

Research review

Maternal effects provide phenotypic adaptation to local environmental conditions

Author for correspondence:
Laura F. Galloway
Tel: +1 434 982 5010
Fax: +1 434 982 5626
Email: lgalloway@virginia.edu

Received: 6 August 2004
Accepted: 1 November 2004

Laura F. Galloway

Department of Biology, University of Virginia, Charlottesville VA, 22904–4328, USA

Summary

Key words: adaptive plasticity, environmental heterogeneity, intergenerational plasticity, maternal effects, patch size, phenotypic adaptation, seed dispersal.

In outcrossing plants, seed dispersal distance is often less than pollen movement. If the scale of environmental heterogeneity within a population is greater than typical seed dispersal distances but less than pollen movement, an individual's environment will be similar to that of its mother but not necessarily its father. Under these conditions, environmental maternal effects may evolve as a source of adaptive plasticity between generations, enhancing offspring fitness in the environment that they are likely to experience. This idea is illustrated using *Campanula americana*, an herb that grows in understory and light-gap habitats. Estimates of seed dispersal suggest that offspring typically experience the same light environment as their mother. In a field experiment testing the effect of open vs understory maternal light environments, maternal light directly influenced offspring germination rate and season, and indirectly affected germination season by altering maternal flowering time. Results to date indicate that these maternal effects are adaptive; further experimental tests are ongoing. Evaluating maternal environmental effects in an ecological context demonstrates that they may provide phenotypic adaptation to local environmental conditions.

New Phytologist (2005) **166**: 93–100

© *New Phytologist* (2005) doi: 10.1111/j.1469-8137.2004.01314.x

Introduction

Environmental variation is ubiquitous at a range of spatial scales. However, sessile organisms, such as plants, typically experience a single environment throughout their lives. They may be exposed to other environments between generations through the dispersal of pollen and seeds, or through changes in the local environment. Plants often respond to environmental variation with phenotypic plasticity. This environmentally induced change

in trait expression may represent a passive response to resource limitation, for example reduced biomass under limited light conditions. However more typically, plasticity is a functionally appropriate adjustment of the phenotype that acts to enhance fitness under current environmental conditions (e.g. Dudley & Schmitt, 1996; Weinig, 2000; Van Kleunen & Fischer, 2003). For example, increasing allocation to leaf tissue under limited light conditions will enhance resource uptake, and increase reproductive output relative to individuals that

maintain the same allocation pattern. This adaptive plasticity is the product of selection for different genetically based trait values in different environments.

Plastic response to the environment may extend to an individual's offspring, influencing offspring trait expression. Both paternal and maternal environments may contribute to transgenerational plasticity, although maternal effects are typically greater in magnitude than paternal effects (e.g. Schmid & Dolt, 1994; Lacey, 1996; Etterson & Galloway, 2002). This is because in addition to the prezygotic environmental effects that both parents contribute, the offspring's early growth takes place on the maternal plant. The maternal environment may influence the phenotype of the offspring directly, through maternal provisioning, or through plasticity of traits in the maternal plant that influence offspring trait expression (Roach & Wulff, 1987; Donohue & Schmitt, 1998). As an example of the latter, maternal branching pattern in *Cakile edentula* influences offspring dispersal distance and that, in turn, determines offspring density and consequently branching architecture (Donohue, 1999). Here I focus on these maternal environmental effects but use the phrase interchangeably with maternal effects, although the latter is more broadly defined (Mousseau & Fox, 1998).

Maternal environmental effects may provide adaptive plasticity across generations (Mousseau & Fox, 1998). Adaptive maternal effects, like phenotypic plasticity, are expected to evolve as a mechanism to ameliorate factors that reduce offspring fitness in specific environments. For example, offspring of *Polygonum persicaria* grown under low light allocate proportionately more resources to shoot growth than those from higher light parents, and offspring of limited-nutrient plants allocate proportionately more to root growth than genetically similar individuals with nutrient-rich parents (Sultan, 1996). Three conditions must be met for the evolution of adaptive maternal effects (Donohue & Schmitt, 1998). First, the maternal environment must predict the progeny environment. Second, maternal environmental effects must enhance the fitness of the offspring and parent generations. Third, there must be genetic variation in maternal effects (i.e. maternal genotype–maternal environment interaction). In plants, there is abundant evidence for genetic variation in maternal environmental effects (Donohue & Schmitt, 1998). However, there is less evidence that parental and progeny environments are correlated or that maternal effects are adaptive. The latter is in part because few studies have grown both parental and offspring generations in natural environments. Although potentially adaptive maternal effects have been found when either the parental (Schmitt *et al.*, 1992; Galloway, 1995), or offspring (Lacey & Herr, 2000; Galloway, 2001b), generation was grown in nature.

