

Commentary

An emerging focus on plant ecological development

Long regarded as uninteresting ‘noise’, the influence of environmental conditions on development has emerged over the past decade as a central, shared focus of biological research. Ecological development investigates how organisms develop in their natural contexts – in the ‘real world’ (Gilbert, 2001), which is an inherently variable and sometimes unpredictable place. Eco-devo research addresses how naturally varying environmental factors affect developmental processes at a mechanistic level, how phenotypic expression varies in response to these factors (i.e. phenotypic plasticity), and how the phenotypic variation this creates in natural populations affects ecological and ultimately evolutionary processes (Gilbert & Bolker, 2003; Sultan, 2003a,b). This common focus thus integrates a stunningly broad range of research disciplines that share an empirical basis in plasticity, from developmental genetics, through functional, population and community ecology, to evolutionary biology. These disciplines are featured in this issue of *New Phytologist*, with research and review articles that contribute to exciting empirical, analytical and conceptual directions in plant ecological development.

‘Plant eco-devo integrates molecular/development approaches with ecology in increasingly sophisticated conceptual frameworks for understanding how plants live and evolve in the real world’

Phenotypic plasticity in context

Plant biologists have led the way in this renascent focus on understanding the causes and consequences of development in its environmental context. Decades after A.D. Bradshaw’s path-breaking 1965 article on plant phenotypic plasticity (which met with a puzzled reception by its contemporary neo-Darwinian audience) (Bradshaw, 1965),

studies of plasticity and life-history strategies have compellingly shown that in all kinds of organisms environmentally mediated development can include the expression of adaptive (as well as maladaptive) phenotypes in response to varying conditions (reviewed by Schlichting, 1986; Stearns, 1989; Travis, 1994; Sultan, 2000; Pigliucci, 2001; DeWitt & Scheiner, 2003). Due in part to the continuous organogenesis that makes plant development extraordinarily flexible at all levels (Walbot, 1996), the environmental contingency of phenotypes in both controlled and natural settings has been most intensively studied in plants (Schlichting, 2002).

Studies of plant plasticity have revealed not only immediate morphological and allocational responses to environmental factors, but complex environmental effects on ontogenetic trajectories (Diggle, 1994; Schlichting & Pigliucci, 1998; Weinig & Delph, 2001) and offspring traits (Donohue & Schmitt, 1998; Agrawal *et al.*, 1999; Lundgren & Sultan, 2005). Although testing the functional and fitness consequences of environmentally mediated variation remains a difficult challenge, Schmitt and colleagues have shown that robust tests of adaptive plasticity are possible, by either manipulating environmental cue systems or using transgenic or mutant plants with disabled plastic responses to generate, experimentally, individuals which do and do not alter their phenotypes in contrasting conditions (reviewed by Schmitt *et al.*, 1999, 2003; see also Galen *et al.*, 2004; Huber *et al.*, 2004). These and several other recent studies have built on the well-studied system of developmental responses to red : far-red light ratio mediated by the phytochrome gene family. To date, this system is the one plant case in which the entire ecological development pathway is reasonably well understood, from perception and transduction of the environmental cue to effects on several genes that regulate phenotypic expression (references in Callahan *et al.*, 1997; Schlichting & Smith, 2002). Whereas the genetic basis of other aspects of plasticity remains largely unknown, quantitative trait locus (QTL) mapping is now being used as an initial step to investigate these systems (Pigliucci, 1996; Weinig & Schmitt, 2004).

New directions in eco-devo research

Researchers in diverse aspects of plant ecological development are building rapidly upon this foundation both empirically and conceptually. Along with a growing body of data on plant developmental responses to specific environmental variables are newly available tools for investigating the genetic bases and transduction pathways of those responses, as well as increasingly sophisticated analytical, comparative, and

theoretical frameworks for understanding their ecological and evolutionary consequences. In this issue, articles by Callahan *et al.* (pp. 129–139), Cronk (pp. 39–48), and van Kleunen & Fischer (pp. 49–60) highlight the range of approaches currently available to study the genetic basis of plasticity at increasingly precise levels, from QTL mapping analysis and cDNA microarrays to candidate gene studies in model systems such as *Arabidopsis* and *Populus*. Stanton & Thiede (pp. 319–337) and Rowe & Speck (pp. 61–72), respectively, offer statistical and biomechanical insights to the fitness consequences of eco-devo variation at the population and macroevolutionary levels. Several articles present new data and/or innovatively refined conceptual frameworks for testing environmental effects on plant development in an adaptive, ecological context (de Kroon *et al.* pp. 73–82; Donohue, pp. 83–92; Galloway, pp. 93–99; Griffith & Sultan, pp. 141–147; Moriuchi & Winn, pp. 149–158; Wong & Ackerly, pp. 159–172). The role of plasticity in evolution is explored by de Jong (pp. 101–117) and Delph & Wolf (pp. 119–128), while Brock *et al.* (pp. 173–183) examine its relation to ecological invasiveness.

The genetic basis of eco-devo response

The genetic basis of phenotypic response to environment is inherently an evolutionary as well as a mechanistic issue. Callahan *et al.* and van Kleunen & Fischer argue convincingly that information on specific loci involved in phenotypic response ('plasticity genes') is essential to understand both the pathway from gene expression to phenotype and the resulting selective dynamics on genetic variation for plasticity. van Kleunen & Fischer offer a thought-provoking critique of our presently limited knowledge of evolutionary constraints on adaptive plant plasticity. They discuss promising new tools to determine the genetic architecture of plasticity, its variation, and its potential costs and limits. They also point to timely research strategies to build our surprisingly limited knowledge of adaptive plasticity, including selection experiments on plastic traits (see Scheiner, 2002) and studies of environmental variation at different scales in relation to plasticity.

