

Phenotypic plasticity in plants: a case study in ecological development

Sonia E. Sultan

Biology Department, Wesleyan University, Middletown, CT 06459-0170, USA

Correspondence (e-mail: sesultan@wesleyan.edu)

INTRODUCTION: PHENOTYPIC PLASTICITY AND ECOLOGICAL DEVELOPMENT

Ecological development has been described as “the meeting of developmental biology with the real world” (Gilbert 2001); in other words, the study of development as it occurs in nature and its ecological consequences. One key area in this field is *phenotypic plasticity*: environment-dependent phenotypic expression (Bradshaw 1965; Schlichting 1986; Sultan 1987, 1995, 2000; Scheiner 1993; Travis 1994; Schlichting and Pigliucci 1998; Pigliucci 2001). To determine patterns of individual plasticity, genotypes are cloned or inbred and the genetic replicates raised in a set of controlled environments. Traits of interest can then be measured in each environment to characterize patterns of phenotypic response (termed *norms of reaction*) for each genetic individual. Ecologically meaningful plasticity studies are designed to test genotypes in a range of environments based on naturally occurring variation and to focus on phenotypic traits important to function and therefore fitness in those environments. The greatest wealth of plasticity data is available for plants, which are ideally suited for such studies because they readily produce genotypic replicates and can be grown in diverse experimental environments. However, all organisms express some degree of phenotypic response to environment. Recent studies have documented developmental as well as physiological and behavioral plasticity in amphibians, reptiles, birds, marine and freshwater invertebrates, insects, mammals, and even lichens (references in Sultan 2000; Gilbert 2001; see also Barata et al. 2001; Griffith-Simon and Sheldon 2001; Hammond et al. 2001; Negovetic and Jokela 2001; Jordan and Snell 2002; Relyea 2002).

Although biologists have always been aware that organisms develop differently in different conditions, environmental effects on phenotype were formerly regarded as uninformative “noise” obscuring the “true” expression of the genotype (Allen 1979; Sultan 1992; Schlichting and Pigliucci 1998). In plants, for instance, individuals that encounter low resource levels inevitably grow less—in fact, the effects of resource availability on plant phenotypes are so profound

that neo-Darwinian botanists were often quite frustrated in their attempts to discern genetically based local adaptations through this “environmental noise” (Stebbins 1980; Pianka 1988). This led them to overlook the much more interesting aspect of plastic response to environmental variation: The fact that phenotypic responses to different environments may also include highly specific developmental, physiological, and reproductive adjustments that enhance function in those environments (Bradshaw 1965; Travis 1994; Schmitt et al. 1999; Sultan 2000; and references therein). This capacity for specific functionally appropriate environmental response is called *adaptive plasticity*, as distinct from the inevitable effects of resource limits and other suboptimal environments on phenotypic expression (Sultan 1995).

Both inevitable and adaptive aspects of developmental plasticity are fundamental to ecological development, because they influence the success of organisms in their natural contexts. However, functionally adaptive plasticity is of particular interest because it permits individual genotypes to successfully grow and reproduce in several different environments. Consequently, such plasticity can play a major role in both the ecological distribution of organisms and their patterns of evolutionary diversification. Taxa consisting of adaptively plastic genotypes may inhabit a broad range of environmental conditions; many widespread generalist species may upon examination show this property (Baker 1974; Oliva et al. 1993). Adaptive plasticity may also contribute specifically to species invasiveness by allowing rapid colonization of diverse new habitats without the need to undergo local selection (Williams et al. 1995). Finally, individual plasticity may influence patterns of evolutionary diversification at the population (and ultimately species) level by precluding selective divergence in environmentally distinct sites (Sultan and Spencer 2002).

THE POLYGONUM SYSTEM: A CASE STUDY

Like other products of evolution, genotypic norms of reaction are shaped by phylogenetic history and genetic constraints

(Scheiner 1993; DeWitt et al. 1998; Schlichting and Pigliucci 1998). Consequently, species and even populations may show different patterns of individual plasticity and different capacities for adaptive environmental response. We are just beginning to learn how plastic responses may differ in individuals of related taxa and to understand the ecological and hence evolutionary consequences of these differences. Here I present a case study of phenotypic plasticity in a group of congeneric annual plant species as an example of an ecological developmental approach and the insights it affords to organisms in the “real world.” The four species in this system, members of a monophyletic section within the genus *Polygonum*, are introduced in North America where they have shared a common geographic range for many generations (Sultan 2001 and references therein). Within this common area, *Polygonum persicaria* is found in an extremely broad range of habitats, whereas *P. lapathifolium*, *P. cespitosum*, and *P. hydropiper* inhabit more restricted ranges of light, soil moisture, and/or macronutrient conditions in the field (see Sultan et al. 1998 for complete environmental distribution data). I draw on results from a series of controlled growth experiments on cloned and inbred genotypes of these species, designed to determine individual plasticity patterns for ecologically important aspects of development to these key environmental factors. There are two insights from this case study. First, the plasticity data offer a more complete and complex view of development by revealing the various environmental response capacities of individual genotypes. Second, they illuminate how these individual response patterns influence species’ environmental distributions in the field and thus their relative ecological breadth.

ALLOCATIONAL PLASTICITY

One environmentally labile and ecologically important aspect of plant development is the proportion of biomass allocated to functionally distinct tissues such as roots, leaves, stems, and reproductive structures (Bazzaz 1996). By adjusting the proportions of light-harvesting leaf tissue versus water- and mineral-collecting root tissue, this allocational plasticity may allow plants to adaptively enhance access to a specific resource in short supply. For example, in response to reduced light availability, genetically identical plants of *P. persicaria* sharply increased the proportion of their tissue allocated to leaves (Fig. 1a), effectively maximizing leaf surface area for photon capture in conditions of low photon flux density (Chapin et al. 1987). Thus, although plants grown at moderate and very low light levels produce much less total biomass, this developmental shift raises the photosynthetic effectiveness of each gram of that biomass so as to promote successful growth and reproduction despite limited light (Gross 1989; Sultan and Bazzaz 1993). Accordingly, the ca-

capacity for this type of allocational plasticity may contribute to the species’ ability to inhabit a broad range of light habitats in the field from open to shaded sites (Sultan et al. 1998).

