary contact with a drought-tolerant related taxon. Hybridization occurs between the two taxa, and introgressed populations of the recipient taxon establish themselves in a new xeric environment. These populations have evolved adaptations to their environment that correspond to drought tolerance traits (e.g. an increase in the extent of branching) introgressed from the donor parental taxon to the recipient taxon.

When the molecular basis of the putatively introgressed trait is not known, robust validation of the adaptive introgression event requires a combination of several lines of evidence (Whitney *et al.*, 2006): evidence for genetic introgression from the donor into the recipient taxon; evidence that introgressed lineages are maintained in the recipient taxon; evidence that phenotypes of the recipient taxon at fitness-related traits have shifted towards those of the donor; and evidence that natural selection has favored recipient genotypes with phenotypes shifted towards those of the donor. In the case of *H. annuus* and *H. debilis*, the transfer of genetic material from the donor into the recipient taxon was confirmed using microsatellite markers (Scascitelli *et al.*, 2010). There is also clear evidence that the introgressed taxon has a long history of occurrence in

**Table 1** Examples of types of traits for which events of adaptive introgression have been demonstrated or suggested; the traits fall into three main categories, depending on the nature of the responsible selective forces

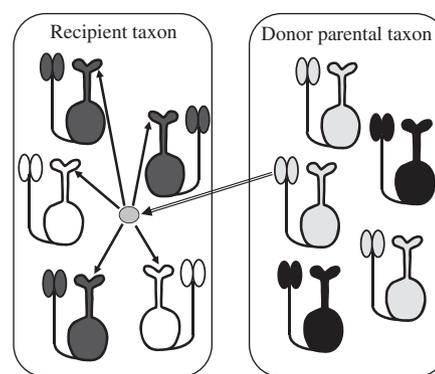
Nature of selection	Relevance of traits	Example taxa	References
Adaptation to the abiotic environment	Shade tolerance	<i>Iris fulva</i> → <i>Iris hexagona</i>	References given in Arnold (2004)
	Drought tolerance	<i>Helianthus debilis</i> → <i>Helianthus annuus</i>	Whitney <i>et al.</i> (2010, this issue)
Adaptation to the biotic environment	Flood tolerance	<i>Iris fulva</i> → <i>Iris brevicaulis</i>	Martin <i>et al.</i> (2006)
	Herbivore resistance	<i>Helianthus debilis</i> → <i>Helianthus annuus</i>	Whitney <i>et al.</i> (2006)
	Invasiveness associated with vegetative growth	<i>Reynoutria sachalinensis</i> ↔ <i>Reynoutria japonica</i>	Pysek <i>et al.</i> (2003)
Mating system dynamics	Outcrossing device (ray floret)	<i>Senecio squalidus</i> → <i>Senecio vulgaris</i>	Kim <i>et al.</i> (2008)
	Self-incompatibility alleles	<i>Arabidopsis lyrata</i> ↔ <i>Arabidopsis halleri</i>	Castric <i>et al.</i> (2008)

southern Texas, USA. Now, Whitney *et al.* provide experimental evidence that many phenotypic traits (ecophysiological, phenological and plant architectural traits) potentially related to drought tolerance differ significantly between introgressed and nonintrogressed populations of the recipient taxon *H. annuus*. In all cases, values of these traits in the introgressed populations were shifted towards the phenotype of the donor *H. debilis*. These comparisons were replicated in two ecologically distinct sites. Finally, two synthetic BC<sub>1</sub> (first generation of backcross with the recipient taxon) hybrid populations were used to specifically test for an association between these traits and individual fitness (as estimated by viable seed production) using the approach of phenotypic selection analysis (Lande & Arnold, 1983). The results highlight that selection in a dry habitat has favored phenotypes in the resynthesized hybrids that are shifted towards those of *H. debilis*. Altogether these results carefully demonstrate that adaptive introgression has resulted in a transfer of traits, allowing rapid growth and reproduction before summer heat and drought, from *H. debilis* to the genomic background of *H. annuus*. More importantly, they show that multiple traits related to adaptation to abiotic features of the environment can be transferred together.

### Evolutionary implications of adaptive introgression

From the many instances of adaptive introgression suggested in the empirical literature, actual demonstrations using the criteria already described are limited to a few reference cases (e.g. Louisiana Iris species (Martin *et al.*, 2006) and sunflower (Whitney *et al.*, 2006, 2010)). It is now essential to investigate this process in other taxa, and for a wide diversity of fitness-related traits, before concluding about the overall evolutionary importance of adaptive introgression. Future successful investigations would combine population genomic approaches and functional analyses, in order to validate the introgression process and to identify the molecular basis of adaptation, with phenotypic selection experiments aimed at demonstrating that the introgression process has been driven by natural selection.