Here I combine the conditions required for adaptive maternal effects with a discussion of the ecological context in which these traits evolve to develop the idea that maternal effects may provide phenotypic adaptation to local habitats. I then illustrate

these concepts using my research on *Campanula americana*. My approach complements a recent review describing how maternal effects provide habitat selection (Donohue, 2003).

Gene dispersal and adaptive maternal effects

The movement of pollen among individuals in a population results in a common gene pool and therefore virtually no opportunity for genetic specialization to local environments within populations. In outcrossing plants, gene movement via pollen is typically greater than that through seed (Levin & Kerster, 1974; McCauley, 1994). Wind and insect vectors may carry pollen throughout a population; however, seed dispersal is often restricted to sites near the maternal plant. Because the spatial scale of pollen and seed movement is different, the patch size that results in dispersal within environments is also expected to differ. In particular, environmental variation that is patchy at a scale that encompasses most seed dispersal, but not necessarily pollen movement, results in individuals that experience an environment similar to their mother but perhaps not their father. If local environments are predictable across generations, environmental maternal effects represent a mechanism by which maternal plants can adjust the phenotype of their offspring to enhance its success in the environment that it is likely to encounter. If seeds happen to disperse into a different habitat patch, environmental maternal effects may miscue offspring trait expression for that location and reduce fitness. However, fitness will be reduced for only a single generation because the plastic response of individuals to the new habitat will induce appropriate maternal effects.

Strictly genetic adaptation, that is a fixed maternal strategy, is expected when environmental variation is at a greater spatial scale than the movement of both pollen and seeds. This is often found between populations with the genetic differentiation referred to as local adaptation (Linhart & Grant, 1996). Pollen dispersal between environments or habitats will instead favor the evolution of adaptive plasticity (e.g. Tufto, 2000; Sultan & Spencer, 2002). By enhancing performance in the environments individuals experience, this plasticity provides phenotypic adaptation. Therefore, in a population occupying a heterogeneous environment, restricted seed dispersal and continuity of habitat patches between generations will select for maternal environmental effects to provide phenotypic adaptation to local environmental conditions.

Maternal environmental effects in an ecological context

To date most research on maternal effects has focused on elucidating patterns of offspring response to maternal environments. Studies have demonstrated most environments elicit maternal effects (Roach & Wulff, 1987), that these effects are environment-specific (Sultan, 1996; Rossiter, 1998; Galloway, 2001a) with their expression often depending on the offspring environment (Schmitt *et al.*, 1992; Munir *et al.*, 2001), and

that maternal effects are expressed throughout the life cycle and may persist for several generations (Alexander & Wulff, 1985; Miao *et al.*, 1991; Case *et al.*, 1996; Lacey & Herr, 2000). However, maternal effects must be studied in an ecological context to establish whether or not they are adaptive.

What attributes of a population are expected to influence the likelihood that maternal effects will evolve as a source of phenotypic adaptation to local environments? One characteristic is the size of habitat patches. For example, soil nutrients may vary over very small spatial scales (10 cm; Lechowicz & Bell, 1991), and individual fitness and selection may also fluctuate in response to microenvironmental variation (Stratton & Bennington, 1998). We do not expect adaptive maternal effects to such fine scale and temporally variable environments because offspring often won't encounter maternal environments. However, populations may span distinct soil nutrient habitats (e.g. serpentine outcrops), water regimes, or light environments (e.g. forest understory and light gaps). Here the environmental differences are at a large enough spatial scale to encompass seed dispersal and are predictable between generations, providing appropriate conditions for the evolution of maternal effects that result in phenotypic adaptation. The frequency of habitat patches will also influence the evolution of adaptive maternal effects. Adaptive cross-generation plasticity is unlikely to evolve in response to rare habitats, even if they represent strong selection, because only a small portion of the gene pool will experience these environments. Selection is expected to mould adaptive responses to common environments encountered by many individuals. As a consequence, maternal environmental effects that enhance fitness are less likely in response to extreme drought, novel temperature, or elevated CO₂ levels, than to more mundane environmental variation.