Callahan *et al.* describe an innovative way to combine developmental and quantitative genetics methods to investigate the genetic basis of plasticity. By using recombinant inbred lines of *Arabidopsis* that are polymorphic at the FRIGIDA locus (which influences flowering response to vernalization regime), they detected an environment-specific plasticity cost. They also unexpectedly found evidence for maladaptive plasticity for delayed flowering in response to partial vernalization, compared with genotypes that constitutively flowered earlier. These data suggest the intriguing possibility that such plasticity may be selectively maintained as a result of pleiotropic positive effects of loci influencing environmental response, indicating greater than expected complexity to the issue of plasticity costs. Cronk

highlights the potential value of *Populus tricharpa* as a model system for molecular eco-devo investigations, now that the complete genome sequence of this widespread, ecologically important tree is available. Because this species has ecologically diverse but cytologically similar congeners, this technical achievement may allow comparative work at the genome level to study how nucleotide variation influences ecologically important aspects of plant development.

Ecological development and adaptation

Studies of potentially adaptive plant responses to environment are beginning to extend beyond straightforward growth and allocational effects to more complex aspects of the phenotype such as architecture, functional anatomy, life history and even effects on offspring traits. Galloway and Rowe & Speck synthesize their recent studies to explore how these diverse aspects of ecological development can contribute to adaptation. Galloway asks whether maternally transmitted environmental effects can provide a means of fine-scale local adaptation in natural plant populations. Her ongoing work on *Campanula americana*, a herb native to patchy light habitats, demonstrates how the maternal plant's light environment influences offspring life-history schedule. Preliminary field data confirmed an adaptive hypothesis: for offspring produced by genetically similar parents grown in either canopy gap or understory sites, rates of fall germination were enhanced when the offspring's light environment matched that of the maternal parent.

From a larger perspective, Rowe & Speck argue that both ecological and phylogenetic effects on development are key to understanding growth form diversity in plants. They consider how little-studied environmental effects such as mechanical perturbation can alter the heterochronic expression, architecture, and wood anatomy of self-supporting vs climbing plant growth forms through specific effects on the cambium. Rowe & Speck propose that this capacity for ontogenetic, biomechanical and hydraulic plasticity in itself may be one of the key innovations provided by the evolution of the bifacial vascular cambium, and discuss how phylogenetic constraints on these traits may influence potential plastic responses to these and other environmental factors.

Stanton & Thiede provide a very different type of insight to the adaptive significance of ecological development: a critique of standard statistical methods for assessing the fitness of phenotypes produced in different environments. Because favorable conditions increase both mean reproductive output and its variance (especially in indeterminate organisms such as plants), researchers usually log-transform fitness data to meet homoscedasticity assumptions. Yet this standard method can distort fitness results and lead to incorrect evolutionary predictions. The authors' clear demonstration of this neglected problem and their proposed alternatives constitute a useful step toward adjusting statistical techniques

to match the particular goals and quirks of eco-devo studies (see also Scheiner *et al.*, 2002; Stinchcombe *et al.*, 2002).

Conceptual frameworks for plant development in the environmental context

Understanding ecological development demands a way of framing the organism–environment relationship, with its complex feedbacks, so as to allow precise, testable hypotheses incorporating multiple levels of investigation. Evolutionary ecologists are continuing to incorporate new ideas into an emerging body of conceptual approaches to this challenging problem (references in Schlichting & Pigliucci, 1998; Lewontin, 2001; Nijhout, 2001; Schlichting & Smith, 2002; Sultan & Stearns, 2005). In this issue, several authors contribute novel and perhaps controversial perspectives to this ongoing synthesis.

de Kroon and colleagues present a modular rather than whole-plant framework for understanding eco-devo response, critically reviewing the literature on plasticity at the level of functional modules such as individual leaves and roots. When heterogeneous conditions occur within the plant individual, the developmental integration of these modular responses can profoundly affect whole-plant resource uptake and growth. As a result, they argue, mechanisms of modular integration can be seen as a key aspect of ecological development. Donohue focuses instead on life-history plasticity as a fundamental aspect of eco-devo variation from which a distinctive formulation of the organism–environment relationship emerges. Through developmental and phenological plasticity, plants alter not only their own phenotypic expression but the environments they subsequently encounter. This ‘niche construction’ is most dramatic in the case of life-history traits such as reproductive timing, dispersal and germination, which directly influence the seasonal and competitive environment of offspring and consequently their selective regime. Donohue synthesizes new results from naturally evolved *Arabidopsis* ecotypes to show how niche-constructing traits can interact to both produce novel life histories in the field, and constrain adaptive evolutionary change in these and related traits.

Moriuchi & Winn address a knotty interpretive question regarding the developmental basis of phenotypes expressed in contrasting environments: do plants in poor vs rich conditions express distinct developmental trajectories, or simply differences in developmental rate that are interpreted as distinct phenotypes when plants are measured at the same age? (See Coleman *et al.*, 1994; McConnaughay & Coleman, 1999.) Moriuchi & Winn’s data show that, in contrast to earlier work on annuals, perennial *Viola* plants grown at low resource levels were not simply developmentally delayed, but expressed distinct, adaptive ontogenetic patterns for traits such as storage allocation to rhizomes. In further contrast to annuals studied previously, these perennials

maintained the ability to alter developmental trajectories beyond the first few weeks of growth in response to changing conditions. The interplay of ontogeny and plasticity in natural ecological contexts remains an important area for further study.