In contrast, *P. hydropiper*, a species that is restricted to consistently high light sites, shows far more limited plasticity for this shade-adaptive trait. In a comparative experiment using inbred lines drawn from a sample of five populations of each species, *P. hydropiper* plants grown at low light increased leaf allocation by 52%, compared with a mean increase of 115% percent in plants of *P. persicaria* (Fig. 1b). Notice that proportional allocation to leaves in these species is identical at favorable high light conditions: The salient difference between the species is not their leaf allocation in general but the capacity for appropriate plastic response to the particular challenge of low light intensity. It is important too to note that this leaf allocation change is not some kind of generalized stress-induced phenotype but rather occurs specifically in response to low light. For instance, plants of both species respond to low macronutrient levels by slightly *decreasing* leaf allocation. It is precisely because of their resource specificity that patterns of plasticity for functionally important traits can shape the environmental distributions of species in very specific ways.

A second ecologically important aspect of allocational plasticity in plants is increased biomass allocation to root tissue in response to limited soil resources, such as water or mineral nutrients. By increasing the relative size of root systems and therefore their absorptive surface area, plants may enhance the availability of these soil resources (Fitter 1994; Rodrigues et al. 1995). Annual *Polygonum* species also differ in this aspect of adaptive plasticity in ways that correspond to their contrasting field distributions. Bell and Sultan (1999) tested allocational response to experimental soil moisture treatments in inbred genotypes of *P. persicaria*, a moisture generalist that occurs in very dry to flooded soils, and *P. cespitosum*, a shade-distributed species restricted to moist soils (Sultan et al. 1998). Plants in both species increased proportional biomass allocation to roots in soil allowed to dry out, compared with plants in a favorable constantly moist treatment (Fig. 2). Once again, however, plants of the more environmentally tolerant *P. persicaria* expressed greater allocational plasticity, in this case increasing root allocation significantly more in the dry soil treatment (58% vs. 48% increase; Fig. 2).

DYNAMIC ASPECTS OF PLASTIC RESPONSE

This experiment also examined a more subtle but equally important aspect of plastic response to soil conditions: the ability of plants to spatially redistribute their root systems (through adjustments in local proliferation) to track change over time in the location of soil resources and hence maximize effective soil foraging (Caldwell 1994 and references

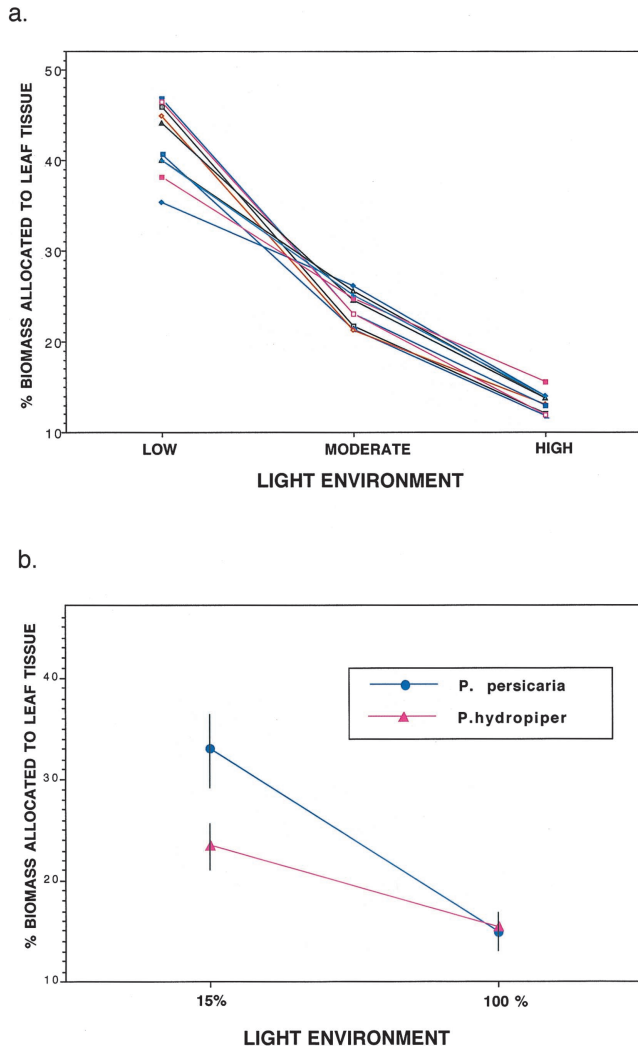


Fig. 1. Plasticity for biomass allocation to leaf tissue in response to contrasting light levels. (a) Individual norms of reaction are shown for 10 *Polygonum persicaria* genotypes raised in three greenhouse light treatments admitting high (100%), moderate (37%), and low (8%) levels of midsummer photosynthetically active radiation (PAR). Proportional biomass allocation to leaves is calculated for fully mature plants as leaf biomass divided by total plant biomass (the sum of leaf, root, stem, reproductive support, and reproductive tissue biomass). Data points indicate means of six clonal replicates per genotype in each treatment; effect of light level on leaf allocation significant at $P \leq 0.000$ (according to a univariate F-test following multivariate analysis of variance for total biomass allocation). (Redrawn from Sultan and Bazzaz 1993.) (b) Mean norms of reaction (± 2 SEs) are shown for *Polygonum persicaria* and *P. hydropiper*, based on six replicates per line of eight inbred lines per species raised in each of two greenhouse light treatments admitting, respectively, 15% and 100% of midsummer PAR (treatment details in Sultan 2001). The species' responses differ significantly, according to a univariate F-test for the species \times light interaction effect on leaf allocation ($P \leq 0.000$) following multivariate analysis of variance for total biomass allocation. (From S. E. Sultan and A. M. Wilczek, unpublished data.)