What aspects of the maternal plant influence the likelihood that maternal environmental effects will serve as a source of phenotypic adaptation? One of the most important attributes is the range of seed dispersal. For plants where long distance seed dispersal is common, the maternal environment may not be a very good predictor of the offspring environment. Therefore maternal effects that convey adaptations to specific environments are less likely to evolve. (The exception is where the maternal plant directs dispersal to a specific habitat; Donohue, 2003.) Mating system is a second attribute that will influence the importance of maternal effects in adaptive evolution. In obligately selfing species with limited seed dispersal, the limited movement of both pollen and seeds is expected to favor genetic specialization to local environments (e.g. Schmitt & Gamble, 1990). Whereas in species where gene movement by pollen occurs across habitats, maternally determined trait expression will more effectively confer adaptation to local environments.

Several studies provide evidence suggesting maternal effects serve as a source of phenotypic adaptation to local environments. For example, *P. lanceolata* is found in mowed and

long-grass areas. Offspring of individuals from unmowed areas have greater fitness than those from mowed areas in both habitats (Donohue & Schmitt, 1998). However, the cumulative fitness, considering both parent and offspring generations, is greatest when offspring are planted into their maternal environment. Similarly, Hangelbroek *et al.* (2003) found local adaptation of an aquatic macrophyte to substrate type (clay vs sand) was mediated by maternally determined tuber size. In both cases, the study of maternal effects in an ecological context permitted a better understanding of their contribution to adaptive evolution.

Maternal effects as phenotypic adaptation to local environments: a case study

I will use our work on *Campanula americana*, an understory forest herb, as an example of how maternal effects may serve as a source of phenotypic adaptation to local environmental conditions. *Campanula americana* L. (= *Campanulastrum americana* Small) individuals grow as either annuals or biennials; the life history schedule is determined by the season of germination (Baskin & Baskin, 1984). Vegetative rosettes require a cold period to induce flowering, therefore seedlings that germinate in the fall are vernalized immediately, bolting and flowering the following summer as annuals. However, plants from spring germinating seeds grow for a season and flower their second summer as biennials. Annual and biennial plants co-occur, flowering at the same time, and an individual's seeds may germinate in either or both seasons. In addition to life span, annuals and biennials may differ in fecundity and experience different patterns of selection because they differ in age and size (cf. Donohue, 2002). Maternal effects may be important in the evolution of *C. americana* because timing of germination, like most seed traits (Roach & Wulff, 1987), is likely to be maternally influenced and has profound consequences for individual life history and fitness.

Campanula americana populations are often found in habitats where light is a patchily distributed resource. In southwestern Virginia, populations typically span distinct light environments with some individuals growing under the forest canopy and others in light gaps or road cuts. Understory individuals receive no direct sun while plants in gap areas are typically in full sun for part of the day. Light availability in gaps ranges from eight times that of under-canopy areas in the early morning, to 50 times greater in the afternoon (J. R. Etterson & L. F. Galloway, unpublished). Individuals are rarely found in complete full sun, and these plants exhibit signs of stress including short stature, reduced foliage and branching, and expression of anthocyanin in the leaves and stems. In light gaps *C. americana* are on average 10 times larger than under the forest canopy (mean biomass \pm SE of full-sibs grown in gap areas 8.27 ± 0.82 g, $n = 70$, and under canopy 0.57 ± 0.06 g, $n = 68$; see also Galloway, 2001a). In addition, the specific leaf

area for these gap plants was half that of the individuals under the forest canopy (L. F. Galloway & J. R. Etterson, unpublished). Larger specific leaf area is associated with thinner leaves and is a classic plastic response to reduced light (Björkman, 1981, e.g. Steinger *et al.*, 2003).

To evaluate whether adaptive maternal effects are likely to be found in response to local light environments, we first need to know whether maternal habitats predict offspring habitats. Specifically, what is the scale of seed dispersal in relation to light gap size? and are these habitats predictable between generations? Seed dispersal in *C. americana* occurs in late summer following the opening of four pores at the top of each capsule. Seeds have no special dispersal structures and passively fall out when the wind blows or animals jostle the plants. Therefore primary seed dispersal is expected to be limited (< 1 m). However, secondary dispersal (seed movement once on the ground) may exceed primary dispersal because *C. americana* is frequently found in steep areas and seeds may move downhill, especially during rainfall. We measured secondary seed dispersal by establishing 10 plots in a natural population growing on an incline and 10 plots in a level area 3.6 km away. Plots in both sites were located in areas without leaf litter. We included the two sites to determine the extent to which incline influences secondary seed dispersal. At two times in the growing season 400 seeds were placed in the center of each plot. Seeds are small (*c.* 1.4 mm long) and therefore we lightly coated them with fluorescent spray paint to make them easier to find. About 2 wk later we carefully searched each plot at night using a black light and marked seed locations.

