Developmental Homeostasis and Floral Form: Evolutionary Consequences and Genetic Basis

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DEVELOPMENTAL HOMEOSTASIS AND FLORAL FORM: EVOLUTIONARY CONSEQUENCES AND GENETIC BASIS

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Plant biologists have largely ignored the role of developmental homeostasis in the evolution of floral traits. In this brief review, we discuss the relationship between floral form and developmental homeostasis, emphasizing that developmental homeostasis, as any other character, may respond to natural selection. We discuss the implications of developmental homeostasis being a selectively labile trait for the evolution of floral characters. A trait's ability to respond to selection is in part determined by its genetic basis. Therefore, we also discuss evidence for the genetic basis of developmental homeostasis and how it influences the evolution of developmental homeostasis and ultimately floral diversity. We conclude with a series of suggestions for future research, calling for a synthetic approach utilizing ecological, morphological, quantitative genetic, and molecular methodologies.

Introduction

There is great variation in floral form, including patterns of symmetry, among flowering plants. The dilemma is that we often consider flowers to express a high degree of constancy for symmetry and other aspects of floral form, including petal number, placement of floral parts, and so on. How then can this diversity arise if at many taxonomic levels it appears to be highly conserved? In this article, we discuss mechanisms responsible for the origin of floral diversity and emphasize that a complete understanding of the evolution of floral diversity must include an understanding of the evolution of the underlying developmental pathways. We suggest that the developmental mechanisms underlying floral evolution may include developmental homeostasis.

The ability of organisms to withstand genetic and environmental disturbances encountered during development and to produce predictable phenotypes is known as developmental homeostasis (Waddington 1942; Lerner 1954). Developmental homeostasis has two major outcomes: canalization and developmental stability. Canalization is the ability of a genotype to express the same phenotype across environments, whereas developmental stability reflects the repeatability of the same character within a specific environment. Canalization acts to reduce phenotypic variation, itself a by-product of environmental and genetic variation. Developmental stability reflects processes that reduce phenotypic variation arising from developmental accidents (see review in Zakharov 1989).

The distinction between developmental homeostasis and plasticity, the extent to which the developmental pathway is modified by external environmental conditions, representing predictable adaptive responses to the environment (Bradshaw 1965), can be obscure.

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Empirical work on *Drosophila* (Scheiner et al. 1991), *Daphnia* (Yampolsky and Scheiner 1994), and *Arabidopsis* (Bagchi and Iyama 1983) demonstrates that developmental stability and plasticity are genetically independent and thus represent different phenomenon. However, canalization and plasticity are contrasting endpoints of a continuous expression of phenotypic variability. Plasticity, as an adaptive response, reflects selection to maintain high fitness across environments. It seems likely that the evolution of plasticity itself reflects a breakdown of mechanisms that ensure developmental homeostasis across environments.

An example of the relevance of developmental homeostasis for floral evolution is floral symmetry patterns. Perhaps some of the most extreme forms of symmetry are expressed in the Caesalpinioideae, e.g., *Chamaecrista,* where the flowers are highly asymmetrical. Furthermore, alternating flowers of an inflorescence are antisymmetrical, being mirror images of each other. The question is, How did this asymmetrical flower evolve from a likely radially symmetrical ancestor and then evolve a high degree of homeostasis? (Similarly, one could ask how differences in floral parts or placement of organs have evolved.)

Symmetry within a flower is expressed early in floral development and is one of the most canalized of floral features, responsible for differentiating higher order taxa at the family level and higher (Tucker 1984). Does this indicate that patterns of symmetry are less likely to evolve, or can symmetry respond rapidly to selection? Is high developmental homeostasis for symmetry established because selection places a premium on consistency of expression, thus variants for symmetry are rarely seen? Can selection to decrease developmental homeostasis lead to evolutionary change in the pattern of symmetry? Continuing this train of thought, we can also ask how variation within a plant for homologous organs arises. For example different forms of flowers on the same plant (cleistogamous vs. chasmogamous, male vs. female, or ray vs. disk florets) or variation in vegetative characters (e.g., heterophylly). In all cases, the likely ancestral condi-

tion are organs with similar morphologies. It would seem that a disruption of developmental homeostasis might be key to homologous organs taking on new form and function.

It is surprising that the role of developmental homeostasis in plant evolution has received so little attention. A review of the literature reveals much more study of developmental homeostasis in animals versus plants, e.g., only 3.5/23 papers in a 1993 issue of *Genetica* (89:1–316) devoted to developmental instability were focused on plants. Because of the modular construction of plants, whereby homologous organs may experience different environments, the extent to which plants exhibit developmental homeostasis may be fundamentally different than animals and should have important fitness consequences.

