

## Editorial

### Plant form and function

A favourite phrase in architectural debate is that *form follows function* – that the form of a building should be based on the functional activities housed within. I am sure that everyone can readily imagine buildings where this tight coupling does not occur. However, in biological organisms the connection should be much more certain, as the form of an organism primarily depends on internal function, as represented by the genome and its translation into cellular metabolism. Modern plant biology easily demonstrates the connection, for example when genetic changes in starch metabolism lead to orders of magnitude changes in plant size (Rasse & Tocquin, 2006), when herbicide-resistance genes allow virulent weeds to survive in the face of applied herbicides (Menchari *et al.*, 2006) and in identifying how many genes appear to be required to confer the capacity to hyperaccumulate toxic heavy metals (Hammond *et al.*, 2006). Processes that are difficult to investigate become much easier with modern genomic approaches. Examples include the involvement of auxin in establishing ectomycorrhizal symbiosis (Reddy *et al.*, 2006) and the action of calmodulin for antioxidant defense in leaves (Hu *et al.*, 2007).

Research published in *New Phytologist* covers many orders of magnitude in time and space (Woodward, 2007), and aspects of the form and function relationships are generally visible but not always in the direction of form following function. Function often follows form and in a manner that does not appear easily possible to dissect by the modern techniques of molecular plant biology. Invisible to the naked eye is the critically important convective flow of air through leaves to rhizomes in anoxic, waterlogged soils (Armstrong *et al.*, 2006) and the lateral movement of carbon dioxide within the air spaces of leaves, important for photosynthesis during drought (Pieruschka *et al.*, 2006). In forest canopies form follows function that follows form, in that the light intercepted by an individual tree is influenced by its size and form and also by the size and form of surrounding trees. However, effective optimization of form and light interception require flexibility in branch form as the tree grows up into the forest canopy (Osada, 2006).

The interaction of form and function can change sign. Nurse plants can protect smaller individuals during their early stages of establishment, a feature that may benefit either genetically related or genetically unrelated species. Nurse plant protection is primarily an above-ground function of shelter that appears to be most effective during drought (Stultz *et al.*, 2007). If well-watered, then the nurse plant protection

changes to a competitive function, outgrowing and increasing the mortality of establishing plants. This change in plant form is an aspect of phenotypic plasticity. A major feature of plasticity in growth form is that it is reduced as environmental conditions become more limiting for growth (Valladares *et al.*, 2007). As function becomes more restricted, so also does the capacity to change form in response to environmental challenges. So, for example, change in form through leaf herbivory affects function and reduces the capacity to obtain the optimum form for a particular environment (Valladares *et al.*, 2007).

The reverse situation of function following form has a long history in plant science that still continues, with the specific aim of attempting to discern critical, but hidden, aspects of function that constrain observable form. The area of the xylem lumen in 51 woody species present in California is positively correlated with plant height (Preston *et al.*, 2006), a functional relationship perhaps associated with the increasing resistance to water flow with plant height. However, in tropical rainforests of Central America, vessel diameter was uncorrelated with precipitation, while vulnerability to drought-induced embolism increased as precipitation decreased (Choat *et al.*, 2007). Species-specific differences in the responses of both form and function to the environment diminish the capacity to generalize accurately. Yet, surveys of large numbers of species do reveal some generalities. For example leaf mass per area is positively correlated with shade tolerance in evergreen tree species (Lusk & Warton, 2007). The close tie between leaf form and function is an area of high current activity (Leishman *et al.*, 2007), again with a focus on leaf structure, but also in terms of functional components – leaf photosynthesis, nitrogen and phosphorus. When applied to invasive plants, the approach clearly identified that exotic invasive species modified function to enable faster growth than native invasive species, with a potential connection to reductions in leaf defence.

Form and function are much like yin and yang, opposing but complementary forces in plant development. The field of 'eco-devo' investigates this relationship in situations where changing functional responses to the environment (opposing current development) elicit a response of form to something potentially adaptive. Casson & Gray (2008) describe such responses by stomata in changing environments. Deep investigation of plant systems also indicate that functions are connected as networks, from the interactions of systemic signals in plants (Demidchik & Maathuis, 2007; Roberts *et al.*, 2007), to mycorrhizal symbioses (Paszkowski, 2006) and to the spread of pathogens through plant populations (Jeger *et al.*, 2007). So, in fact, form and function are joined within a complex network of co-occurring components, interacting

on a range of timescales yet to be fully investigated. *New Phytologist*, with the breadth of subjects that it publishes, is constantly working at identifying these network components, through our emphasis not only on mechanisms but also on the diversity of plant form.

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**Key words:** form, function, network, molecular plant biology, leaf traits, plasticity, eco-devo, mycorrhiza.