We found secondary seed movement is limited (Fig. 1). On the sloped site, not surprisingly, most seeds (83%) moved downhill. The maximum distance moved was 1.45 m, while the median distance was 0.26 m. On the level site the maximum seed movement was slightly less, 0.81 m, but the median distance was similar, 0.20 m. Although secondary dispersal may continue until seeds germinate, further seed movement may be reduced by leaf litter or obstacles (e.g. rocks, sticks). Light areas in natural populations range from gaps *c.* 12 m in diameter to stream and road cuts that run the length of populations (pers. obs.). Therefore even with additional movement, seed dispersal is typically on a smaller scale than light patches. As a consequence, while gene movement through insect-vectored pollen is undoubtedly substantial in this highly outcrossing species (Galloway *et al.*, 2003), seeds are likely to remain in their mother's light environment. Therefore selection may increase the frequency of maternal environmental effects that enhance offspring fitness in maternal light habitats.

We conducted two studies to investigate whether maternal effects associated with plastic responses to light affect offspring trait expression. In the first, seeds were created on *C. americana* grown in a glasshouse under full sun ('high'), 30% neutral shade ('medium'), and 73% neutral shade ('low'). The seeds were planted into an understory area of their home

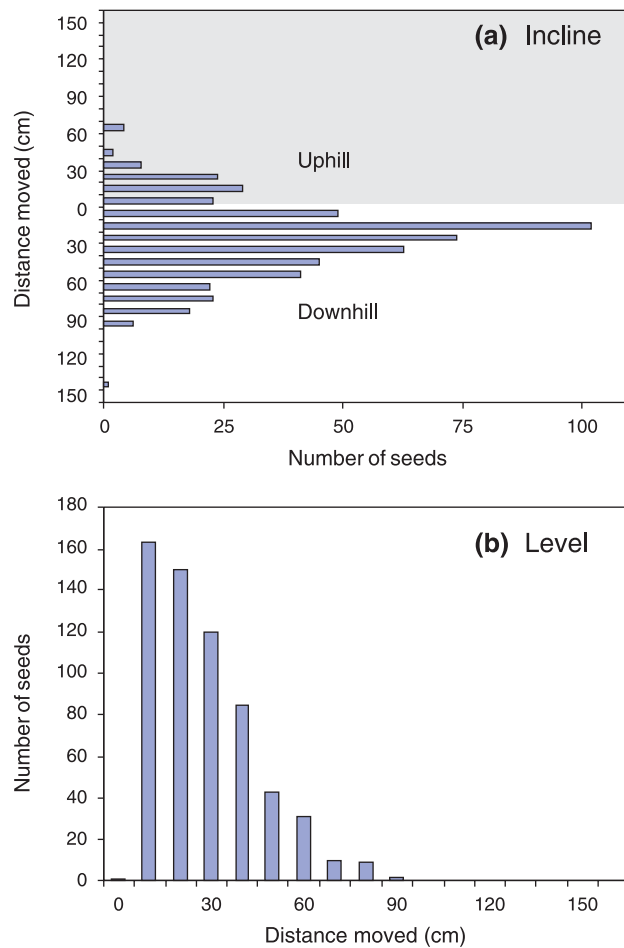


Fig. 1 Secondary seed dispersal distance in *Campanula americana*. Seed movement over *c.* 2 wk was measured (a) both uphill and downhill in a natural population and (b) in a nearby level site. Note that the axes differ between the plots.