Breakdown of developmental homeostasis is often considered to be maladaptive (Palmer and Strobeck 1986). However, here we focus on how the breakdown of developmental homeostasis may constructively contribute to the evolution of floral characters. Throughout this article, we treat developmental homeostasis as a trait and consider how its evolution may effect the evolution of floral traits. We first briefly describe methods of quantifying developmental homeostasis and then demonstrate that the evolution of developmental homeostasis can be studied fruitfully with quantitative genetic approaches. We follow with a discussion of whether the basic assumptions of a neo-Darwinian approach are met (i.e., genetic variation, selection) and how the genetic basis of developmental homeostasis will influence its evolution. Finally, we conclude by suggesting future directions for research.

Quantifying developmental homeostasis

For clarity, it is helpful to provide a brief overview of the methodology by which developmental homeostasis is quantified. More detailed descriptions can be found in Palmer and Strobeck (1986) and Graham et al. (1993). Perhaps the most common measure of the developmental stability component of developmental homeostasis is fluctuating asymmetry, the degree of nondirectional departure from symmetry of bilaterally symmetrical traits. Other measures include the extent to which a trait departs from the norm on individuals (e.g., abnormal petal number on some flowers of a plant, or flower size variation on the same plant) or varies in its expression among identical genotypes across different environments (e.g., flower size of clones grown under different environmental conditions). Depending on the degree to which the environment is uniform for developing meristems, the former is a measure of both components of developmental homeostasis, while the latter is solely a measure of canalization.

Variation of expression of developmental homeostasis

EMPIRICAL EVIDENCE

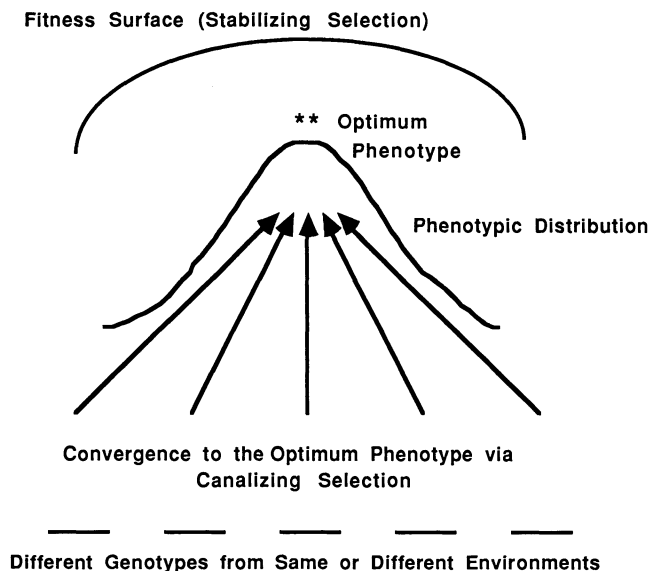If the evolution of developmental homeostasis for floral form follows a neo-Darwinian process, there must be variation in expression among individuals. Variation in number and symmetry of floral parts on plants has been documented in a number of studies (Berg 1959; Ellstrand 1984; Møller and Erickson 1994). Different degrees of breakdown of developmental homeostasis for floral traits among individuals are often associated with increased levels of genetic (mutation, inbreeding, hybridization) or environmental stress (heat, drought, nutrition, herbivory) (Waddington 1942; Parsons 1990, 1993; reviewed in Møller and Swaddle 1996). Below, we briefly discuss empirical quantification of variation in developmental homeostasis, focusing on genetic and environmental factors.

GENETIC STRESS

Genetic stress contributes to the disruption of developmental homeostasis in plants. Specific mutations can be associated with reduced developmental homeostasis. The peloric mutation (a general name describing the action of a number of mutations) in *Antirrinhum* and related species, first described by Linneaus (Cronk and Moller 1997), results in two forms of flowers being produced on an inflorescence, the normal bilateral symmetrical form and a radially symmetrical form at the terminus. Recent work with *Arabidopsis* has also demonstrated that a mutation altering floral organ number also is associated with variation of floral organ number expression within the plant (Running and Meyerowitz 1996; for *Drosophila,* cf. Rendel 1967). Evidence for inbreeding effects on developmental homeostasis in plants is not consistent, mirroring the animal literature. Inbred lines or populations sometimes demonstrate decreased developmental homeostasis, e.g., variation in style length between flowers of the same plant in *Primula sinensis* (Mather 1950) or consistency of expression of leaf length in populations of *Clarkia tembloriensis,* which differ in their outcrossing rates (Sherry and Lord 1996). However, inbred plants often do not differ from F_1 hybrids or outcrossed individuals in their degree of developmental homeostasis (reviewed in Grant 1975). Furthermore, even when some characters may demonstrate lower developmental homeostasis in more inbred genotypes, other characters do not, e.g., *Clarkia tembloriensis* (Sherry and Lord 1996) and *Mimulus gutattus* (C. B. Fenster, D. E. Carr, and M. R. Dudash, unpublished data). Hybridization among related species has also been shown to reduce developmental homeostasis of floral characters, e.g. *Liatris* (Levin 1970b and citations within).