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## Commentary

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### Stealth tactics of galling parasites and their potential indirect effects

Associations between higher plants and their gall-forming arthropod parasites are among the most specific, intimate and tightly co-evolved interspecific interactions known in macroscopic organisms. Galling insects, by definition, do

not merely feed upon their host plants, but induce their hosts to form a bewildering array of highly specific tumor-like structures via biochemical interactions with plant hormones and regulatory mechanisms of gene expression (Fig. 1; Price *et al.*, 1987). Recent research has demonstrated that in addition to inducing gross morphological changes, these gall-forming parasites often employ a diversity of more subtle manipulations of plant physiology and chemistry. These include the induction of sugary secretions (Fernandes *et al.*, 1999), increased concentrations of defensive compounds in external gall tissues (e.g. Hartley, 1998), decreased concentrations of



**Fig. 1** An example of the goldenrod ball gall formed by the tephritid fly *Eurosta solidaginis* on *Solidago* species.

defensive chemicals and increased concentrations of nutrients (e.g. amino acids and lipids) in gall-nutritive tissues (Koyama *et al.*, 2004), and suppression of the release of volatile organic compounds (VOCs) (Tooker & De Moraes, 2007).

In this issue of *New Phytologist*, John Tooker and colleagues (pp. 657–671) provide evidence that the manipulation of plants by galling insects may be even more subtle and complex than previously appreciated. Using a combination of laboratory and field experiments, Tooker *et al.* demonstrated that not only does the stem-galling tephritid fly *Eurosta solidaginis* fail to elicit a significant local volatile response in its perennial host, *Solidago altissima* (Tall Goldenrod), it also appears to systemically inhibit the emission of VOCs typically induced in response to a generalist folivorous caterpillar, *Heliothis virescens*.

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*‘... the intimate relationships of gall-formers with plants and their immobility may have selected for strategies to avoid detection by natural enemies; strategies that may include the manipulation of VOC release.’*

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## Volatile organic compounds as indirect defenses?

Volatile phytochemicals induced by herbivore feeding have been shown to be attractive to natural enemies of the herbivores, particularly parasitoids, for a variety of specific plant–herbivore associations (e.g. De Moraes *et al.*, 1998). Whether VOC release attracts natural enemies remains to be determined for this particular system, but it is probable given the widespread reliance of insect natural enemies on plant-derived VOCs (e.g. De Moraes *et al.*, 1998). It is unclear in these systems whether the interactions between natural enemies and volatile chemical cues produced by plants is an evolved response to herbivore pressure; however, the conclusions of Tooker *et al.* do not rest upon the assumption that the emission of VOCs by *S. altissima* represents an adaptive indirect defense, only that such chemical cues may alter the mortality rates of herbivores by their enemies.

## Insights from a comparative approach

A highlight of the study carried out by Tooker *et al.* is its comparative approach. By comparing volatile release among *S. altissima* plants with different herbivores, the authors were able to demonstrate that (1) not all galling herbivores inhibit volatile release in response to the exophytic caterpillar, and (2) the observed response is unlikely to occur as a result of resource depletion associated with feeding, as a xylem-feeding herbivore (spittlebug) failed to suppress volatile release. There has been relatively little study of volatile induction in response to gallers (but see Tooker & De Moraes, 2007), but the intimate relationships of gall-formers with plants and their immobility may have selected for strategies to avoid detection by natural enemies – strategies that may include the manipulation of VOC release. The failure of the gall-forming *Gnorimoschema* moth to suppress volatile release may be a result of its feeding mechanism (chewing mandibles rather than sucking or rasping), its phylogenetic proximity to the exophytic herbivore, or because, in contrast to *Eurosta*, its dominant enemies attack early in development before the gall is fully formed (Heard *et al.*, 2006).

## Mechanisms of suppression of induced indirect defenses

Tooker *et al.* suggest that alteration in the accumulation of salicylate may be part of the biochemical mechanism that suppresses induced VOC release. Induced volatile production in maize by a generalist folivorous caterpillar is associated with jasmonate accumulation in wounded tissues (e.g. Schmelz *et al.*, 2003), but it remains to be demonstrated whether the same is true in *S. altissima*. If it is, salicylate accumulation in the tissues galled by *Eurosta* could be involved in the suppression of volatiles, given its known antagonism of the

induction of jasmonate-mediated defenses (Cipollini *et al.*, 2004). There is a need to determine where volatiles are made in the stem, which is important in order to know whether altered accumulation of salicylate in inner vs outer tissues of the gall could be part of the suppressive mechanism. Moreover, salicylate and jasmonate contents in leaves attacked by the exophytic herbivore, where volatile production was systemically suppressed by *Eurosta* galls in the stem, need to be assessed to determine the involvement of these defense hormones there. Alternatively, *Eurosta* may use other mechanisms, including salivary or fecal components, to silence volatile production, at least locally in the gall. Some herbivores can silence direct defenses of plants through the use of glucose oxidase in the saliva, although such mechanisms may ultimately rely on salicylate accumulation in the plant for the actual mechanism of suppression (Musser *et al.*, 2002).