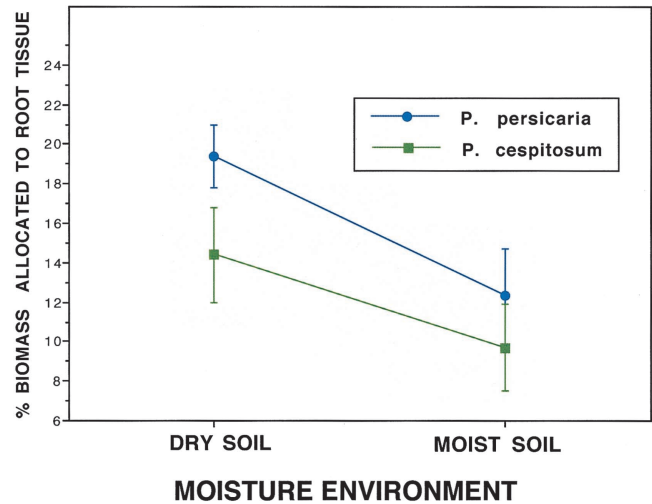


Fig. 2. Contrasting patterns of plasticity for biomass allocation to root tissue in *Polygonum persicaria* and *P. cespitosum*. Mean norms of reaction (± 2 SEs) are shown for proportional biomass allocation to roots (calculated for fully mature plants as root biomass divided by total plant biomass) in 10 inbred lines per species, based on one replicate per line in each of two greenhouse moisture treatments, dry and moist soil. Root allocation in the two species differed significantly in the dry treatment (species effect significant at $P \leq 0.004$) but not in the moist treatment ($P \leq 0.237$), based on nested analysis of variance within each treatment. (Redrawn from Bell and Sultan 1999.)

therein). In temporally varying conditions that demand this kind of dynamic plastic response, the timing as well as the magnitude of response is critical. Because rapid adaptive response to environmental changes may be essential to withstanding those changes in nature, differences in these dynamic aspects of developmental plasticity may influence the ecological distribution of species in important ways.

In the *Polygonum* study, we tested dynamic root responses to spatial changes in soil moisture availability by growing inbred replicate plants of both species in flat Plexiglas containers that allowed us to monitor the spatial distribution of roots to different soil layers over time (Bell and Sultan 1999). In one treatment, initially moist upper soil layers were allowed to become progressively drier, whereas moisture was supplied only to the lowermost layers. In response to this change in the location of available water, *P. persicaria* plants rapidly and increasingly deployed roots to the moist lower soil layers and reduced the proportion of their root systems in the increasingly dry upper layers (Fig. 3). *Polygonum cespitosum* plants showed a similar type of adaptive redeployment, but it was both slower and less pronounced (Fig. 3). As a result, after 8 weeks of growth in this dry-down soil treatment, *P. persicaria* plants had deployed on average 65% of their root systems to the lowest soil layers where water remained available, compared with 44% in *P. cespitosum* (Fig. 3). Plants of *P. persicaria* showed a sim-

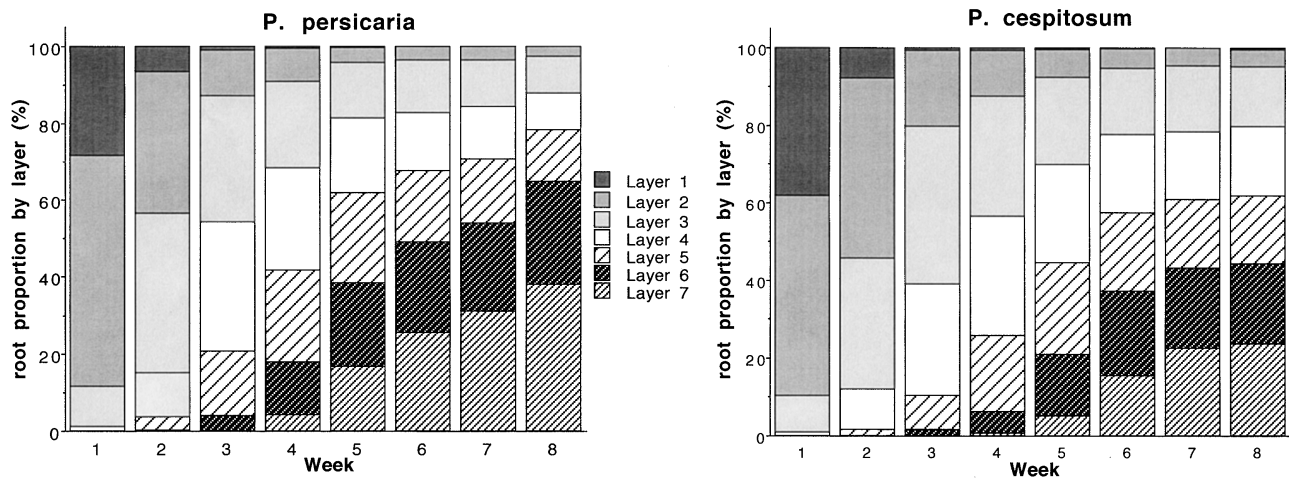


Fig. 3. Contrasting patterns of dynamic plasticity for vertical root deployment in *Polygonum persicaria* and *P. cespitosum*. Mean root deployment patterns over time of 10 inbred lines per species grown in a dry soil treatment (one replicate per line). The percent of each plant's root system located in each of seven soil layers from container top to bottom was calculated from digitized weekly root-system tracings. By week 3 of the experiment, moisture was available only in layers five to seven of the dry treatment containers. The species differed significantly in the timing and final amount of root redeployment to these moist soil layers and in root system reduction in the dry uppermost soil layers (species \times week interaction effects on root proportion within upper and lower soil layers significant at $P \leq 0.05$ and $P \leq 0.02$, respectively, based on nested repeated-measures multivariate analysis of variance for vertical root deployment). (From Bell and Sultan 1999.)

ilar capacity for rapid redeployment of roots to track spatial changes in the availability of a second critical soil resource, oxygen, in response to soil flooding. In this case, *P. persicaria* individuals rapidly and dramatically increased root deployment to the soil–air interface layer, a key way for flooded plants to maintain oxygen supply when soil pores fill with water (Etherington 1984; Blom and Voesenek 1996). Plants of *P. cespitosum* showed a significantly slower and less marked redeployment to the soil surface in response to flooding and suffered a 40% reduction in total growth compared with only 10% reduction in the flooded *P. persicaria* plants (Bell and Sultan 1999). Recall that in nature, only *P. persicaria* inhabits sites subject to either flooding or very dry conditions (Sultan et al. 1998). Thus, species' differences in the timing of ecologically important plastic responses, as well as in the magnitude of those responses, may influence their environmental tolerances and hence their realized distributions in the field.