Precise hypotheses about ecological development also require a clear focus on the environmental cues that initiate developmental responses in natural habitats. Griffith & Sultan distinguish perception of an environmental cue from subsequent developmental response as separate components of phenotypic plasticity, and present comparative data illustrating this decoupling in two closely related taxa. Because these components can have different genetic bases and evolutionary potential, they can differ among populations and species in ways that contribute to ecological differences. At present, little is known about either mechanisms of cue perception and transduction (Gilroy & Trewavas, 2001) or the correlations between specific cues and selective conditions that shape the evolution of adaptive response in natural populations (Tufto, 2000; Sultan, 2004). Wong & Ackerly approach the role of cue reliability in the selective maintenance of plasticity from a theoretical perspective. They present an optimality model testing variation in reproductive allocation in relation to predictable vs unpredictable season lengths. Their model and accompanying simulations confirmed that when environmental information poorly predicted selective conditions, plasticity for reproductive allocation was disadvantageous relative to a random bet-hedging strategy.

Broad evolutionary and ecological implications

Starting with Bradshaw (1965), it has been clear that ecological developmental variation in nature has profound implications for the process of adaptive evolution in plants. Two articles in this issue contribute, respectively, to empirical and theoretical knowledge of these broad-scale implications. Delph & Wolf consider how life-history plasticity may either promote or constrain the evolution of genetically dimorphic plant breeding systems. They review existing data to conclude that sex expression (relative seed or pollen output) in subdioecious species is often resource-dependent, a fact overlooked in models of breeding system evolution. Their overview of the literature shows that selection may act differently when the plastic morph is predominantly male rather than predominantly female: gender plasticity can prevent the evolution of complete dioecy from gynodioecy by reducing the cost of producing seeds, while plasticity can act to maintain gender dimorphism in androdioecious species that otherwise might evolve toward hermaphroditism. de Jong’s provocative theoretical paper argues against the notion that plasticity may play a macroevolutionary role as a mechanism of adaptive species diversification, an idea which has lately sparked a great deal of interest among evolutionary biologists. According to this conceptual model (termed the

'Baldwin effect' by G.G. Simpson in 1953), the adaptive flexibility of genotypes produces phenotypes able to invade new habitats, so that new ecotypes and ultimately species result if these phenotypes become genetically fixed under subsequent selection in the new environment (West-Eberhard, 2003; Pigliucci & Murren, 2003; Schlichting, 2004). de Jong extends existing quantitative genetic approaches to propose instead that observed patterns of ecotypic variation can be explained by conventional, neo-Darwinian selective mechanisms operating on adaptive plasticity in the context of limited migration. The possibility of a unique role for plasticity in evolutionary diversification is likely to remain an area of controversy, particularly because empirical data on this intriguing issue are scarce.

Environmentally mediated development also holds important ecological implications. Adaptive plasticity can enlarge a species' environmental tolerances and hence contribute to broad, generalist distributions. Such adaptive plasticity can also allow the spread of an invasive into new habitats without a selective lag time. Brock *et al.* tested the relation of shade plasticity to invasiveness in two sympatric *Taraxacum* species. Their study confirms the key point that environmentally induced variation *per se* is not likely to explain invasiveness; rather, invasiveness may involve adaptive plasticity for traits that enhance fitness in relevant environments, along with constancy for traits such as high dispersal potential.

A synthesis in progress

These diverse avenues of research are part of an emerging synthesis in plant ecological development: the integration of molecular/development approaches with ecology in increasingly sophisticated conceptual frameworks for understanding how plants live and evolve in the real world. This synthetic approach accords with the growing recognition that, in general, gene interaction and regulation by both internal and external factors is of primary importance for phenotypic determination (Carroll, 2000; Nijhout, 2001). However, this synthesis is very much a work in progress. To achieve this integrated understanding of plant ecological development from concordant mechanistic, ecological and evolutionary points of view requires further research on the rich array of subjects addressed in this issue, as well as studies of higher-order effects on species' interactions (Agrawal, 2001). It will also require continuing efforts to refine our empirical, statistical, and modelling techniques for assessing and interpreting environmentally mediated variation.

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In this brief overview I have not attempted to provide comprehensive references to this vast multidisciplinary literature. Please see individual papers in this issue and the listed references for more complete citations.