Tooker *et al.* also suggest that resource limitations caused by galling could play a role in the systemic suppression of volatile responses by *Eurosta*. Systemic induction of direct defenses in young leaves of some plants relies on the import of carbon from other leaves in a source–sink relationship (Arnold & Schultz, 2002). Because *Eurosta* galls can alter the patterns of carbohydrate translocation among organs of *S. altissima* (McCrea *et al.*, 1985), disruption of source–sink relationships between stem and leaves could be part of the mechanism of the systemic suppression of exophytic herbivore-induced volatiles (but presumably not local *Eurosta*-induced volatiles). The authors address this possibility by comparing the suppressive effects of *Eurosta* with those of two other herbivores, but found that feeding by the galling moth *Gnorimoschema* and the xylem-feeding spittlebug failed to suppress VOC release. However, as the authors recognize, these organisms may not be appropriate controls given their different feeding modes and resources. Systemic suppression as a result of resource limitation also seems unlikely because the release of low-molecular-weight volatiles is thought to be among the least costly forms of plant defense (Halitschke *et al.*, 2000). A parallel examination of the induction or suppression of ‘costly’ direct defenses and ‘cheap’ indirect defenses by gallers or associated leaf-feeders would help to clarify this possibility.

### Trait-mediated indirect community effects

Although the study of Tooker *et al.* is preliminary in several respects, the local and systemic suppression of VOC release by *E. solidaginis* points to potential community-wide trait-mediated indirect effects of this gall-maker. If suppression of VOC release results in lower mortality rates of relatively stationary leaf-chewing insects, as the authors suggest, then this could significantly affect the community of insect herbivores feeding on *S. altissima*. In contrast to most examples of host-mediated indirect interactions, which tend to be negative (Kaplan & Denno, 2007), the interactions

between galling *Eurosta* flies and the exophytic *Heliothis* caterpillars may be positive. Similar consequences have been observed with indirect interactions between above-ground and below-ground herbivores in maize, in that attractiveness to enemies is reduced in doubly infected plants as a result of changes in VOC release (Rasmann & Turlings, 2007). Such facilitative interactions among herbivores could result in positively correlated distributions of herbivores, a contagious distribution of herbivore damage and unstable population dynamics via negative density dependence of herbivore mortality. Given the growing evidence that VOCs released from one plant can induce or prime neighboring individuals for the induction of defense, suppression of VOC release in a galled ramet could also increase the susceptibility of neighboring ramets or genets by preventing this priming response.

### Future directions

The study of Tooker *et al.* represents an initial incursion into a relatively new and potentially insightful area of research involving the tritrophic, plant-mediated facilitation of insect herbivores. Yet, there are many conceptual and empirical gaps in our knowledge that need to be filled before the ecological importance of these interactions can be fully appreciated. For example, in this particular system, it remains to be shown that the VOCs are attractive to enemies and that inhibition of these ‘indirect defenses’ results in lower mortality risk for both endophytic and exophytic herbivores. As outlined above, the physiological mechanisms of VOC induction by exophytic herbivores and suppression by gall-makers need to be clarified, especially with regard to the roles of salicylic acid and jasmonic acid pathways and their potential antagonism. Finally, the effects of these interactions on the community need to be explored in the field to determine whether these tritrophic interactions significantly influence community structure and dynamics. Taking a broader view, these interactions need to be explored in additional tritrophic systems to understand whether such plant-mediated facilitative effects are widespread, and, if so, whether they function by similar or distinct mechanisms. While there has been growing recognition of community-wide effects of structural changes in plants caused by herbivores (e.g. Crawford *et al.*, 2007), the diverse, yet visually inconspicuous, biochemical and physiological interactions between plants and gall-making herbivores may prove to be even more pervasive and ecologically significant.

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**Key words:** indirect defense, plant gall, trait-mediated indirect effects, tritrophic interactions, volatile organic compounds.

## The genetic diversity of intraterrestrial aliens

In this issue of *New Phytologist*, Croll *et al.* (pp. 672–687) describe a study in which they sampled over 40 individuals

from a field population and scored each individual for its genotype at each of 13 polymorphic molecular loci. Such studies have been the routine fodder of population genetics since the 1970s, so why is this paper noteworthy? It is because the subjects of this study are arbuscular mycorrhizal fungi (AMF). These are strange organisms, and it has become obligatory to open every paper on AMF with two true statements: AMF are vital for the normal growth of most plants, and AMF are fiendishly difficult to study.