In general, differences in the timing of plastic developmental responses may influence ecological distributions in surprisingly important ways. For example, a flood-intolerant strain of cultivated rice was found to differ from its flood-tolerant wild progenitor not in its ability to adaptively elongate in response to shoot submergence, as originally assumed, but rather in the lag time to elongation after the initial submergence cue. In the cultivated rice genotype, the shoot elongated equally, but it did so too late to ensure survival when flooding occurred early in the life cycle (Eiguchi et al. 1993). The timing of shoot elongation in response to shade may also influence plant growth and fitness, depending on

the identity and elongation characteristics of co-occurring species competing for light (Weinig 2000). In general, when environmental conditions fluctuate unpredictably, taxa that express long lag times for functionally important plastic traits may be unable to accurately match their responses to environmental demands (Kingsolver and Huey 1998; Tufto 2000). Species may also differ in the degree to which individuals alter ontogenetic timing in response to environmental conditions, directly affecting both functional success and reproduction (see Reproductive and Cross-Generational Plasticity, below).

MORPHOLOGICAL PLASTICITY

In addition to proportional allocation and dynamic developmental responses, plants express plasticity for a number of morphological traits, such as organ size and structure. One ecologically important example is the size of leaves produced in different light conditions. Given that decreased light availability inevitably reduces the total number of leaves plants produce, a second adaptive response to low light (along with increased proportional leaf biomass allocation) is to make individual leaves as large as possible under those growth limits to maximize surface area for light capture. The *Polygonum* species differed in this aspect of plasticity as well (Fig. 4): in *P. hydropiper*, a species excluded in nature from shaded sites, individuals grown in shade maladaptively decreased leaf size by 40% compared with plants in full sun, whereas light-deprived individuals of the broadly distributed *P. persicaria* maintained close to equivalent

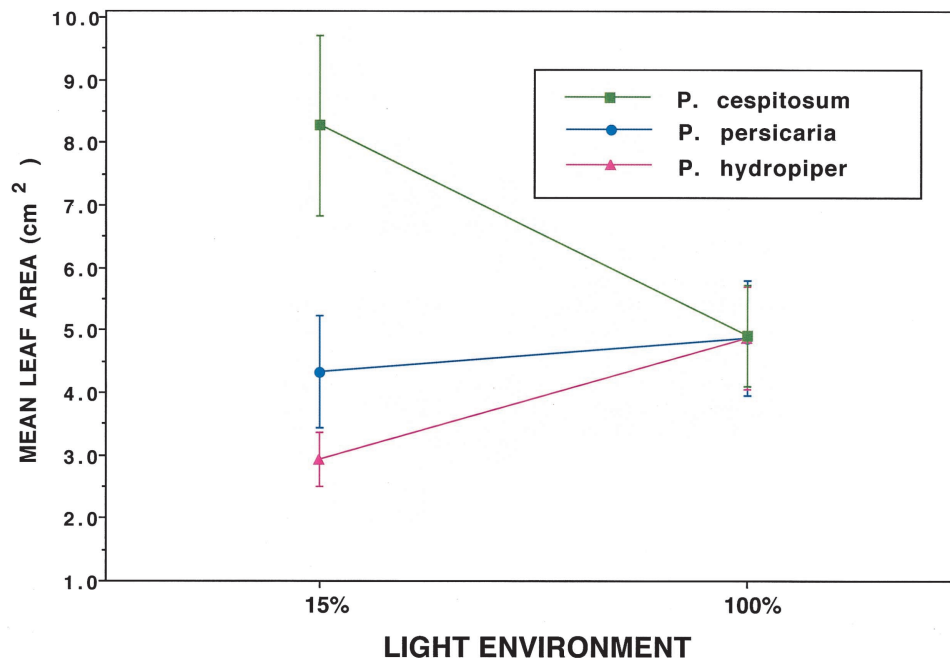


Fig. 4. Contrasting patterns of plasticity for leaf size in *Polygonum persicaria*, *P. cespitosum*, and *P. hydropiper*. Mean norms of reaction (± 2 SEs) are shown for area of individual leaves in eight inbred lines per species, based on six replicates per line raised in each of two greenhouse light treatments admitting, respectively, 15% and 100% of midsummer photosynthetically active radiation (treatment details in Sultan 2001). The species' responses differ significantly (species \times light interaction effect significant at $P \leq 0.000$ according to analysis of variance). (From S. E. Sultan and A. M. Wilczek, unpublished data.)

leaf size (statistically nonsignificant size decrease from high to low light; Fig. 4). The shade-inhabiting species, *P. cespitosum*, expressed a completely different plastic response: When grown in low light, these plants increased leaf size by nearly 70% (Fig. 4). In this case, congeneric species differed in the direction as well as the magnitude of plastic response, in ways corresponding to their differences in environmental distribution.

In addition to species-specific adjustments in leaf size, shaded plants also express developmental plasticity for leaf thickness, reflecting anatomical and ultrastructural changes that enhance the light-harvesting efficiency of leaf tissue under conditions of low photon-flux density (references in Sultan and Bazzaz 1993; Ryser and Eek 2000). Indeed, shade-induced increases in leaf specific areas are one of the most well-known and universal aspects of morphogenetic plasticity in plants (Björkman 1980; Fitter and Hay 2002). For instance, individual genotypes from two field populations of *P. persicaria* increased specific leaf area nearly 2-fold at moderate light and 2.5- to 3-fold at very low light, relative to the far thicker leaves produced at full sun (Sultan and Bazzaz 1993). Equally dramatic changes in leaf structure are also expressed by shaded individuals of *P. cespitosum*, *P. hydropiper*, and *P. lapathifolium* (S. E. Sultan and A. M. Wilczek, unpublished data), suggesting that this functionally critical aspect of plasticity may be shared among species that differ in numerous other aspects of developmental response.