ENVIRONMENTAL STRESS

Environmental factors are associated with a breakdown of expression of floral traits in *Linanthus* (Heuther 1969) and *Eichhornia paniculata* (Barrett and Harder 1992), and anthropogenic sources of pollution have been documented to result in reduced levels of developmental homeostasis for vegetative characters (Freeman et al. 1993). Resource limitation associated with defoliation or later flowers on a plant

Fitness Surface (Stabilizing Selection)

Fig. 1   Role of canalizing selection in causing the convergence of developmental pathways on the optimum phenotype. Shown on *top* is the fitness surface, which reflects stabilizing selection. Canalizing selection favors the evolution of developmental pathways that converge on the optimum phenotype despite genetic and environmental differences among individuals.

is associated with decreasing size of floral organs, e.g., *Mimulus guttatus* (Macnair and Cumbes 1990; Mossop et al. 1994), *Solanum hirtum* (Diggle 1991), and *Chamaecrista fasciculata* (Frazee and Marquis 1994). Different factors can also interact to further reduce developmental homeostasis. For example, Heuther (1968), working with natural populations of *Linanthus*, observed that both phenology (later flowers) and herbivory caused decreased constancy of expression of petal number on plants. However, he observed the greatest degree of variable expression of floral parts on plants exposed to both simulated herbivory and selection for petal number.

Quantitative genetics and developmental homeostasis

BACKGROUND AND THEORY

Developmental homeostasis may evolve through the action of canalizing selection (fig. 1); Waddington 1940; Schmalhausen 1949). If the average or normal expression of a trait is favored by stabilizing selection, canalizing selection will favor the development of a trait to converge on the optimum. Note that canalizing and stabilizing selection are interchangeable in terms of their outcomes: both lead to the decreased expression of phenotypic variability. However, canalizing selection refers to the developmental mechanism underlying the reduced variability when the trait is under stabilizing selection.

Models (Slatkin and Lande 1976; Bull 1987; Møller and Pomiankowski 1993; Gravilets and Hastings 1994) predict that, if the mean phenotype is favored through stabilizing selection, canalizing selection will act to increase developmental homeostasis if the po-

sition of the optimum does not change. However, selection favors the reduction of developmental homeostasis if the position of the optimum fluctuates. In addition, if the degree of sensitivity of a genotype to the environment is correlated to the mean expression of a trait, directional selection on a trait can cause the correlated evolution of developmental homeostasis (Gravilets and Hastings 1994). Thus, if a trait has been under the influence of stabilizing and canalizing selection and then is exposed to either directional or disruptive selection, selection favoring a change in the mean would act to disrupt developmental homeostasis. Individuals expressing the extreme of a trait in the favored direction(s) would have higher fitness. The role of a breakdown of developmental homeostasis in contributing to the response of a trait to directional and disruptive selection is evaluated below in the discussion of selection experiments on developmental homeostasis.

HERITABLE VARIATION FOR LEVELS OF DEVELOPMENTAL HOMEOSTASIS

The presence of genetic variation for developmental homeostasis is a prerequisite for evolution of this trait in natural populations. What evidence is there that variation in developmental homeostasis among individuals can respond to selection, i.e., has a heritable component? Surprisingly few plant studies have attempted to document the degree to which stability of expression varies among genotypes. Paxman (1956) demonstrated a genetic component to the stability of stamen and pistil length (in addition to leaf characters) at three levels for *Nicotiana rustica:* among identical individuals in (1) different environments, (2) the same environment, and (3) within individuals. Jinks and colleagues (summarized in Jinks and Pooni 1988) found ubiquitous genetic variation for micro- and macroenvironmental sensitivity in *Nicotiana.* Most recently, Winn (1996), in a study of a wild or native species, demonstrated a genetic component for within-individual environmentally determined leaf variation in *Dicearandra linearifolia* (Lamiaceae). Evans and Marshall (1996) determined the genetic contribution to variation in fluctuating asymmetry for foliar and floral traits in two populations of *Brassica campestris.* Although between-population differences were observed, the within-population, or heritable, component of fluctuating asymmetry was low and was often not significantly different from zero. In contrast, Møller (1996) quantified low but significant heritability for fluctuating asymmetry of petal length in *Epilobium angustifolium.* Genetic factors also influence the stable expression of the anther position relative to the stigma in *Eichhornia paniculata* (Barrett and Harder 1992). In sum, these studies demonstrate genetic variation in stability of expression.

ROLE OF SELECTION

Given genetic variation in developmental homeostasis, is there evidence that it is a target of natural se-

lection? Yes. A number of studies have demonstrated that floral traits exhibit greater symmetry than do foliar characters (Berg 1959; Møller and Erikson 1994; Evans and Marshall 1996), presumably because of the greater importance of symmetry in flowers, which facilitates the pollination process. Fenster (1991) observed lower phenotypic variation for corolla tube length in species with longer corolla tubes, which was attributed to higher intensity of stabilizing selection imparted by specialized pollinators. Extending to the relationship among two or more characters, allometric relationships during development among functionally interacting floral characters are more highly correlated during development than are floral traits, which do not interact with regard to pollination (Kirchoff 1983). In addition, larger phenotypic correlations have been observed among floral characters that have functional significance to pollination (Conner and Sterling 1995). Overall, these patterns have been interpreted as selection favoring a higher degree of developmental homeostasis in organs that require precise shape or placement for their proper functioning.