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*‘AMF are exceptional in that there is no stage in the life history where an individual is reduced to a single nucleus, because the large spores contain hundreds of nuclei.’*

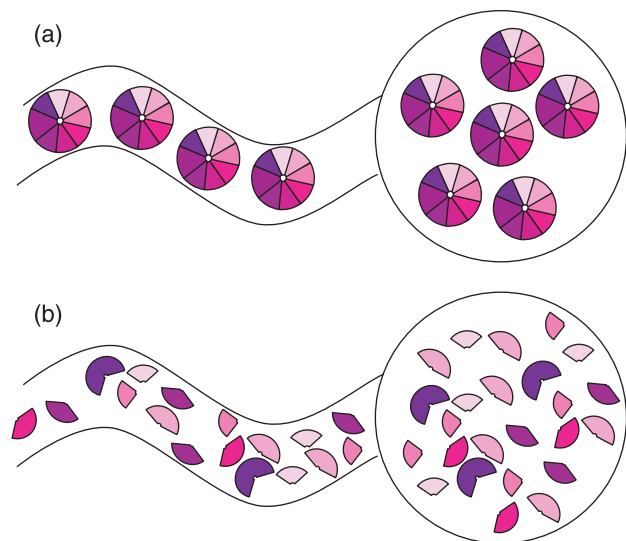
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The first challenge in AMF population genetics is to sample a set of individuals from the tangled web of root infections in the field, which Croll *et al.* did by establishing multiple *in vitro* cultures. Nobody has yet succeeded in growing AMF in pure culture, as the fungus does not grow unless attached to plant roots, but it is possible to propagate AMF on root organ cultures *in vitro*, although only a few AMF species have so far been grown successfully in this way. This indirect approach is bound to introduce some bias reflecting culturability in the chosen hosts and conditions, but has major advantages. A simpler approach would be to collect spores from the field (Stukenbrock & Rosendahl, 2005), but this is the equivalent of studying a plant community by digging up the seeds in the soil; spore numbers are a poor reflection of fungal biomass and activity. The other problem with a spore is that it only has enough DNA for a small number of analyses (Stukenbrock & Rosendahl, 2005), whereas an *in vitro* culture can be multiplied indefinitely. Croll *et al.* were therefore able to type each isolate reliably at 13 genetic loci. Furthermore, each locus was targeted by AMF-specific PCR primers, so we can be confident that all the products are from the fungus itself rather than from the bacteria or nonAMF fungi that are frequently closely associated with AMF.

The first surprise is that, at all the loci described by Croll *et al.*, they report just one allele in each isolate. This might seem a normal expectation for a fungus, given that most fungi are haploid most of the time, but in fact the authors did find some loci that had more than one allele in some individuals, although they did not use them in the study because this would have complicated the analysis (I. Sanders, pers. comm.).

The history of multiple sequences within AMF began with the discovery that a single isolate may have two or more distinct sequences for the ribosomal RNA gene region (Sanders *et al.*, 1995; Lloyd-Macgilp *et al.*, 1996). Usually these differences are fairly small, but in the *Glomus mosseae* group of species, two internal transcribed spacer (ITS) sequences are found, and these are so different that one might expect them to indicate different genera, except that they have been reported to co-occur in the same isolate (Clapp *et al.*, 2002). Nor is within-isolate diversity confined to the ribosomal RNA genes: it has also been seen for other genes (Helgason *et al.*, 2003; Corradi *et al.*, 2004). Whether this diversity reflects the cohabitation of genetically distinct nuclei within the same cytoplasm (a heterokaryon) or identical nuclei, each of which contains all the genetic variants (a homokaryon), is the subject of ongoing debate (Kuhn *et al.*, 2001; Hijri & Sanders, 2004; Pawlowska & Taylor, 2004; Hijri & Sanders, 2005; Pawlowska, 2005; Corradi *et al.*, 2007; Rosendahl, 2008). AMF have few cross-walls within their hyphal networks, so nuclei inhabit a common cytoplasm (a syncytium). This is not so unusual in fungi, but AMF are exceptional in that there is no stage in the life history where an individual is reduced to a single nucleus, because the large spores contain hundreds of nuclei. The nuclei in a spore, and in the mycelium derived from a spore, are therefore better considered as a population rather than as an individual. If they are collectively a homokaryon, we have to explain how the variation generated by mutation is purged, while if they are a heterokaryon, we must explain how diversity is maintained in the face of genetic drift.