An analogous type of morphogenetic plasticity occurs in root systems. Plants may decrease root diameter when grown under limiting moisture or nutrient conditions, which effectively increases the length and therefore surface area of roots for resource uptake per gram of tissue invested (Fitter and Hay 2002; Ryser and Eek 2000). Root systems of flooded plants may show one of several adaptive plastic adjustments, including the production of extremely fine superficial root systems located at the soil-air interface (Blom and Voesenek 1996) and the formation of aerenchyma tissue containing large air-filled lacunae that permit oxygen to reach submerged parts of the plant (Blom et al. 1994). Morphological plasticity in plant organs thus may reflect plastic changes to underlying anatomical traits (Dubé and Morisset 1996; Cordell et al. 1998). At the whole-plant level, environmentally induced changes in meristem initiation and fate, as well as organ and branch size and structure, can lead to plastic change in architecture (Wu and Stettler 1998; Huber et al. 1999).

REPRODUCTIVE AND CROSS-GENERATIONAL PLASTICITY

In addition to functionally important aspects of plasticity, ecological distributions are influenced by developmental adjustments to traits that directly affect reproductive success

in various environments. These traits include reproductive timing, biomass allocation to reproduction, total reproductive output, and the size and quality of offspring. Differences in these aspects of plasticity affect the abilities of diverse taxa to maintain reproduction in resource-poor stressful conditions and/or to maximize reproductive output in favorable conditions, both important elements in ecological breadth (Ford and Siegal 1989; Travis 1994; Sultan 2001). We tested these fitness-related aspects of developmental plasticity in the *Polygonum* system through a large multifactorial experiment, in which replicates of inbred lines of the four species were grown in all possible combinations of high and low light, rich and poor macronutrients, and dry, moist, and flooded soil. As with the functional traits discussed above, the *Polygonum* species differed in their patterns of reproductive plasticity in ways that may help explain their contrasting environmental distributions.

With respect to reproductive timing, the *Polygonum* species differed in the extent to which plants delayed reproduction when subjected to particular environmental stresses, compared with plants in favorable conditions. Species that express such stress-induced delays may be unable to maintain populations in habitats where those stressful conditions occur. For instance, plants of *P. lapathifolium* (a species that does not occur in shaded habitats) expressed very delayed and consequently strongly reduced reproduction in low light treatments, in contrast with shade-tolerant congeners that maintained rapid reproduction despite limited light availability (Sultan 2001). Conversely, in certain species environmentally induced changes to reproductive timing may be adaptive, as in the case of *Mimulus* plants that flower earlier when stressed (Galloway 1995). Ontogenetic plasticity may also include adaptive changes in sex expression: For instance, plants of *Solanum hirtum* adjust the proportions of staminate (functionally male) versus hermaphroditic flowers depending on their resource status (Diggle 1994).

Plasticity in total reproductive output reflects the organism's patterns of environmental response in numerous underlying characters. In some species, plants in poor growth conditions may increase proportional allocation to reproduction so as to maintain a given level of reproductive output despite reduced total biomass. The *Polygonum* data show that this type of compensatory developmental response can differ among related species (Sultan 2001 and references therein). Although to some extent negative effects of environmental stresses on total reproduction are inevitable, the magnitude of those negative effects, and the extent to which they can be avoided entirely, will thus depend on several aspects of adaptive plasticity likely to vary among species: responses in functional traits that affect plant growth and total biomass, together with positive versus negative changes in reproductive allocation. Indeed, the results of the multifactorial *Polygonum* experiment revealed complex and idiosyncratic differences in

plasticity for reproductive output (measured as total biomass of achenes, one-seeded fruits). The four species differed in both the magnitude and direction of reproductive responses to contrasting levels of light, moisture, and nutrients, as well as to specific combinations of these factor levels (Fig. 5). These complex patterns of plasticity for reproductive output may influence the species' abilities to maintain viable populations under different combinations of resource stresses in the field and hence are likely to influence their ecological distributions in quite specific ways (Sultan 2001).

Along with diverse patterns of plasticity for total reproductive output, species may differ in the effects of contrasting environments on ecologically important traits of individual offspring, such as the quantity and quality of seed provisions. The provisions stored by the maternal plant in the seed fuel the seedling's initial root and shoot extension and are therefore essential to its survival and successful establishment (Roach and Wulff 1987 and references therein). Increased provisioning enhances each offspring's probability of success, particularly in sites with dry or nutrient-poor soils or with dense competition for light, where seedlings must produce extensive root or shoot systems to gain adequate access to resources (Thompson and Hodgkinson 1998 and references therein). In certain species, resource-deprived plants express adaptive plasticity for offspring size and quality by enhancing provisioning to each seed they produce (Donohue and Schmitt 1998 and references therein). Conversely, in other species parent plants may respond to specific environmental stresses by producing smaller as well as fewer offspring (a response that exacerbates the negative effects on fitness of reduced offspring number by decreasing each offspring's chance of success; Sultan 1996).

Depending on precisely how these positive and negative provisioning changes affect offspring growth and competitive success, species differences in this *cross-generational* aspect of plasticity may significantly influence seedling establishment in particular habitats and consequently shape species' ecological distributions (Sultan 2001). For example, because *P. hydropiper* is restricted to very moist habitats whereas its congeners inhabit both moist and somewhat dry sites (Sultan et al. 1998), we were interested to know whether cross-generational effects of dry soil in *P. hydropiper* differed from those effects in the other *Polygonum* species. We found that drought-stressed *P. hydropiper* plants produced smaller, less well-provisioned offspring than did genetically identical, amply watered parent plants, whereas drought-stressed individuals of *P. persicaria*, *P. cespitosum*, and (to a lesser extent) *P. lapathifolium* all increased provisioning to produce heavier individual offspring (Fig. 6). Subsequent studies have demonstrated that these contrasting cross-generational effects on provisioning entail specific changes to seedling morphology, root extension rates, and total growth that may influence the success of seedlings in their own environments