References

- Agrawal AA. 2001. Phenotypic plasticity in the interactions and evolution of species. *Science* **294**: 321–326.
- Agrawal AA, Laforsch C, Tollrian R. 1999. Transgenerational induction of defenses in animals and plants. *Nature* **401**: 60–63.
- Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**: 115–155.
- Brock MT, Weinig C, Galen C. 2005. A comparison of phenotypic plasticity in the native dandelion *Taraxacum ceratophorum* and its invasive congener *T. officinale*. *New Phytologist* **166**: 173–183.
- Callahan HS, Pigliucci M, Schlichting CD. 1997. Developmental phenotypic plasticity: where ecology and evolution meet molecular biology. *Bioessays* **19**: 519–525.
- Callahan HS, Dhanooolal N, Ungerer MC. 2005. Plasticity genes and plasticity costs: a new approach using an *Arabidopsis* recombinant inbred population. *New Phytologist* **166**: 129–139.
- Carroll SB. 2000. Endless forms: the evolution of gene regulation and morphological diversity. *Cell* **101**: 577–580.
- Coleman JS, McConnaughay KDM, Ackerly DD. 1994. Interpreting phenotypic variation in plants. *Trends in Ecology and Evolution* **9**: 187–191.
- Cronk Q. 2005. Plant eco-devo: the potential of poplar as a model. *New Phytologist* **166**: 39–48.
- Delph LF, Wolf DE. 2005. Evolutionary consequences of gender plasticity in genetically dimorphic breeding systems. *New Phytologist* **166**: 119–128.
- DeWitt TJ, Scheiner SM, eds. 2003. *Phenotypic Plasticity: Functional and Conceptual Approaches*. New York, USA: Oxford University Press.
- Diggle PK. 1994. The expression of andromonoecy in *Solanum hirtum* (Solanaceae): phenotypic plasticity and ontogenetic contingency. *American Journal of Botany* **81**: 1354–1365.
- Donohue K. 2005. Niche construction through phenological plasticity: life history dynamics and ecological consequences. *New Phytologist* **166**: 83–92.
- Donohue K, Schmitt J. 1998. Maternal environmental effects in plants. In: Mousseau, TA, Fox, CW, eds. *Maternal Effects as Adaptations*. New York, USA: Oxford University Press, 137–158.
- Galen C, Huddle J, Liscum E. 2004. An experimental test of the adaptive evolution of phototropins: blue-light photoreceptors controlling phototropism in *Arabidopsis thaliana*. *Evolution* **58**: 515–523.
- Galloway LF. 2005. Maternal effects provide phenotypic adaptation to local environmental conditions. *New Phytologist* **166**: 93–99.
- Gilbert SF. 2001. Ecological developmental biology: developmental biology meets the real world. *Developmental Biology* **233**: 1–12.
- Gilbert SF, Bolker JA. 2003. Ecological developmental biology: preface to the symposium. *Evolution and Development* **5**: 3–8.
- Gilroy S, Trevas A. 2001. Signal processing and transduction in plant cells: the end of the beginning? *Nature Reviews (Molecular and Cell Biology)* **2**: 307–314.
- Griffith TM, Sultan SE. 2005. Shade tolerance plasticity in response to neutral vs green shade cues in *Polygonum* species of contrasting ecological breadth. *New Phytologist* **166**: 141–147.
- Huber H, Kane NC, Heschel MS, von Wettberg EJ, Benton J, Leuck A-M, Schmitt J. 2004. Frequency and microenvironmental