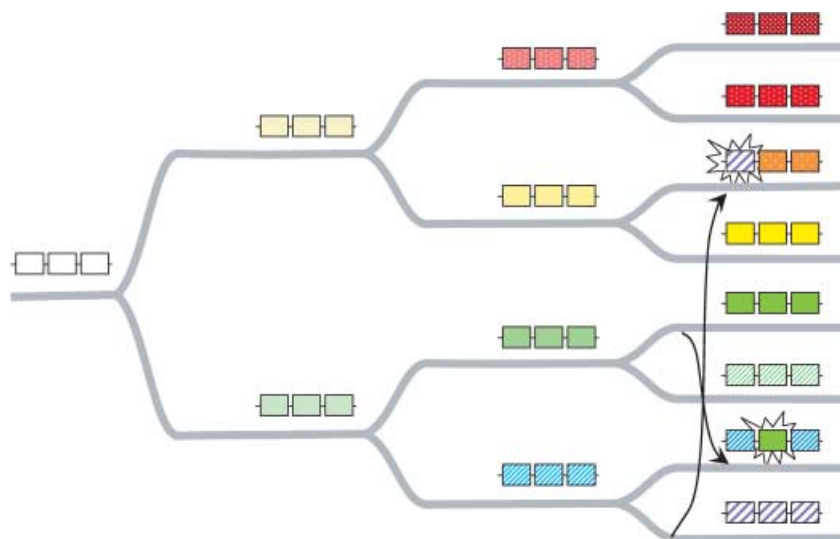
There is not space here for a full discussion of all the evidence, so I shall merely point out that the most-cited study supporting the homokaryon hypothesis is far from conclusive. Pawlowska & Taylor (2004) studied two genes in *Glomus etunicatum*. The first, PLS1, was unusual in that 13 allelic variants coexisted in a single isolate. All the variants were maintained through successive generations, which would be unlikely if each variant were in a separate, independently segregating nucleus. However, under some models for heterokaryosis, such as the selfish nucleus hypothesis (Fig. 1), independent segregation of nuclei is not expected. Secondly, Pawlowska & Taylor (2004) amplified the ribosomal ITS from a number of individual nuclei, and showed that, whenever they succeeded in getting amplification, a nucleus carried all three of the ITS variants seen in that isolate. Ribosomal genes are unusual in that they are in multiple copies in the genomes of all organisms, and sometimes in several arrays that may diverge in sequence. Admittedly, the sequences in different nuclear lineages within a permanent heterokaryon would be expected to diverge, but Pawlowska & Taylor (2004) only succeeded in obtaining amplification for a handful of nuclei, which might have represented a particularly favourable genotype (perhaps with a large number of rDNA copies), rather than a random sample of all the nuclei in the spore.



**Fig. 1** Two hypotheses for genome organization in arbuscular mycorrhizal fungi. (a) The polyploid nucleus hypothesis (Pawlowska & Taylor, 2004) explains how multiple allelic variants can coexist in a homokaryon. Each nucleus has multiple copies of the genome, although massive gene loss frequently follows the formation of a polyploid, so it is likely that individual genes vary widely in copy number. (b) The selfish nucleus hypothesis (proposed here) explains how multiple genetically different nuclei can persist in a heterokaryon without segregational loss. In a syncytium, a nucleus may replicate faster if it loses part of its genome and relies on its neighbours to provide the missing products in the common cytoplasm. The evolutionary result will be a consortium of mutually complementary nuclear lineages, none of which can survive without the others. Other scenarios are also possible for both homokaryons and heterokaryons.

Indeed, in a syncytium, it is theoretically possible for some nuclei to survive even if they have no rDNA at all.

Multiple genetic markers allow a good number of genotypes to be distinguished, and Croll *et al.* discuss their spatial distribution and association with host species. Furthermore, with multiple loci in multiple individuals, patterns of association between loci can be explored. Here things start to get really interesting. AMF have been described as anciently asexual, because no convincing structures associated with sexual reproduction have been seen, and no unambiguous evidence for genetic recombination (Rosendahl & Taylor, 1997). Ancient asexuals are of interest because most asexual lineages are thought to be short-lived (Gandolfi *et al.*, 2003). This issue, and others raised in this commentary, have been discussed in a recent Tansley review (Rosendahl, 2008). A completely asexual organism evolves as a branching tree of clonal lineages. A genetic variant that arises in one lineage is forever associated with the set of genotypes characteristic of that lineage. Without recombination, it cannot get together with an allele at another locus that arose in a different lineage (Fig. 2). On the face of it, the table of genotypes presented by Croll *et al.* seems to contradict this expectation. There are several instances where the same allele crops up in genotypes



**Fig. 2** Genetic evidence for asexuality and recombination. In an asexual organism, clonal lineages gradually diverge from each other at all loci. Since all loci share a common ancestry, they all have a consistent phylogeny. The effect of recombination between lineages (indicated by black arrows) is to introduce alleles that have a discordant phylogeny.

that, on the evidence of the other loci, clearly belong to different lineages. Is this evidence for genetic recombination in the supposedly asexual AMF?