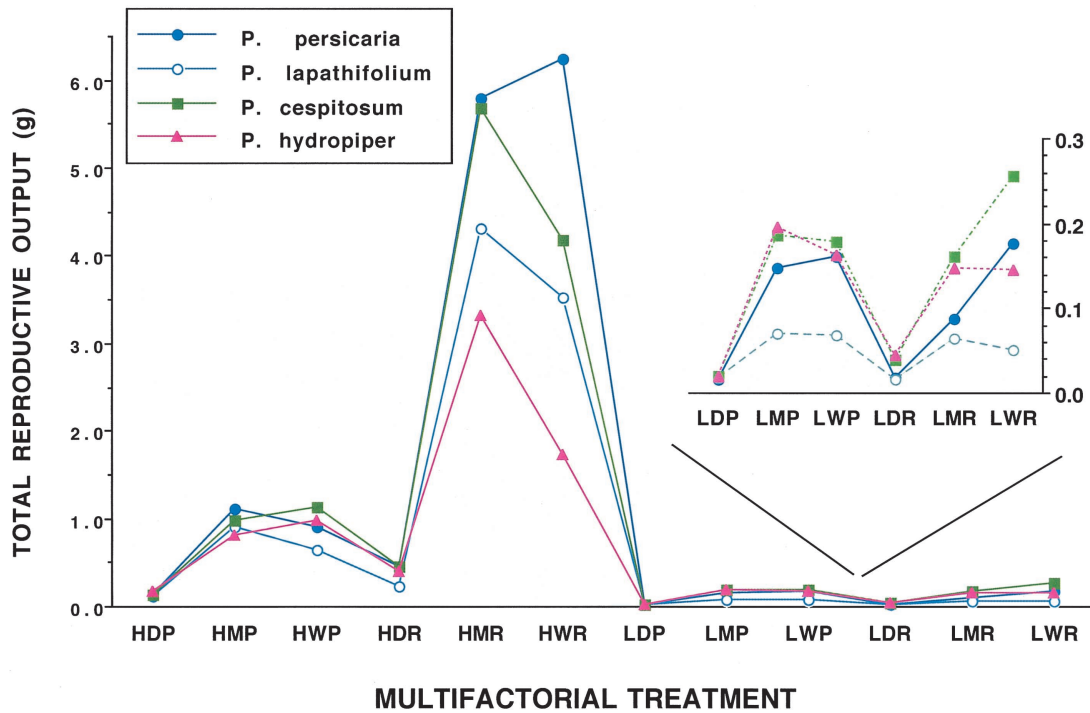


Fig. 5. Plasticity for total lifetime reproductive output (total achene biomass) in four *Polygonum* species, showing complex environmental effects. Species means shown are based on single replicates of the same eight inbred lines per multifactorial treatment in each species, in all combinations of high (H) vs. low (L) light; dry (D), moist (M), or wet (W) soil; and poor (P) vs. rich (R) macronutrients. The inset shows total achene mass of plants grown in low light treatments on an expanded scale. The species differ significantly in their patterns of response to all three environmental factors (light, moisture, and nutrients) and to all two- and three-way combinations of factors (all interaction effects of species \times environmental factor(s) are significant at $P \leq 0.005$ according to a four-way mixed analysis of variance). (From Sultan 2001.)

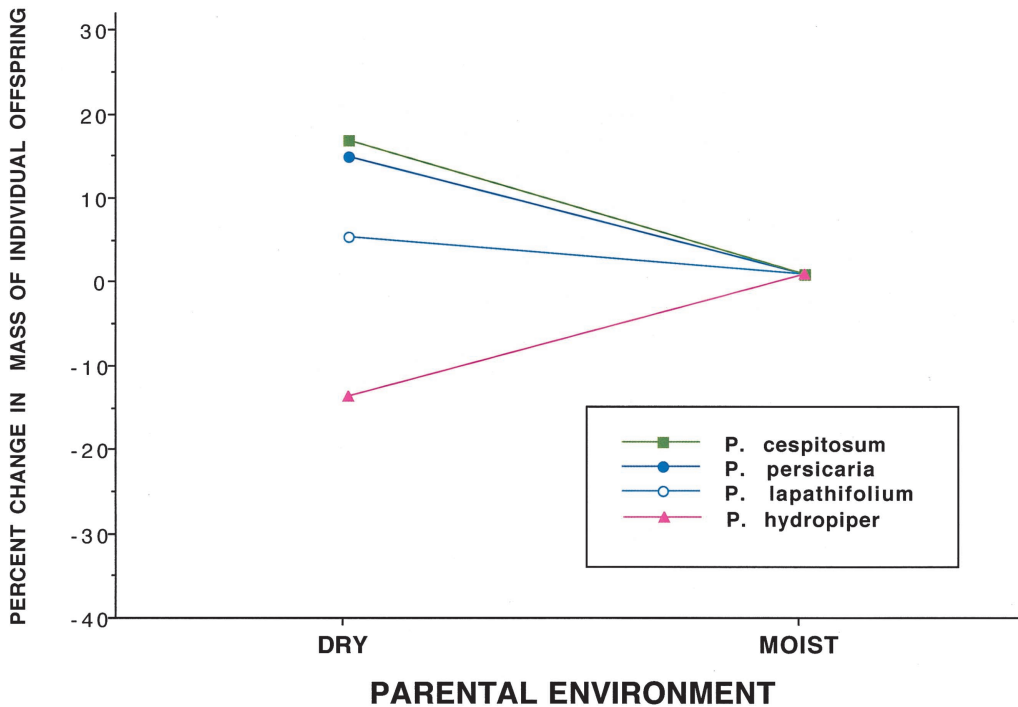


Fig. 6. Plasticity for mass of individual offspring (achenes) in four *Polygonum* species, showing contrasting patterns of change in the mean mass of offspring produced by plants of each species in dry soil relative to those produced by parent plants of the same eight inbred lines in favorable, moist soil. Plasticity is expressed as percent change to correct for average species differences in achene mass. The species differ significantly in their patterns of response (species \times moisture effect on mean achene mass significant at $P \leq 0.001$ according to four-way mixed analysis of variance). (From Sultan 2001.)