- pattern of selection on plastic shade-avoidance traits in a natural population of *Impatiens capensis*. *American Naturalist* **163**: 548–563.
- de Jong G. 2005. Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. *New Phytologist* **166**: 101–117.
- van Kleunen M, Fischer M. 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist* **166**: 49–60.
- de Kroon H, Huber H, Stuefer JF, van Groenendael JM. 2005. A modular concept of phenotypic plasticity in plants. *New Phytologist* **166**: 73–82.
- Lewontin RC. 2001. Gene, Organism and Environment: A New Introduction. In: Oyama, SG, Griffith, PE, Gray, RD, eds. *Cycles of Contingency*. Cambridge, MA, USA: The Massachusetts Institute of Technology Press, 55–66.
- Lundgren MR, Sultan SE. 2005. Seedling expression of cross-generational plasticity depends on reproductive architecture. *American Journal of Botany* **92**. (In press.)
- McConaughay KDM, Coleman JS. 1999. Biomass allocation in plants: ontogenetic or optimality? A test along three resource gradients. *Ecology* **80**: 2581–2593.
- Moriuchi KS, Winn AA. 2005. Relationships among growth, development and plastic response to environment quality in a perennial plant. *New Phytologist* **166**: 149–158.
- Nijhout HF. 2001. The ontogeny of phenotypes. In: Oyama, SG, Griffith, PE, Gray, RD, eds. *Cycles of Contingency*. Cambridge, MA, USA: The Massachusetts Institute of Technology Press, 129–140.
- Pigliucci M. 1996. How organisms respond to environmental changes: from phenotypes to molecules (and vice versa). *Trends in Ecology and Evolution* **11**: 168–173.
- Pigliucci M. 2001. *Phenotypic Plasticity: Beyond Nature and Nurture*. Baltimore, MD, USA: Johns Hopkins University Press.
- Pigliucci M, Murren CJ. 2003. Genetic assimilation and a possible evolutionary paradox. *Evolution* **57**: 1455–1464.
- Rowe NP, Speck T. 2005. Plant growth forms: an ecological and evolutionary perspective. *New Phytologist* **166**: 61–72.
- Scheiner SM. 2002. Selection experiments and the study of phenotypic plasticity. *Journal of Evolutionary Biology* **15**: 889–898.
- Scheiner SM, Donohue K, Dorn LA, Mazer SJ, Wolfe LM. 2002. Reducing environmental bias when measuring natural selection. *Evolution* **56**: 2156–2167.
- Schlichting CD. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* **17**: 667–693.
- Schlichting CD. 2002. Phenotypic plasticity in plants. *Plant Species Biology* **17**: 85–88.
- Schlichting CD. 2004. The role of phenotypic plasticity in evolutionary diversification. In: DeWitt, TJ, Scheiner, SM, eds. *Phenotypic Plasticity: Functional and Conceptual Approaches*. New York, USA: Oxford University Press, 191–200.
- Schlichting CD, Pigliucci M. 1998. *Phenotypic Evolution: a Reaction Norm Perspective*. Sunderland, MA, USA: Sinauer Associates, Inc.
- Schlichting CD, Smith H. 2002. Phenotypic plasticity: linking molecular mechanisms with evolutionary outcomes. *Evolutionary Ecology* **16**: 189–211.
- Schmitt J, Dudley SA, Pigliucci M. 1999. Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade avoidance responses in plants. *American Naturalist* **154**: S43–S54.
- Schmitt J, Stinchcombe JR, Heschel MS, Huber H. 2003. The adaptive evolution of plasticity: phytochrome-mediated shade avoidance responses. *Integrative and Comparative Biology* **43**: 459–469.
- Stanton ML, Thiede DA. 2005. Statistical convenience vs biological insight: onsequences of data transformation for the analysis of fitness variation in heterogeneous environments. *New Phytologist* **166**: 319–337.
- Stearns SC. 1989. The evolutionary significance of phenotypic plasticity. *Bioscience* **39**: 436–445.
- Stinchcombe JR, Rutter MT, Burdick DS, Tiffin P, Rausher MD, Mauricio R. 2002. Testing for environmentally induced bias in phenotypic estimates of natural selection: Theory and practice. *American Naturalist* **160**: 511–523.
- Sultan SE. 2000. Phenotypic plasticity for plant development, function and life-history. *Trends in Plant Science* **5**: 537–542.
- Sultan SE. 2003a. The promise of ecological developmental biology. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* **296B**: 1–7.
- Sultan SE. 2003b. Phenotypic plasticity in plants: a case study in ecological development. *Evolution and Development* **5**: 25–33.
- Sultan SE. 2004. Promising research directions in plant phenotypic plasticity. *Perspectives in Plant Ecology, Evolution and Systematics* **6**: 227–233.
- Sultan SE, Stearns SC. 2005. Environmentally contingent variation: phenotypic plasticity and norms of reaction. In: Hall, B, Hallgrímsson, B, eds. *Variation: a Hierarchical Examination of a Central Concept in Biology*. London, UK: Elsevier Academic Press. (In press.)
- Travis J. 1994. Ecological genetics of life-history traits: variation and its evolutionary significance. In: Real, L, ed. *Ecological Genetics*. Princeton, NJ, USA: Princeton University Press, 171–204.
- Tufto J. 2000. The evolution of plasticity and nonplastic spatial and temporal adaptations in the presence of imperfect environmental cues. *American Naturalist* **156**: 121–130.
- Walbot V. 1996. Sources and consequences of phenotypic and genotypic plasticity in flowering plants. *Trends in Plant Science* **1**: 27–32.
- Weinig C, Delph LF. 2001. Phenotypic plasticity early in life constrains developmental responses later. *Evolution* **55**: 930–936.
- Weinig C, Schmitt J. 2004. Environmental effects on the expression of quantitative trait loci and implications for phenotypic evolution. *Bioscience* **54**: 627–635.
- West-Eberhard MJ. 2003. *Developmental Plasticity and Evolution*. New York, USA: Oxford University Press.
- Wong TG, Ackerly DD. 2005. Optimal reproductive allocation in annuals and an informational constraint on plasticity. *New Phytologist* **166**: 159–172.

Key words: eco-devo, phenotypic plasticity, plant life history, phenotypic expression, environmental cues, plasticity costs.

Ancient and recent polyploidy in angiosperms

One of the most startling results of recent genomics studies is the near ubiquity of polyploidy – even in organisms not suspected to have undergone genome doubling. The small genome of *Arabidopsis* may have been derived from three rounds of polyploidization (Vision *et al.*, 2000; Bowers *et al.*, 2003), and most other model plants are either ancient or recent polyploids (Blanc & Wolfe, 2004). Most recently, *Oryza* has been shown to have an anciently duplicated genome (Paterson *et al.*, 2004; Wang *et al.*, 2005; see also the commentary by Paterson, 2005), and it seems likely that all angiosperms are polyploid – the question is only one of

scale. Of course, as stunning as these results are, plant biologists are not totally surprised: they have long recognized the importance of polyploidy as a speciation mechanism (e.g. Stebbins, 1950, 1966; Grant, 1971, 1981). However, the fact that yeast (Wolfe & Shields, 1997) and vertebrates (e.g. Ohno, 1970; Gu *et al.*, 2002; McLysaght *et al.*, 2002; Furlong & Holland, 2004) are also ancient polyploids is a bit more difficult for some to accept. Given the important role that polyploidy plays in plant evolution – and the decades of study devoted to polyploid plants – it seems likely that studies of recent polyploidy in targeted plant groups will provide clues to the causes and consequences of genome duplication. In this issue, Guo *et al.* (pp. 273–289) address the recurrent formation of polyploid lineages in *Achillea*, and Skalická *et al.* (pp. 291–303) report rapid and repeated changes in genome content in synthetic allotetraploid tobacco. Both processes, (i) multiple origins of a polyploid ‘species’ from genetically different diploid parent individuals and (ii) rapid genomic change immediately after polyploid formation, may contribute to genetic diversity in polyploid plants, preventing their fate as ‘evolutionary dead-ends’ (Wagner, 1983).