Direct evidence that high developmental homeostasis is at a selective premium (or that symmetry is favored by selection) has been provided mostly by the animal literature in the context of both natural and sexual selection (reviewed in Markow 1995). Evidence that developmental homeostasis for floral characters is indeed under the influence of natural selection is provided by a study demonstrating bumblebee preference for symmetrical flowers in Epilobium angustifolium (Møller 1995). Floral symmetry was positively associated with both the size of the flower and the amount of nectar reward. Bees visited flowers that were more symmetrical compared to neighboring flowers. This preference for large and symmetrical flowers was also observed in experiments where flowers were manipulated with scissors to be either more or less symmetrical, independent of size. Preferential pollinator visitation to symmetrical flowers was also observed in 10 different European flowering plant species (Møller and Erikson 1995). Clearly, more work of this type needs to be conducted to determine the role of selection in maintaining current levels of developmental homeostasis.

In addition, a number of studies demonstrate that developmental homeostasis can readily evolve. The stability of yield in Nicotiana can respond to selection (Jinks and Pooni 1988). Several other examples of selection for levels of developmental homeostasis are particularly revealing. Heuther (1969) performed selection on petal number in pentamerous Linanthus androsaceus (Polemoneaceae). He was able to both increase and decrease petal number in his high and low selection lines, respectively. However, over the course of selection, he also uncovered natural genetic variation underlying the constancy of expression of the pentamerous state. Low levels of inconstancy for petal number are found in natural populations of L. androsaceus (Heuther 1968). However, after selection, both

high and low lines consisted of individuals that had, on average, more or less petals than five but also had greater variability of expression of petal number on the same plant. Individual plants in either selection line had greater variation in petal number than previously observed in the whole population. Thus, inadvertent selection for decreased developmental homeostasis released genetic variation for petal number. Thoday (1958) observed similar results: selection for high and low chaetae number in Drosophila melanogaster resulted in greater expression of asymmetries between the left and right side of the body.

Selection for petal number in Linanthus and chaetae number in D. melanogaster reveals that selection can reduce developmental homeostasis. Is there evidence that selection can increase developmental homeostasis? Yes. Rendel (1967) demonstrated that individuals homozygous (or hemizygous, sex linked) for the sc mutation in Drosophila had both lower number of scutellar bristle number and greater variation of expression of scutellar bristles compared to the wildtype. However, through selection, Rendel was able to increase the developmental homeostasis of individuals homozygous for the scute mutation so that they produced a lower number of bristles with very little variation in expression. Thus, he was able to disrupt developmental homeostasis and then, through selection, recanalize the trait at a different mean level of expression.

A natural selection equivalent has been observed during the evolution of diazinon resistance in the Australian sheep blowfly, Lucilia crupina (McKenzie and O'Farrell 1993; Clarke 1997). Initially, pesticide-resistant flies demonstrated asymmetries in bristle counts between the left and right sides of a number of different tissues. However, the levels of fluctuating asymmetry of pesticide resistant and susceptible flies are currently the same, indicating that natural selection has favored the evolution of modifiers to restore symmetry to flies that are diazinon resistant.

Breakdown of developmental homeostasis and consequences for the evolutionary process

HIDDEN VARIABILITY RELEASED BY GENETIC AND ENVIRONMENTAL INTERACTIONS

The ability of an organism to express a trait consistently across environments was recognized early to have a genetic component (Waddington 1942; Schmaulhausen 1949). Waddington (1953, 1960) and Mather (1953) demonstrated that differences among individuals for expression of a trait, following stress or environmental changes, could be used to select successfully for alteration of a trait, where no phenotypic variation previously existed. This phenomenon has been termed "genetic assimilation of an acquired character" (Waddington 1953). Analogous to the effect of a mutation, environmental stress can lead to the expression of new variation by disruption of developmental homeostasis in some genotypes. Referring to

figure 1, imagine the variability that might be expressed if development did not always converge on the same optimum. Thus, the breakdown of developmental homeostasis under environmental stress can significantly increase the amount of variability on which selection can act. Indeed, a number of animal studies indicate that the heritable component of traits increases with increasing stress (Parsons 1993). Thus, developmental homeostasis may effectively reduce selection on genetic variation by buffering the individual from the inappropriate expression of genes, allowing for the maintenance of larger standing genetic variation (Vogel 1996). Consequently, the breakdown of homeostasis may "unmask" genetic variation for floral variation, allowing the population to respond to novel selection pressures on floral features (Levin 1970a).