(S. Elmendorf and S. E. Sultan, unpublished data; K. Barton, S. E. Sultan, and A. M. Wilczek, unpublished data). Much remains to be learned about this extraordinary cross-generational aspect of plant plasticity and the extent to which it may confer specific adaptations on seedlings in environments similar to those of their parents (Donohue and Schmitt 1998; Sultan 2000 and references therein). Such adaptive cross-generational plasticity may be a particularly significant ecological factor in gravity-dispersed plants such as *Polygonum* and other organisms in which offspring remain close to their parents early or throughout life.

CONCLUSIONS

In the real world, the development of organisms (like other aspects of their phenotypes, such as physiology and behavior) is shaped and modulated in response to environmental circumstances. These variations in phenotypic expression have profound ecological consequences, which to date have been particularly well studied in plants. Ecologically important plant developmental responses to environment include specific adjustments to proportional tissue allocation, morphology and underlying anatomy, dynamic traits such as root deployment and ontogeny, components of reproduction, and cross-generational effects on offspring traits. Of course, organisms are integrated developmental systems, and these responses are not independent. A particular environmental stress may initiate a suite of plastic changes involving several salient aspects of development, such as the “shade avoidance syndrome” (Smith and Whitelam 1997), which includes altered allocation, stem elongation, suppressed branching, and accelerated reproduction. Furthermore, plasticity expressed early in ontogeny may constrain developmental plasticity for other aspects of the phenotype later in life (Weinig and Delph 2001).

Comparative norm of reaction studies in the genus *Polygonum* have demonstrated both the tremendous versatility of individual development and the diversity of response patterns for ecologically meaningful traits that may characterize individuals of congeneric species. Although closely related species may share patterns of plasticity for certain traits, they may also differ in the amount, direction, and timing of plastic responses to a given environmental cue. Because these response patterns are specific to particular environmental factors and indeed to particular combinations of factor levels, they influence specific aspects of environmental tolerance and hence realized distribution in the field. Thus, differences among taxa in patterns of developmental plasticity may be an important aspect of adaptive diversity contributing to their ecological narrowness or breadth.

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REFERENCES

- Allen, G. E. 1979. Naturalists and experimentalists: the genotype and the phenotype. In W. Coleman and C. Limoges (eds.), *Studies in the History of Biology*. Vol. 3. Johns Hopkins Press, Baltimore, pp. 179–209.
- Baker, H. G. 1974. The evolution of weeds. *Annu. Rev. Ecol. Syst.* 5: 1–24.
- Barata, C., Baird, D. J., and Soares, A. M. V. M. 2001. Phenotypic plasticity in *Daphnia magna*: variable maturation instar as an adaptive response to predation pressure. *Oecologia* 129: 220–227.
- Bazzaz, F. A. 1996. *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology*. Cambridge University Press, Cambridge.
- Bell, D. L., and Sultan, S. E. 1999. Dynamic phenotypic plasticity for root growth in *Polygonum*: a comparative study. *Am. J. Bot.* 86: 807–819.
- Björkman, O. 1981. Responses to different flux densities. In: O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler (eds.), *Encyclopedia of Plant Physiology*, new series Vol. 12A, *Physiol. Plant Ecology I*. Springer-Verlag, Berlin, pp. 57–107.
- Blom, C. W. P. M., and Voeseek, L. A. C. J. 1996. Flooding: the survival strategies of plants. *Trends Ecol. Evol.* 11: 290–295.
- Blom, C. W. P. M., Voeseek, L. A. C. J., Banga, M., Engelaar, W. M. H. G., Rijnders, J. H. G. M., van de Steeg, H. M., and Visser, E. J. W. 1994. Physiological ecology of river-side species: adaptive responses of plants to submergence. *Ann. Bot.* 74: 253–263.
- Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* 13: 115–155.
- Caldwell, M. M. 1994. Exploiting nutrients in fertile microsites. In M. M. Caldwell and R. W. Pearcy (eds.), *Exploitation of Environmental Heterogeneity by Plants*. Academic Press, New York, pp. 325–347.
- Chapin, F. S. III., Bloom, A. J., Field, C. B., and Waring, R. H. 1987. Plant responses to multiple environmental factors. *Bioscience* 37: 49–57.
- Cordell, S., Goldstein, G., Mueller-Dombois, D., Webb, D., and Vitousek, P. M. 1998. Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. *Oecologia* 113: 188–196.
- DeWitt, T. J., Sih, A., and Wilson, D. S. 1998. Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* 13: 1–8.
- Diggle, P. K. 1994. The expression of andromonoecy in *Solanum hirtum* (Solanaceae): phenotypic plasticity and ontogenetic contingency. *Am. J. Bot.* 81: 1354–1365.
- Donohue, K., and Schmitt, J. 1998. Maternal environmental effects in plants. In T. A. Mousseau and C. W. Fox (eds.), *Maternal Effects as Adaptations*. Oxford University Press, New York, pp. 137–158.
- Dubé, M., and Morisset, P. 1996. La plasticité phénotypique des caractères anatomiques foliaires chez le *Festuca rubra* L. (Poaceae). *Can. J. Bot.* 74: 1708–1718.
- Eiguchi, M., Sano, R., Hirano, H.-Y., and Sano, Y. 1993. Genetic and developmental bases for phenotypic plasticity in deepwater rice. *J. Hered.* 84: 201–205.
- Etherington, J. R. 1984. Comparative studies of plant growth and distribution in relation to waterlogging. X. Differential formation of adventitious roots and their experimental excision in *Epilobium hirsutum* and *Chamerion angustifolium*. *Journal of Ecology* 72: 389–404.
- Fitter, A. H. 1994. Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In M. M. Caldwell and R. W. Pearcy (eds.), *Exploitation of Environmental Heterogeneity by Plants*, Academic Press, New York, NY, pp. 305–323.
- Fitter, A. H., and Hay, R. 2002. *Environmental Physiology of Plants* (3rd edition). Academic Press, San Diego, CA.
- Ford, N. B., and Seigel, R. A. 1989. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. *Ecology* 70: 1768–1774.