‘Analysis of the complete genome sequences of Arabidopsis and rice is forcing us to accept that probably all angiosperms – and maybe all plants – are polyploid to some extent’

Evolutionary patterns of polyploid formation

Although the mechanisms of polyploid formation are not entirely clear (see Ramsey & Schemske, 1998), the production of unreduced gametes is typically involved. Polyploid species that form through the combined processes of interspecific hybridization and chromosome doubling are considered *allopolyploids*, and those polyploids that arise within a single species are *autopolyploids*, which are much less common in nature. Polyploid complexes, such as the *Achillea millefolium* L. aggregate, may comprise diploid species, diploid hybrids, and auto- and allopolyploids of multiple ploidal levels (Guo *et al.*). Superimposed on this diversity is the fact that most polyploid species have formed recurrently from genetically distinct diploid progenitors, yielding a potentially large gene pool for the derivative polyploid.

Over five decades ago, Ownbey and colleagues (Ownbey, 1950; Ownbey & McCollum, 1953, 1954) suggested that multiple populations of the allotetraploid *Tragopogon mirus*

Ownbey had formed independently from local parental individuals of *T. dubius* Scop. and *T. porrifolius* L.; the same was proposed for the allotetraploid *T. miscellus* Ownbey and its progenitors, *T. dubius* and *T. pratensis* L. Ownbey and colleagues used a number of characteristics – morphological and cytogenetic – to infer multiple origins of each of these allotetraploid species. Unfortunately, such morphological and chromosomal signatures of multiple origins are not always evident, and several decades passed before the generality of Ownbey’s observations was recognized. Landmark papers by Werth *et al.* (1985a, 1985b) elegantly used isozyme polymorphisms to document recurrent formation of polyploid species, and since then, increasingly sensitive genetic tools have been applied to polyploid systems to test hypotheses of recurrent formation. Nearly all polyploid species that have been examined using isozyme or DNA markers have formed recurrently, often dozens of times (for example, see reviews of *Tragopogon*, Soltis *et al.*, 2004; *Senecio*, Abbott & Lowe, 2004; and the Arctic flora, Brochmann *et al.*, 2004).

Traditional models of allopolyploid formation predict a genetically uniform polyploid species that results from the genetic contributions of a single plant of each parental species. This mode of formation, coupled with the perceived buffering capacity of a duplicated genome, caused noted plant evolutionary biologists such as Stebbins and Wagner to consider polyploidy as an evolutionary dead-end: a genetically uniform species could not respond to a changing environment and would therefore face extinction when conditions changed. Current views of polyploid species, however, reveal instead genetic variability both among and, sometimes, within populations, due to the varied contributions of multiple parental individuals. Furthermore, crossing among genetically distinct individuals of separate origin may generate even greater genetic diversity through independent assortment. The result may be a pool of genetically different polyploid individuals that may respond differentially to various selection pressures, providing more opportunities for polyploid species to survive changing environments.

Genetic and ploidal diversity in the *Achillea millefolium* species complex

Guo *et al.* present a staggering view of genetic and ploidal diversity in the *Achillea millefolium* species complex (Asteraceae). Decades of research, tracing back to Ehrendorfer’s work in the 1950s, have documented numerous cases of polyploidy ($2x-4x-6x-8x$) and ‘... suggest that reticulate evolution is not only involved in recent radiations but must have been active already in the early diversification of *Achillea*.’ Therefore, understanding more recent polyploid radiations, such as the *A. millefolium* complex, may provide clues as to the processes and conditions that lead to both polyploid formation and persistence across geologic time. In their paper, Guo *et al.* used AFLP markers to tease apart

historical patterns of hybridization and polyploidy in the *A. millefolium* complex. Hybridization across ploidal levels, the origins of several polyploid species, recurrent formation and patterns of worldwide migration of the complex were all detected with these sensitive markers (as demonstrated in other groups, for example by Hedrén *et al.*, 2001). Although complex, the evolutionary patterns observed for *A. millefolium* and relatives are similar to those that have been reported for other complexes that have been studied in detail (e.g. *Tragopogon*, Soltis *et al.*, 2004; *Draba* and other Arctic species, Brochmann *et al.*, 2004; species of *Glycine*, Doyle *et al.*, 2004; *Veronica*, D. Albach, University of Vienna, unpublished). With few exceptions, recurrent formation – resulting in genetically distinct derivative individuals – appears to characterize polyploid species of plants, and of other organisms as well.

Rapid genomic consequences of polyploidy

Views on the stability of the polyploid genome are also changing (see Matzke *et al.*, 1999). Synthetic allotetraploids of *Brassica napus* L. (Song *et al.*, 1995) and synthetic allopolyploids and diploid F1 hybrids of *Aegilops* and *Triticum* (Ozkan *et al.*, 2001; Shaked *et al.*, 2001; reviewed by Levy & Feldman, 2004) exhibited nonrandom genetic changes, including chromosome-specific and genome-specific gains and losses of loci. These genomic changes occurred rapidly, within a few generations of polyploid formation. Likewise, the naturally occurring *Nicotiana tabacum* L. (tobacco) has undergone genome reorganization (Kenton *et al.*, 1993). However, not all polyploids display genomic rearrangement relative to their diploid progenitors: the recently formed polyploids of *Tragopogon* (Pires *et al.*, 2004) and *Spartina* (Baumel *et al.*, 2002) exhibit genome stability, as do older tetraploids in *Gossypium* (Liu *et al.*, 2001) and *Brassica juncea* (L.) Czern. (and, interestingly, synthetic *B. juncea*; Axelsson *et al.*, 2000). The small number of species examined for chromosomal repatterning makes it difficult at present to identify trends and form generalities, and more data are clearly needed.