Interestingly, several cases of adaptive introgression have been suggested recently for traits that are subsequently maintained as polymorphisms within the recipient taxon. One case corresponds to the transfer of the radiate inflorescence form from *S. squalidus* to *S. vulgaris* (see earlier). This introgressed trait seems to be maintained as a stable polymorphism within the recipient taxon and contributes potentially to an increase in population levels of outcrossing (Kim *et al.*, 2008). A second case corresponds to the transfer of individual alleles at the multiallelic self-incompatibility locus between *Arabidopsis lyrata* and



**Fig. 2** Adaptive introgression under negative frequency-dependent selection of an allele at the self-incompatibility locus. A pollen grain carrying a given allele at the self-incompatibility locus can only successfully fertilize individuals carrying a different allele (with a different color). Through hybridization, an allele specific to the donor parental taxon (light gray) is introduced (as a pollen grain) in the recipient taxon (double arrow) where it will benefit from the advantage of the rare as it can fertilize potentially all extant individuals (adapted from Schierup & Vekemans, 2008).

*Arabidopsis halleri* (Castric *et al.*, 2008; Fig. 2). High allelic diversity at this locus is maintained within species through negative frequency-dependent selection (advantage of the rare), but hybridization has caused transfers of alleles between species driven by natural selection. Outside the plant literature, a third case has been described corresponding to a transfer of a mutation from domestic dogs to North American gray wolf populations, causing skin color change (melanistic K locus mutation; Anderson *et al.*, 2009). These examples suggest that adaptive introgression, coupled with some form of balancing selection, might constitute a recurrent evolutionary scenario. Interestingly, in each case, the introgressed allele did not seem to have evolved in the donor parental taxon but was inherited from an ancestor, yet it was absent or lost in the lineage leading to the recipient species. Hence, it has been argued that adaptive introgression is an important mechanism for the long-term maintenance of many alleles in multi-allelic systems subject to balancing selection (e.g. plant self-incompatibility; Schierup & Vekemans, 2008), or for the recovery of ancestral characters that may have been lost in some lineages (e.g. ray florets in *Senecio*; Kim *et al.*, 2008).

Finally, adaptive introgression may also have evolutionary implications as a process leading to the transfer of traits from domesticated gene pools to wild gene pools. A key concern is constituted by the risk for increased weediness associated with the potential transfer of herbicide- or insect-resistance alleles from genetically modified crops to wild populations of related species (Stewart *et al.*, 2003). However, the North American gray wolf case also suggests that, for an endangered species, 'hybridization with another species or a domesticated relative can provide

genetic variation that has important adaptive consequences' (Hedrick, 2009).

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**Key words:** drought tolerance, hybridization, introgression, natural selection, plant adaptation, plant evolution.

## Letters

### Naturally occurring ectopic growths in certain *Xanthosoma* and *Begonia* cultivars and the problem of leaf dorsiventral polarity

The morphologically dorsiventral polarity of leaves of higher plants has become a major subject of interest in plant development. Wardlaw (1949) suggested that an inhibitor from the apical meristem prevents the proximal leaf cells from forming those cell types that are usually located in the distal region. This hypothesis was experimentally supported by Sussex (1955) when isolated leaf primordia were found to have radial, and not bilateral, symmetry. This idea was later discounted when Whittier (1962) found apogamous leaves in the fern *Pteridium*, where no apical

meristem is present in the gametophyte, and concluded that 'dorsiventral symmetry of the isolated leaf is inherent in the leaf primordium.' I have found that apogamous leaves in the fern *Thelypteris* come from polarized gametophytic cells where upper sides form papillae and lower sides produce rhizoids, that is, a possible symmetry pre-pattern exists outside the leaf (Korn, 1993). Hagemann (1970) supported Wardlaw's contention of the upper region arising as either a part of, or continuous with, the shoot apical meristem (SAM). Recently Wardlaw's hypothesis was re-activated by Nogueira *et al.* (2007) who found that one class of small RNAs were spatially restricted to the apical meristem and part of a leaf primordium. Through a series of ablation experiments, Reinhardt *et al.* (2005) identified a role of the L1 (epidermal) cells in establishing leaf polarity.

Lately this phenomenon has been inspected using mutation analysis. Waites & Hudson (1995) described the *phantastica* (*phan*) mutation in *Antirrhinum* in which older leaves have ectopic axes of growth. These growths are on the upper surface of leaves and are characterized as a trough of