HIDDEN VARIABILITY AND SHIFTING BALANCE

The contribution of the breakdown of developmental homeostasis and the associated increase in phenotypic variation to the evolutionary process have been explicitly modeled by Whitlock (1995). Sewall Wright's vision of evolution (1931, 1988) included populations evolving to higher fitness by first drifting through maladaptive valleys of lower fitness. This process was described by Wright as shifting balance—populations are able to shift to higher adaptive peaks, given the proper balance between gene flow, genetic drift, and selection. Although Wright's shifting balance has been a useful paradigm for evolutionary biologists for close to 70 yr, it has been a difficult concept to test, especially the notion of populations evolving lower fitness (Coyne et al. 1997). One hypothetical process by which populations might be able to come under the influence of a higher adaptive peak is variance-induced peak shifts (Whitlock 1995). This is the phenomenon whereby any process that increases phenotypic variation will facilitate a shift to a different adaptive peak. Using *Linanthus* as an example, imagine that the five-petal condition conveys intermediate fitness. Imagine also that 10 petals confer higher fitness, but intermediate character states of 6, 7 , 8, and 9 petals confer lower fitness. How can the population evolve across this maladaptive valley? If there is a breakdown of developmental homeostasis such that some plants are capable of producing up to 10 petal flowers, the population will come under the selective influence of the 10-petal peak.

MATING SYSTEM EVOLUTION IN *EICHHORNIA PANICULATA*

Is there an example where evolution of developmental homeostasis is crucial to the evolution of floral traits? Yes. We think the best example is that of Barrett and colleagues with *Eichhornia paniculata,* a neotropical aquatic herb that is commonly tristylous and highly outcrossing (reviewed in Barrett 1993). Normally, the midmorph is highly outcrossing, with its stigma sandwiched between a high and low rank of anthers. However, throughout its range are midindividuals on which some of the flowers are modified so that the

outside filament of the lower rank anthers is elongated (Richards and Barrett 1987) such that the anther is juxtaposed to the stigma, allowing for automatic self-pollination. The elongated anther is the first step in the breakdown of tristyly to homostyly and selfing. The breakdown of developmental homeostasis for the position of the lower anther rank in the midmorph is under recessive gene control (Fenster and Barrett 1994). Either environmental stress and/or factors that promote inbreeding, including population bottlenecks, which are frequent in *E. paniculata* (Husband and Barrett 1992), may increase the probability of expression of the modified midform. These same bottlenecks may also be associated with the loss of the short morph though drift, pollinator scarcity, and the purging of genetic load that normally prevents the evolution of selfing (Barrett 1993). Consequently, the frequency of modified midexpression increases via natural selection and spreads throughout the population. Eventually, the modified mid itself becomes highly canalized and developmentally stable and is associated with the dramatic evolution of floral features common to the evolution of selfing, including reduced flower size and reduction in allocation to male function. The breakdown of developmental homeostasis for anther placement initiates the dramatic evolution of selfing in *E. paniculata.*

Genetic basis of developmental homeostasis

The contribution of genetic variation to a trait can be partitioned into further components reflecting the different modes of gene action, including V_A (additive), V_D (dominance), and V_I (interaction or epistasis). Note that the contribution of each of the components is very sensitive to gene frequencies. Thus, little phenotypic variation can be explained by any one component, although the expression of any trait might be greatly affected by one of the three modes of gene action. Two contrasting hypotheses have been put forward to explain the genetic basis of developmental homeostasis: heterozygosity (V_D; Lerner 1954) and coadapted gene complexes (V_I; Dobzhansky 1970). Distinguishing between these hypotheses will affect our understanding of the importance of heterozygosity and the role of selection acting on groups of interacting coadapted genes. Below, in our discussion of the contribution of each component of genetic variation to developmental homeostasis, we demonstrate that the simple dichotomy between heterozygosity and coadapted genes may be an oversimplification.

ADDITIVE GENETIC VARIATION

The resemblance between parents and offspring is mostly due to additive genetic variation. Thus, selection acting on differences among individuals will result in an evolutionary response, i.e., change in the mean across generations due to change in allele frequencies, depending on the degree to which additive genetic variation underlies phenotypic variation. The experiments discussed above have documented signif-

icant genetic variation for developmental homeostasis and response to selection, demonstrating that developmental homeostasis has an additive component.

DOMINANCE OR HETEROZYGOSITY

The role of heterozygosity in developmental homeostasis was first emphasized by Lerner (1954). He popularized the term "phenodeviants" to describe individuals whose development is more prone to environmental fluctuation and proposed that accidents of development because of environmental fluctuation were more likely to occur in individuals with less heterozygosity. He viewed stabilizing selection as favoring heterozygotes, while homozygotes were more likely to express extreme characters resulting in lower fitness. He ascribed heterozygote superiority to a greater buffering capacity of heterozygotes. Thus, an individual heterozygous at a locus has two alleles, and the two together are more likely to be expressed across environments than is either of the homozygotes individually. Note that Lerner used an overdominance model to describe the relationship between heterozygosity and developmental homeostasis. However, a simple dominance model, with deleterious recessive mutations decreasing homeostasis, is also likely to underlay the expression of developmental homeostasis.