Genomic rearrangements in tobacco

Skalická *et al.* used an elegant approach to re-examine genomic rearrangements in tobacco. Although generation of synthetic polyploids of tobacco is difficult, success was obtained in 1973 (see Skalická *et al.*) by crossing the parental diploid species *N. sylvestris* Speng. (maternal) and *N. tomentosiformis* Goodsp. (paternal), with chromosome doubling occurring in tissue culture, from which a single regenerated plant was obtained (the S0 generation). Repeated selfing of plants from this regenerant resulted in the S4 plants used by Skalická *et al.*; these plants represent lines that were produced close to the time of polyploid formation and thus offer the potential to compare immediate genomic

consequences of polyploidy with those observed in naturally occurring *N. tabacum* (Kenton *et al.*, 1993). Repeated sequences derived from *N. tomentosiformis* (the paternal parent) were selectively eliminated from the synthetic S4 tobacco tetraploids. Furthermore, intergenomic translocation has occurred subsequent to polyploid formation. Both this translocation and the loss of *N. tomentosiformis* loci in these synthetic plants are similar to observations of natural tobacco, which exhibits an intergenomic translocation similar to that reported for the synthetics (along with several others; Kenton *et al.*, 1993; Kitamura *et al.*, 1997) and which showed less similarity to its paternal parent, *N. tomentosiformis*, than to the maternal parent, *N. sylvestris*, in Genome *In Situ* Hybridization studies (Kenton *et al.*, 1993; Jakowitsch *et al.*, 1998). These results demonstrate the remarkable facts that (i) genomic changes may occur very early – within the first few generations – in a polyploid lineage (as shown for *B. napus*, *Aegilops*, and wheat), and (ii) at least some of these genomic changes are repeatable, that is, they occurred in both synthetic and natural polyploid derivatives. Understanding the ‘rules’ of genetic and genomic change in polyploids is one of the next great frontiers in the study of polyploidy.

Emerging view of plant polyploids

The last five years have witnessed a reawakening in the study of polyploidy. The complete genome sequences of *Arabidopsis* and rice have revealed multiple and complex episodes of genome duplication during the diversification of the angiosperms, forcing us to accept that probably all angiosperms – and maybe all plants – are polyploid to some extent. This recognition brings with it new questions. How do polyploids form? What happens to their duplicate gene copies? Are there ‘rules’ that govern the behavior of homoeologous genes and chromosomes when united in a single nucleus? How does the genetic diversity observed in recent polyploids of multiple origin relate to the diversity observed in ancient polyploids? The papers by Guo *et al.* and Skalická *et al.* attempt to bridge this gap through comparisons and inferences of ancient vs recent polyploid events. More such studies will be welcome additions to the rapidly accumulating data on genetic and genomic diversity of polyploid plants.