- Galloway, L. F. 1995. Response to natural environmental heterogeneity: maternal effects and selection on life-history characters and plasticities in *Mimulus guttatus*. *Evolution* 49: 1095–1107.
- Gilbert, S. F. 2001. Ecological developmental biology: developmental biology meets the real world. *Dev. Biol.* 233: 1–12.
- Griffith-Simon, C., and Sheldon, B. C. 2001. Phenotypic plasticity in the expression of sexually selected traits: neglected components of variation. *Anim. Behav.* 6: 987–993.
- Gross, L. J. 1989. Plant physiological ecology: a theoretician's perspective. In R. M. May, J. Roughgarden, and S. A. Levin (eds.), *Perspectives in Ecological Theory*. Princeton University Press, Princeton, NJ, pp. 11–24.
- Hammond, K. A., Szweczek, J., and Krol, E. 2001. Effects of altitude and temperature on organ phenotypic plasticity along an altitudinal gradient. *J. Exp. Biol.* 204: 1991–2000.
- Huber, H., Lukacs, S. and Watson, M. A. 1999. Spatial structure of stoloniferous herbs: an interplay between structural blue-print, ontogeny and phenotypic plasticity. *Plant Ecol.* 141: 107–115.
- Jordan, M. A., and Snell, H. 2002. Life history trade-offs and phenotypic plasticity in the reproduction of Galapagos lava lizards (*Microlophus delanonis*). *Oecologia* 130:44–52.
- Kingsolver, J. G., and Huey, R. B. 1998. Evolutionary analysis of morphological and physiological plasticity in thermally variable environments. *Am. Zool.* 38: 545–560.
- Negovetic, S., and Jokela, J. 2001. Life-history variation, phenotypic plasticity, and subpopulation structure in a freshwater snail. *Ecology* 82: 2805–2815.
- Oliva, G., Martinez, A., Collantes, M., and Dubcovsky, J. 1993. Phenotypic plasticity and contrasting habitat colonization in *Festuca pallescens*. *Can. J. Bot.* 71: 970–977.
- Pianka, E. 1988. *Evolutionary Ecology*. 4th Edition. Harper and Row, New York.
- Pigliucci, M. 2001. *Phenotypic Plasticity: Beyond Nature and Nurture*. Johns Hopkins University Press, Baltimore.
- Relyea, R. A. 2002. Local population differences in phenotypic plasticity: predator-induced changes in wood frog tadpoles. *Ecol. Monogr.* 72: 77–93.
- Roach, D. A., and Wulff, R. D. 1987. Maternal effects in plants. *Annu. Rev. Ecol. Syst.* 18: 209–235.
- Rodrigues, M. L., Pacheco, C. M. A., and Chaves, M. M. 1995. Soil-plant water relations, root distribution, and biomass partitioning in *Lupinus albus* L. under drought conditions. *J. Exp. Bot.* 46: 947–956.
- Ryser, P., and Eek, L. 2000. Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of above-ground and belowground resources. *Am. J. Bot.* 87: 402–411.
- Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* 24: 35–68.
- Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. *Annu. Rev. Ecol. Syst.* 17: 667–693.
- Schlichting, C. D., and Pigliucci, M. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer Associates, Sunderland, MA.
- Schmitt, J., Dudley, S. A., and Pigliucci, M. 1999. Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade-avoidance responses in plants. *Am. Nat.* 154: S43–S54.
- Smith, H., and Whitelam, G. C. 1997. The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. *Plant, Cell and Environment* 20: 840–844.
- Stebbins, G. L. 1980. Botany and the synthetic theory of evolution. In E. Mayr and W.B. Provine (eds.), *The Evolutionary Synthesis*. Harvard University Press, Cambridge, pp. 139–152.
- Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evol. Biol.* 21: 127–178.
- Sultan, S. E. 1992. Phenotypic plasticity and the neo-Darwinian legacy. *Evol. Trends Plants* 6: 61–71.
- Sultan, S. E. 1995. Phenotypic plasticity and plant adaptation. *Acta Bot. Neerl.* 44 (Special Plants and Evolution Jubilee issue): 363–383.
- Sultan, S. E. 1996. Phenotypic plasticity for offspring traits in *Polygonum persicaria*. *Ecology* 77: 1791–1807.
- Sultan, S. E. 2000. Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci.* 5: 537–542.
- Sultan, S. E. 2001. Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. *Ecology* 82: 328–343.
- Sultan, S. E., and Bazzaz, F. A. 1993. Phenotypic plasticity in *Polygonum persicaria*. I. Diversity and uniformity in genotypic norms of reaction to light. *Evolution* 47: 1009–1031.
- Sultan, S. E., and Spencer, H. G. 2002. Metapopulation structure favors plasticity over local adaptation. *Am. Nat.* 160: 271–283.
- Sultan, S. E., Wilczek, A. M., Hann, S. D., and Brosi, B. J. 1998. Contrasting ecological breadth of co-occurring annual *Polygonum* species. *J. Ecol.* 86: 363–383.
- Thompson, K., and Hodgkinson, D. J. 1998. Seed mass, habitat, and life history: a re-analysis of Salisbury (1942, 1974). *New Phytol.* 138: 163–176.
- Travis, J. 1994. Ecological genetics of life-history traits: variation and its evolutionary significance. In L. Real (ed.), *Ecological Genetics*. Princeton University Press, Princeton, NJ, pp. 171–204.
- Tufto, J. 2000. The evolution of plasticity and nonplastic spatial and temporal adaptations in the presence of imperfect environmental cues. *Am. Nat.* 156: 121–130.
- Weinig, C. 2000. Differing selection in alternative competitive environments: shade-avoidance responses and germination timing. *Evolution* 54: 124–136.
- Weinig, C., and Delph, L. F. 2001. Phenotypic plasticity early in life constrains developmental responses later. *Evolution* 55: 930–936.
- Williams, D. G., Mack, R. N., and Black, R. A. 1995. Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. *Ecology* 76: 1569–1580.
- Wu, R., and Stettler, R. F. 1998. Quantitative genetics of growth and development in *Populus*. III. Phenotypic plasticity of crown structure and function. *Heredity* 81: 299–310.