As cited in the discussion of genetic stress (and summarized in Clarke 1993), there is no clear relationship between levels of developmental homeostasis and levels of heterozygosity in outcrossing organisms. Lerner claimed that breakdown of developmental homeostasis would be seen only where there is departure from the mating system (loss of heterozygosity in normally outcrossing individuals). However, his theory should also apply across breeding systems, such that species with higher selfing rates should exhibit less developmental homeostasis. A number of studies have demonstrated that heterozygosity does not enhance homeostasis in self-pollinating crops (Grant 1975). Given the variety of mating systems in plants and the fixed heterozygosity that is found in allopolyploids versus their lower ploidy ancestors, it would seem plants would be ideal organisms to test Lerner's ideas further.

## EPISTASIS OR COADAPTED GENE COMPLEXES

Defined as the phenomenon by which genes are selected for their joint effect on fitness (Wright 1969; Fenster et al. 1997), Dobzhansky (1970) first suggested that coadapted gene complexes are responsible for the expression of developmental homeostasis. Perhaps the strongest evidence in support of the role of genetic coadaptation in developmental homeostasis is Thoday's (1955, 1958) work with *Drosophila*. He demonstrated that intrapopulation hybrids have lower levels of bristle number asymmetries than interpopulation hybrids and that lines selected for asymmetries maintain the asymmetries when hybridized. In addition, strong evidence for the role of coadaptation is provided in both the animal and plant literature, whereby single mutations alter the mean expression of a trait as

well as the developmental homeostasis of that trait or other traits. This implies that the balance between the wildtype allele and genetic modifiers that normally result in the canalized expression of that trait has been disrupted. For example, the effects of the scute mutation in *Drosophila* (Rendel 1967), insecticide resistance in blowfly (McKenzie and O'Farrell 1993), perianthia mutation that alters floral organ number in *Arabidopsis* from wildtype four to five (Running and Meyerowitz 1996), and the peloric class of mutations that determine symmetry patterns in *Antirrhinum* flowers (Coen et al. 1995) depend on the genetic background of the mutations. In addition, in *Eichhornia paniculata* lower consistency of expression of anther height of the modified midmorph was observed in progeny derived from longer distance crosses, indicating an important role of genetic background or epistatic interactions (Fenster and Barrett 1994).

In natural or artificial hybrid populations, coadapted gene complexes may be broken up by the mixing of the parental genomes. Therefore, hybrid studies have been used to demonstrate the presence of coadapted genes. Most of the evidence associated with decreased developmental homeostasis is in animal hybrid populations (reviewed in Clarke 1993). Although Levin (1970b) demonstrated that some hybrids of *Liatris* demonstrated less developmental homeostasis than did their parents, many plant examples (reviewed in Grant 1975 and Levin 1970b) demonstrate that F_1 hybrids are often more uniform and more consistent in their expression of traits than are parents, contrary to the coadapted gene complex argument. However, these F_1 studies fail to account for the increased level of heterozygosity in hybrids. Quantitative genetic approaches that account for heterozygosity and coadaptation are discussed below.

QUANTITATIVE GENETIC APPROACHES TO DETERMINE THE UNDERLYING GENETIC BASIS OF DEVELOPMENTAL HOMEOSTASIS

Many types of gene action are likely responsible for developmental homeostasis, and specific patterns may differ among traits and organisms (Clarke 1995, 1997). Developmental homeostasis certainly is in part determined by additive gene action, since it can respond to selection (see above). Unfortunately, many of the previous studies to determine the role of heterozygosity and coadapted genes in developmental homeostasis have been flawed because they do not completely factor out the role of either. In addition, they are not able to distinguish the role of dominance versus overdominance in the relationship between heterozygosity and developmental homeostasis. To discriminate between the hypotheses of gene action underlying developmental homeostasis, approaches are required whereby dominance and overdominance contributions to heterozygosity, as well as coadaptation, can be examined factorially. Several approaches exist and have been mostly applied to crop breeding. First, the North Carolina III design (reviewed in Lawrence 1984), crossing