The evidence is not conclusive, and the potential problem is homoplasy; that is, the possibility that the same allele arose independently more than once. This is a particularly prevalent problem with microsatellites (simple sequence repeats, SSR), and most of the loci in the study were of this kind. An SSR locus consists of a number of tandem repeats of a very short DNA motif, typically two or three bases. Mutations that increase or decrease the number of repeats occur frequently by strand-slippage during replication, so such loci are typically highly polymorphic in populations. This makes them handy as genetic markers, but homoplasy is rife at SSR loci because a variant with a particular number of repeats can be generated in many ways. Hence, SSRs do not seem a good choice for a critical study of interlocus associations. However, an examination of the allele sequences that Croll *et al.* provide in their supplementary material reveals that, although they chose loci because they included SSR motifs, most of the allelic differences that they observed are not the result of typical SSR length variation. In fact, the alleles differ in multiple ways, including short insertions or deletions and single nucleotide substitutions. When an allele has multiple unique features, it is very unlikely to have arisen more than once, so we can discount homoplasy. Some ambiguity remains, though, because Croll *et al.* do not provide a complete sequence for every gene in every individual. Most individuals are only characterized by the overall length of the PCR product from each locus. It is easy to see that quite different sequences can happen to be of the same overall length and, in the case of the nuclear intron locus, the authors demonstrate exactly this. Nevertheless, Croll *et al.* appear to have the tools for a rigorous assessment of recombination in AMF. Will we soon have to reassess the assumption that AMF are ancient asexuals?

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## Meetings

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### Whither plant evo-devo?

**Investigating the evolution of plant form: conceptual integration from the molecular to the ecological – Boulder, Colorado, USA, December 2007**

Plant evolutionary developmental biology has come a long way in the years since its transformation at the beginning of the molecular era. Gone are the naïve hopes that developmental genetics would provide unambiguous solutions to questions of homology and evolutionary novelty that had stymied plant biologists for centuries. Also gone is the simplistic notion that understanding the molecular genetics of *Arabidopsis thaliana* might reveal universal properties of plant (or even just angiosperm) development (Jaramillo & Kramer, 2007). On the other hand, life's complexity is surely what makes all of us enjoy being biologists. So perhaps, while plant evo-devo has not answered all (or even many) of the questions it initially set out to address, it is timely to ask where this young field is going, or perhaps more importantly, where this young field could and should go. Such was the vision of a recent meeting of plant evolutionary biologists with strong interests in integrating plant developmental biology into the broader spectrum of botanical disciplines.

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*'... we risk the sophistication and power of genetic tools outstripping our ability to interpret the data and "know" the phenotype.'*

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*Investigating the evolution of plant form: conceptual integration from the molecular to the ecological*, was an intensive, three-day minicourse organized by the Molecular and Organismic Research in Plant History (MORPH) Research Coordination Network (part of the US National Science Foundation Research Coordination Network Program) that took place in mid-December at the University of Colorado in Boulder. The overarching goal of MORPH has been to promote interdisciplinary research on the evolution of plant form through the integration of concepts and approaches from across the hierarchy of biological organization. This has primarily been accomplished over the last five years through the sponsorship of more than 40 interdisciplinary research training experiences for undergraduates, graduate students, postdoctoral individuals and junior faculty; through assistance to 95 students to attend interdisciplinary plant evo-devo symposia at national and international meetings; and development of a website for the highly diverse and international community of plant evolutionary developmental biologists (<http://www.colorado.edu/eeb/MORPH/>). The MORPH minicourse represented a new tack in attempting to bridge interdisciplinary chasms and engage the next generation of plant evolutionists and developmentalists.

This minicourse provided the opportunity for a select group of 14 doctoral students, from across the USA and Mexico, to interact with 11 seasoned researchers (Scott Armbruster, University of Portsmouth, UK; Spencer Barrett, University of Toronto, Canada; Peter Crane, University of Chicago, USA; Pamela Diggle, University of Colorado, USA; Michael Donoghue, Yale University, USA; Peter Endress, University of Zurich, Switzerland; William Friedman, University of Colorado, USA; Larry Hufford, Washington State University, USA; Vivian Irish, Yale University, USA; Amy Litt, New York Botanical Garden, USA; and Michael Purugganan, New York University, USA), whose work spans the spectrum from



evolutionary ecology to developmental genetics (for a listing of talks, go to <http://www.colorado.edu/eeb/MORPH/grants/minicourses/minicourse2007.html>). Both researchers and students gave research presentations that were followed by extensive discussions of best approaches, potential pitfalls and interdisciplinary insights on the evolution of plant form.