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References

- Abbott R, Lowe AJ. 2004. Origins, establishment and evolution of new polyploid species: *Senecio cambrensis* and *S. eboracensis* in the British Isles. *Biological Journal of the Linnean Society* 82: 467–474.
- Axelsson T, Bowman CM, Sharpe AG, Lydiate DJ, Lagercrantz U. 2000. Amphidiploid *Brassica juncea* contains conserved progenitor genomes. *Genome* 43: 679–688.
- Baumel A, Ainouche M, Kalendar R, Schulman AH. 2002. Retrotransposons and genomic stability in populations of the young allopolyploid species *Spartina anglica* C.E. Hubbard (Poaceae). *Molecular Biology and Evolution* 19: 1218–1227.
- Blanc G, Wolfe KH. 2004. Widespread paleopolyploidy in model plant species inferred from age distributions of duplicate genes. *Plant Cell* 16: 1667–1678.
- Bowers JE, Chapman BA, Rong JK, Paterson AH. 2003. Unravelling angiosperm genome evolution by phylogenetic analysis of chromosomal duplication events. *Nature* 422: 433–438.
- Brochmann C, Brysting AK, Alsos IG, Borgen L, Grundt HH, Scheen A-C, Elven R. 2004. Polyploidy in arctic plants. *Biological Journal of the Linnean Society* 82: 521–536.
- Doyle JJ, Doyle JL, Rauscher JT, Brown AHD. 2004. Evolution of the perennial soybean polyploid complex (*Glycine* subgenus *Glycine*): a study of contrasts. *Biological Journal of the Linnean Society* 82: 583–597.
- Furlong RF, Holland PWH. 2004. Polyploidy in vertebrate ancestry: Ohno and beyond. *Biological Journal of the Linnean Society* 82: 425–430.
- Grant V. 1971. *Plant Speciation*. New York, USA: Columbia University Press.
- Grant V. 1981. *Plant Speciation*, 2nd edn. New York, USA: Columbia University Press.
- Gu X, Wang Y, Gu J. 2002. Age distribution of gene families shows significant roles of both large- and small-scale duplications in vertebrate evolution. *Nature Genetics* 31: 205–209.
- Guo YP, Saukel J, Mettermayr R, Ehrendorfer F. 2005. AFLP analyses demonstrate genetic divergence, hybridisation, and multiple polyploidisation in the evolution of *Achillea* (Asteraceae-Anthemideae). *New Phytologist* 166: 273–289.
- Hedrén M, Fay MF, Chase MW. 2001. Amplified fragment length polymorphisms (AFLP) reveal details of polyploid evolution in *Dactylorhiza* (Orchidaceae). *American Journal of Botany* 88: 1868–1880.
- Jakowitsch J, Papp I, Matzke MA, Matzke AJ. 1998. Identification of a new family of highly repetitive DNA, NTS9, that is located predominantly on the S9 chromosome of tobacco. *Chromosomal Research* 6: 649–651.
- Kenton A, Parokony AS, Gleba YY, Bennett MD. 1993. Characterization of the *Nicotiana tabacum* L. genome by molecular cytogenetics. *Molecular and General Genetics* 240: 159–169.
- Kitamura S, Inoue M, Ohmido N, Fukui K. 1997. Identification of parental chromosomes in the interspecific hybrids of *Nicotiana rustica* L. × *N. tabacum* L. & *N. gossei* Domin × *N. tabacum* L., using genomic in situ hybridization. *Breeding Science* 47: 67–70.
- Levy AA, Feldman M. 2004. Genetic and epigenetic reprogramming of the wheat genome upon allopolyploidization. *Biological Journal of the Linnean Society* 82: 607–613.
- Liu B, Brubaker CL, Mergeai G, Cronn RC, Wendel JF. 2001. Polyploid formation in cotton is not accompanied by rapid genomic changes. *Genome* 44: 321–330.
- Matzke MA, Scheid OM, Matzke AJ. 1999. Rapid structural and epigenetic changes in polyploid and aneuploid genomes. *Bioessays* 21: 761–767.
- McLysaght A, Hokamp K, Wolfe KH. 2002. Extensive genome duplication during early chordate evolution. *Nature Genetics* 31: 200–204.
- Ohno S. 1970. *Evolution by Gene Duplication*. Berlin, Germany: Springer-Verlag.
- Ownbey M. 1950. Natural hybridization and amphiploidy in the genus *Tragopogon*. *American Journal of Botany* 37: 487–499.
- Ownbey M, McCollum GD. 1953. Cytoplasmic inheritance and reciprocal amphiploidy in *Tragopogon*. *American Journal of Botany* 40: 788–796.
- Ownbey M, McCollum GD. 1954. The chromosomes of *Tragopogon. Rhodora* 56: 7–21.
- Ozkan H, Levy AA, Feldman M. 2001. Allopolyploidy-induced rapid genome evolution in the wheat (*Aegilops-Triticum*) group. *Plant Cell* 13: 1735–1747.
- Paterson AH. 2005. Ancient duplication of cereal genomes. *New Phytologist* 165: 658–661.
- Paterson AH, Bowers JE, Chapman BA. 2004. Ancient polyploidization predating divergence of the cereals, and its consequences for comparative genomics. *Proceedings of the National Academy of Sciences, USA* 101: 9903–9908.
- Pires JC, Lim KY, Kovarik A, Matyasek R, Boyd A, Leitch AR, Leitch IJ, Bennett MD, Soltis PS, Soltis DE. 2004. Genome size and distribution of tandem repetitive DNA in allopolyploid *Tragopogon* (Asteraceae). *American Journal of Botany* 91: 1022–1035.
- Ramsey J, Schemske DW. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* 29: 467–501.
- Shaked H, Kashkush K, Ozkan H, Feldman M, Levy AA. 2001. Sequence elimination and cytosine methylation are rapid and reproducible responses of the genome to wide hybridization and allopolyploidy in wheat. *Plant Cell* 13: 1749–1759.
- Skalická K, Lim KY, Matyasek R, Matzke M, Leitch AR, Kovarik A. 2005. Preferential elimination of repeated DNA sequences from the paternal, *N. tomentosiformis* genome donor of a synthetic, allotetraploid tobacco. *New Phytologist* 166: 291–303.
- Soltis DE, Soltis PS, Pires JC, Kovarik A, Tate JA, Mavrodiev E. 2004. Recent and recurrent polyploidy in *Tragopogon* (Asteraceae): cytogenetic, genomic and genetic comparisons. *Biological Journal of the Linnean Society* 82: 485–501.
- Song K, Lu P, Tang K, Osborn TC. 1995. Rapid genome change in synthetic polyploids of *Brassica* and its implications for polyploid evolution. *Proceedings of the National Academy of Sciences, USA* 92: 7719–7723.
- Stebbins GL. 1950. *Variation and Evolution in Plants*. New York, USA: Columbia University Press.
- Stebbins GL. 1966. Chromosomal variation and evolution; polyploidy and chromosome size and number shed light on evolutionary processes in higher plants. *Science* 152: 1463–1469.
- Vision T, Brown D, Tanksley S. 2000. The origins of genomic duplications in *Arabidopsis*. *Science* 290: 2114–2117.
- Wagner WH Jr. 1983. Reticulistics: the recognition of hybrids and their role in cladistics and classification. In: Platnick, NI, Funk, VA, eds. *Advances in Cladistics* 2. New York, USA: Columbia University Press, 63–79.
- Wang X, Shi X, Hao BL, Ge S, Luo J. 2005. Duplication and DNA segmental loss in the rice genome and their implications for diploidization. *New Phytologist* 165: 937–946.
- Werth CR, Guttman SI, Eshbaugh WH. 1985a. Electrophoretic evidence of reticulate evolution in the Appalachian *Asplenium* complex. *Systematic Botany* 10: 184–192.
- Werth CR, Guttman SI, Eshbaugh WH. 1985b. Recurring origins of allopolyploid species in *Asplenium*. *Science* 228: 731–733.
- Wolfe KH, Shields DC. 1997. Molecular evidence for an ancient duplication of the entire yeast genome. *Nature* 387: 708–713.

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