Genetic basis of developmental homeostasis: Heterozygosity vs. Coadaptation

Quantitative Genetic Approach:
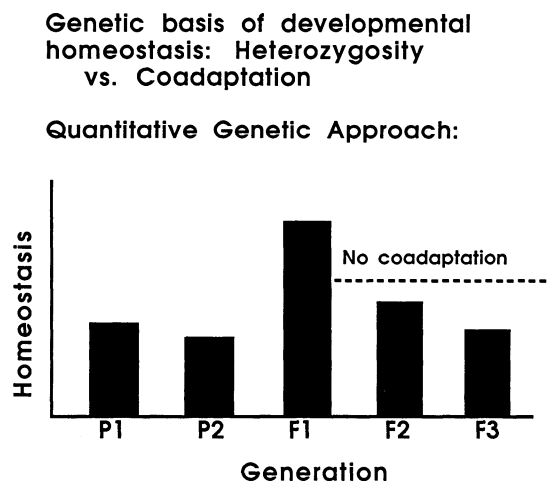
Fig. 2 Quantitative genetic design to determine the role of heterozygosity and genetic coadaptation in developmental homeostasis. Shown are the mean levels of developmental homeostasis for two inbred populations or lines, P_1 (parent 1) and P_2 (parent 2) and their F_1, F_2, and F_3 hybrids. Because of the increased heterozygosity in the F_1, we might expect to see increased developmental homeostasis in the F_1 compared to either parent. Mendelian segregation results in the F_2 and F_3 having a heterozygosity halfway between the average of the two parents and the F_1 (dashed line). Thus, in the absence of coadaptation the F_2 and F_3 should have a level of developmental homeostasis equal to the dashed line. However, the breakup of coadapted gene complexes affecting developmental homeostasis will result in F_2 and F_3 developmental homeostasis significantly lower than the dashed line. If the gene interactions occur over short stretches of the chromosome, F_3 performance will be lower than F_2 because of the additional round of recombination.

inbred lines to the F_2 and then backcrossing the F_2 to the parental inbred lines can be used to distinguish the causal mode of gene action underlying the reduction of developmental homeostasis following inbreeding, i.e., distinguishing dominance from overdominance. One can simultaneously determine the role of heterozygosity and coadaptation in developmental homeostasis by use of hybridization or line-cross methodology (Lynch 1991; Fenster et al. 1997). The experimental design is illustrated in figure 2. When crossing populations, or inbred lines, we expect to see increased developmental homeostasis for traits in the F_1 population if heterozygosity plays an important role in developmental homeostasis. In addition, increased developmental homeostasis in the F_1 population may also be associated with the decreased expression of deleterious recessive mutations. The F_2 and F_3 populations should have half the heterozygosity of the F_1 population, provided the F_3 population is made by randomly crossing the F_2 plants, and thus should have a developmental homeostasis midway between that of the parents and the F_1 population. If the F_2 and F_3 populations have lower than expected developmental homeostasis, recombination has disrupted the coadapted gene complexes.

CONSEQUENCES OF THE ROLE OF HETEROZYGOSITY AND COADAPTATION FOR EVOLUTION AND CONSERVATION

Decreased homeostasis for floral traits may be an important component of inbreeding depression and hence an important factor in preventing the evolution of selfing (Fisher 1941; Charlesworth and Charlesworth 1987). If we accept that the pollination process, either outcrossing or selfing, depends on the precise placement of floral parts in relation to one another, then the breakdown of developmental homeostasis in floral characters should be detrimental to the organism, regardless of the mating system. In addition, many species have intermediate outcrossing rates. Thus, the production of selfed, more highly homozygous offspring is a constant feature of many plant populations. Consequently, greater variation of expression of developmental homeostasis may be found in plant taxa as compared to animal species.

The role of coadapted gene complexes in developmental homeostasis has importance in specific evolutionary phenomenon such as the significance of hybrid zones. For example, do hybrid zones lead to a release of genetic variation because of a breakdown of developmental homeostasis, or will a breakdown of developmental homeostasis at hybrid contact zones help maintain the integrity of a species (prevent introgression)?

Much emphasis has been placed recently on the relationship between heterozygosity and the management of species. With so many threatened and endangered species reduced to small, fragmented populations (Holsinger and Gottlieb 1991), the likelihood of inbreeding increases (Barrett and Kohn 1991; Fenster and Dudash 1994). Consequently, the developmental breakdown of traits associated with adaptation to the environment may be associated with inbreeding in these species, further contributing to their likelihood of extinction. However, if coadaptation among genes is responsible for developmental homeostasis, then mixing gene pools to restore heterozygosity may result in the breakdown of developmental homeostasis of traits conferring adaptations to the environment.

Summary

Understanding the evolution of developmental pathways provides a fuller understanding of how complex traits evolve (Gould 1977; Maynard Smith et al. 1985; Fenster et al. 1995). Thus, we should always strive to integrate questions of development into evolutionary studies. As an example, our survey of the literature demonstrates that the evolution of floral traits may arise through the evolution of developmental homeostasis in the following way. Consistency of expression of floral traits likely reflects the action of canalizing selection. However, the breakdown of developmental homeostasis may be necessary for populations to respond to new selection pressures that favor different floral form.