By bringing together students and faculty from diverse backgrounds, this meeting served to increase the dialogue between botanical subdisciplines that, while fundamentally interested in plant structure and diversity, rarely attend the same meetings or sit at the same table. In a single room, paleobotanists working on reproductive structures in Cretaceous angiosperms and outgroups to flowering plants (e.g. Friis *et al.*, 2006) sat side-by-side with molecular geneticists examining the roles of gene duplication and subfunctionalization in floral evolution (e.g. Irish & Litt, 2005) and ecologists whose goals of explaining floral diversity require fitness assays in wild populations (Barrett, 2008). The two organizers, Larry Hufford (Washington State University, USA) and William Friedman (University of Colorado, USA), hoped that by the end of the meeting, the participants would be able to identify both common ground and difficult areas where future interdisciplinary collaboration is required to develop new paradigms.

### Broadening the macroevolutionary and microevolutionary comparative bases of plant evo-devo

The comfort zone necessary for cross-disciplinary synthesis can be remarkably narrow in any new area. While most biologists recognize the great potential of plant evolutionary developmental biology in this molecular era, it has yet to deliver an understanding of the morphological diversity characteristic of the vast majority of clades in nature. Moreover, plant evo-devo has not as yet forged a meaningful union with ecology and microevolution. Success in plant evolutionary developmental genetics to date has largely involved the use of a limited number of model organisms. Even these few models, however, provide tantalizing glimpses of the possibilities that may be achieved through the power of comparative approaches to developmental and evolutionary biology.

The rapid rate of whole-genome sequencing, currently underway along with the development of new technologies, suggests that plant biologists will soon have many more systems to compare to infer the general rules of plant development (Bowman *et al.*, 2007). However, with the emerging promise of large-scale genomic initiatives, a key challenge will be to link comparative developmental genetics to existing bodies of knowledge, notably the more than 200 yr of plant morphological tradition that date to the work of Goethe (*Versuch die Metamorphose der Pflanzen zu erklären*, 1790) and the hypothesis-driven approaches used in evolutionary

ecological studies of adaptation and population divergence (e.g. Barrett, 2008 and articles contained therein). This integration will be absolutely critical as the phylogenetic, structural and ecological breadth of plant taxa open to study expands, and the sophistication of the questions asked increases in complexity.

Discussions at the MORPH minicourse did indeed focus on the growing recognition that plant evo-devo requires a broad set of study systems and genetic tools that can be readily applied to diverse groups to study the molecular genetic basis of morphological novelty and ecological function. In turn, these new study systems and genetic tools will allow us to examine at what levels regulatory or structural genes, networks and modules change and/or are co-opted for new and different developmental outcomes in different taxa. We need to understand whether there are different ways in which gene networks are recruited for different types of traits (Irish & Benfey, 2004). Are there certain types of traits that arise by frequent recruitment of different genetic pathways, pointing to lability in the ways such traits evolve? Or does most variability arise from redeployment of a basic set of pathways, presumably through evolutionary tweaking of levels and timing of gene expression? And, further, is the 'primacy of regulatory evolution' really primary?

The MORPH minicourse demonstrated that the 'candidate gene approach' remains a common starting point for many of the projects that are attempting to move beyond model systems. Explicit or implicit in this approach are the assumptions that (1) gene function is highly conserved and (2) there is a 'toolkit' of developmental genes (or networks) that have been co-opted repeatedly to perform the same function at a new time or location, or in a new context. Tests of these assumptions (and perhaps tests of the primacy of regulatory evolution) will depend, in part, on the correct assessment of gene function (Ehrenreich *et al.*, 2007) and what 'sameness' is in the context of diverse organisms. Each use of the candidate gene approach depends critically on a careful consideration of how the function of the candidate gene was assessed, how its function is manifest in different model systems and how it might be expressed in the system of interest. These steps, regardless of the genetic tools available, require explicit comparative morphological (and anatomical) analyses as both the starting and ending points (Friedman *et al.*, 2004; Endress, 2006).