The role of developmental homeostasis in evolutionary processes has been explored in much greater depth for animals than for plants. We argue above that the study of developmental homeostasis in plants may be particularly useful for several reasons. First, because of the selective premium placed on plasticity in

sessile plants, it may be easier to quantify the relationship between developmental homeostasis and fitness. Second, the modular construction of plants indicates that developmental homeostasis may differ among the levels of organization within the plant, i.e., from within a flower to among flowers on the same plant. Third, because of the great range of mating and genetic systems found among plant species, the role of genetic architecture for developmental homeostasis may be better quantified than in animals. Below we suggest future directions utilizing a number of approaches to determine the role of developmental homeostasis in the origin of floral diversity.

Future directions

We clearly need more studies documenting the role of selection in determining levels of developmental homeostasis for floral traits. The recent work of Møller (1995, 1996) documenting natural selection on floral symmetry mediated through pollinator behavior preferences is a landmark and should be expanded. Pertinent questions include: Does selection always favor increased developmental homeostasis for floral traits, or is decreased constancy of expression sometimes favored? Does selection favor greater developmental homeostasis of some traits versus others, i.e., floral versus foliar characters? Furthermore, greater understanding of the evolution of floral traits can be attained through more artificial selection studies of developmental homeostasis. Does changing the optimum for stabilizing selection lead to a decrease in developmental homeostasis as theory predicts? In short, we need quantitative, manipulative studies that measure the relationship between fitness of an individual and the degree of developmental homeostasis of a trait.

Variation in resources available to developing floral organs may influence the developmental homeostasis of flowers in terms of their constancy of expression (Diggle 1995). Therefore, we might expect that different constraints may underlay the evolution of variation across floral organs on the same plant versus within a flower. Thus, the ability to evolve variation in petal size or shape across flowers within an inflorescence may be easier than the evolution of petal size variation within a flower because each petal within a flower is exposed to more similar levels of resources than petals on different flowers. We need a greater understanding of the origins of variation in floral organs within a plant and whether different levels of organization are more responsive to selection than others.

The significance of genetic variation for the sensitivity of developmental homeostasis across environments needs to be understood more fully. In particular, we need a better comprehension of the ecological significance of varying expression of developmental homeostasis in different environments. Under what conditions does a breakdown in developmental homeostasis lead to adaptive evolution? We need to contrast the various ways by which developmental ho-

meostasis is broken down, either through relaxed selection or increased stress, and quantify their roles in the evolution of floral traits. For example, does a release from stress via colonization of unoccupied habitat (i.e., island colonization) result in a relaxation of canalizing selection and thus a release of genetic variability for selection to act on? Alternatively, does increased stress resulting in a breakdown of developmental homeostasis lead to adaptive evolution? Parsons (1993) argues for the former, suggesting that extinction is the likely outcome of stress. Additional questions related to the genetics of developmental homeostasis having ecological relevance are such issues as the effect of ploidy level on developmental homeostasis (including the relationship of auto- vs. allopolyploidy with developmental homeostasis) and the levels of developmental homeostasis observed in congeners with contrasting mating systems. Although some of these questions were addressed in the past, the development of new statistical approaches to quantify developmental homeostasis indicate the merit of reexamination.

Utilizing molecular techniques, including marker-assisted techniques in quantitative genetics, and mutations in model plant organisms, such as *Arabidopsis* and *Antirrhinum,* will allow more precise understanding of both the genetic basis and the developmental mechanisms underlying developmental homeostasis. In addition to the traditional biometrical or strictly statistical approaches outlined above, new molecular techniques allow more detailed understanding of the genetic architecture of traits by use of linkage map approaches (Cheverud and Routman 1993). Thus, we can now answer in greater detail than ever before possible such basic questions as to the number, effect (major vs. minor), and mode of expression (additive vs. dominance vs. epistasis) of genes influencing traits such as developmental homeostasis. With the mapping techniques, we can determine which genes influence developmental homeostasis, what pleiotropic effects they may have and, by following their products, determine the developmental mechanisms by which developmental homeostasis is expressed. We need to know whether genes that influence the developmental homeostasis of floral traits are highly conserved like the ones that determine floral organ initiation. Have the same major genes affecting floral symmetry (Coen et al. 1995) or developmental homeostasis for floral traits evolved repeatedly, giving rise to the floral diversity extant today? Or are patterns of floral symmetry and developmental homeostasis general features of an organism effected by the interaction between stress and polygenic systems controlling the development of a trait, rather than associated with specific major genes? Answers to these questions will allow us to determine the relative role of selection and mutation in the evolution of developmental homeostasis and consequently floral evolution.

Finally, in combination with the above molecular

approaches, morphological studies can provide the wealth of detail necessary for a complete understanding of the role of genes in producing a certain level of developmental homeostasis. For example, we can now address such questions as When during development are the genes that influence patterns of symmetry expressed? and Does selection altering developmental homeostasis act by altering events early or late in development? Thus, we can determine the lability of developmental homeostasis to selection. Given the broad consequences of developmental homeostasis to the evolution of floral form, synthetic approaches are re-quired to understand fully the processes underlying its evolution.

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