Conclusions about organism-level developmental evolution depend critically on the correct evaluation of phenotypes and the organism-specific developmental phenomena that underlie those phenotypes. A description (perhaps better yet, hypothesis) of gene function is only as good as the underlying assessment of its associated developmental phenotype. There is a danger in the field of plant evo-devo of overlooking the vast legacies of comparative morphology, systematics and paleobiology. These provide vital analytical tools that are critical for understanding the evolutionary changes that yield morphological

and functional diversity. The MORPH Research Coordination Network has attempted to overcome this problem with interdisciplinary training opportunities for students to move between molecular and organismic labs. However, if we are to achieve the goals of plant evo-devo, training in organismic biology must be sustained in academic institutions – a trend that clearly is not occurring. Relatively few major universities now count trained plant morphologists and anatomists or paleobotanists among their faculty. As it stands now, we risk the sophistication and power of genetic tools outstripping our ability to interpret the data and ‘know’ the phenotype. Ultimately, the recurring themes of many of the presentations of how to analyze homology, homoplasy and structural innovation will require just as much of a look backward to the historical and conceptual depths of morphology as a look forward to the leading edges of technology and genomics.

### Modularity, natural genetic variation and phenotypic plasticity

Developmental geneticists rely on the constancy of certain phenotypes in their analyses; however, it is clear that adaptive plasticity and phenotypic variance are essential prerequisites for evolutionary tinkering (Diggie, 2002; Armbruster *et al.*, 2004; Mitchell-Olds & Schmidt, 2006). Indeed, many questions were raised as to how plant evo-devo can best incorporate the complexities of the extensive natural variation found in highly metamerically continuously developing organisms. To what extent can we capture this type of intra-organism and inter-organism variation through comparative developmental genetic studies? How are such changes translated into phenotypic differences? In fact, what kinds of diversity at the organismic, tissue, cell and genetic levels are there? What kind of diversity is represented in the fossil record? And how does this diversity inform our understanding of extant modes of development resulting in particular morphologies? Does the iterative and indeterminate growth of plants impact the types of developmental processes that can be recruited for such changes?

The use of morphological polymorphisms in which individuals possess alternative states of a trait, but have common genetic backgrounds, might provide powerful experimental systems to relate intraspecific developmental variation to ecological or functional adaptation (Kalisz *et al.*, 2006). Unfortunately, despite their simple Mendelian inheritance, evo-devo studies of polymorphisms have rarely been undertaken. Discussion focused on the future use of polymorphic systems to link developmental genetic differences to trait function in natural environments. The holy grail of ecological evolutionary developmental biology ultimately will be to integrate these contrasting approaches by linking genes through morphology to adaptation and fitness in wild populations. Clearly, if plant evo-devo and plant ecology are to

have a meaningful relationship, much work needs to be accomplished to integrate the vastly different perspectives of these disciplines.

### Je ne comprends pas

Functional analyses differ depending on which level of the genealogical hierarchy is investigated. The language and approach change as one moves from the species, to the population, through the individual organism, to the molecular level. Charles Darwin initiated a functional view of plant diversity by proposing adaptive hypotheses for diverse plant traits, particularly those associated with reproduction. Currently, a significant research program within evolutionary ecology focuses on testing functional hypotheses. Presentations at the meeting on the ecological function of traits used manipulative field studies and measures of fitness to illustrate one approach to examining biological function in the Darwinian tradition.

One of the challenges for an integrative field of biology, such as ‘evo-devo’, is finding a common conceptual framework and language. This issue was a recurrent theme at the Boulder meeting where there were lively discussions on the precise meaning and usage of terms and concepts after several presentations. No better example of the plethora of meanings was evident following the innocent question – what precisely is a module? Ecologists, morphologists and molecular biologists proposed strikingly different definitions that were characterized by what was and what was not included within an individual module. Attempts to formulate universal definitions that will satisfy everyone remain an important challenge. This meeting showed that the next generation of plant biologists is becoming increasingly sophisticated at learning different discipline-specific languages and interweaving information from each field. There is good reason to believe that this intellectual potential will result in a community of scientists that can seamlessly weave these threads into new and dynamic views of how novel plant structures have been fashioned through time.

### Whither to?

In the final analysis, the recent MORPH meeting raised many more issues than it solved – but the issues discussed provided us with a greater appreciation of how traditionally distinct fields of research can interface in new and productive ways. One promising and important theme that emerged from the meeting is that graduate students are becoming savvier – more aware of the interdisciplinary implications of their work. They are thinking about adaptation and developmental variation as important components of their research; they are carefully considering the phylogenetic context of their study systems; and they are worrying about how best to bring new levels of sophistication to our understanding of

the evolutionary diversification of plant life. That is very good news for the field. The key will be to ensure that graduate and postdoctoral training is unburdened from the canalized thinking and intellectual approaches of the subdisciplines of ecology, organismic biology and molecular genetics. Beyond the need for future small meetings that bring diverse perspectives together in a single room, we need to continue to promote interdisciplinary training at every possible venture. As exemplified by the robust and lively interactions at the MORPH meeting, a modest investment in interdisciplinary dialogue and training can pay off handsomely.

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