population and a nearby site with a similar light regime. We then scored germination during the fall and spring (Galloway, 2001b). We found the germination of seeds produced on medium-light mothers was relatively unbiased between seasons. By contrast, seeds from maternal plants grown under either high or low light conditions were more likely to germinate in the spring than the fall (Fig. 2; Galloway, 2001b). In addition when seeds were grown under controlled conditions, the effect of maternal light on timing of germination was analogous to that found in the field and it varied among families (maternal family*maternal light; Galloway, 2001a). These results demonstrate that maternal light environment influences offspring season of germination and therefore life history schedule, and that these maternal effects are genetically variable. However, the interpretation of this study is limited for two reasons. First, maternal plants experienced differences in light quantity but not light quality (i.e. red: far-red ratio). Light quantity and quality typically covary (Smith, 1982) and adaptive plasticity to light quality has been found in other

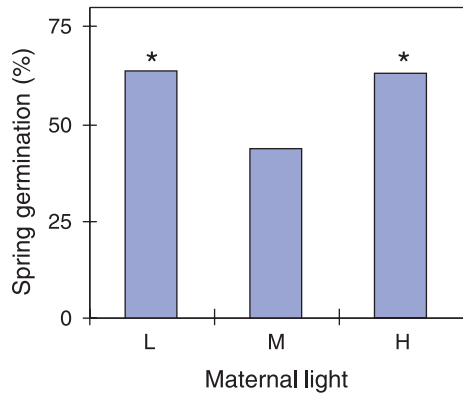


Fig. 2 Percentage of *Campanula americana* seedlings that germinated in the spring for seeds produced under three maternal light environments and planted into the field. Spring germination of 50% indicates no seasonal bias, while > 50% reflects a majority of germination in the spring (*, $P < 0.05$). Modified from Galloway (2001b).

studies (e.g. Schmitt *et al.*, 2003). Second, the offspring were planted into a uniform light environment, therefore it was not possible to determine whether the observed maternal effects were adaptive.

To address these limitations, we conducted a second study in which both generations were grown under natural conditions. The aim of this experiment was first to establish patterns of maternal effects elicited by natural variation in light availability, and second to determine whether these maternal effects enhance the fitness of offspring when grown in the mother's environment. This study is ongoing and therefore I provide a preliminary summary here. Individuals of 70 full-sib families were planted into light gap and understory regions of a natural population to serve as maternal plants. Additional plants were grown in the light gap for use as pollen donors. When the plants flowered, gap and canopy siblings were pollinated with the same pollen donor. This resulted in offspring that were genetically similar (full-sib mothers, the same father) but produced in different maternal light environments. The offspring were planted into both gap and canopy regions of the population just before natural fruit ripening the following year and were scored for germination in the fall and spring.

The influence of maternal light environment on rate of fall germination depended on the offspring light environment (log-linear analysis: offspring light*maternal light $\chi^2 = 24.69$, d.f. = 1, $P < 0.001$). In the fall, twice as many seeds germinated in the light gap if their mother had grown in the gap. Similarly, in the understory twice as many seeds germinated if their mother had also grown under the forest canopy (L. F. Galloway & J. R. Etterson, unpublished). Therefore rates of fall germination were greater when the offspring environment matched the maternal environment. Probability of germination is an important fitness component, and for this stage of the life cycle offspring fitness was greater in their maternal habitat. Maternal environment also influenced season of germination (log-linear analysis: maternal light*season $\chi^2 =$

7.77, d.f. = 1, $P < 0.005$). Fall germination was greater for seeds produced on plants grown in the sun while spring germination was greater for seeds produced on plants grown in the shade (L. F. Galloway & J. R. Etterson, unpublished). To fully evaluate the extent to which these maternal light effects are adaptive we need to estimate offspring survivorship and fecundity in light gap and canopy regions of the population; this work is currently underway.

Maternal flowering time may also influence offspring trait expression. In *C. americana* the date a flower is open is strongly correlated with the date of fruit maturation from that flower ($r_s = 0.88$, $n = 134$, $P < 0.001$; Galloway, 2002). Therefore early flowering plants mature their seeds earlier than late flowering plants. Might the timing of fruit maturation influence offspring season of germination and consequently life history schedule? To answer this question, flowers were labeled every 5 d on plants in a natural population. Fruits were harvested when mature and the seeds grouped into early ripening fruit, intermediate-ripening fruit, and late-ripening fruit. Each group was planted shortly after they were harvested and germination was monitored in the fall and spring (Galloway, 2002). Flowering date was strongly associated with offspring season of germination. Early planted seeds from early season flowers were more likely to germinate in the fall than late-planted seeds from late-season flowers (Fig. 3; germination season*planting time $\chi^2 = 8.03$, d.f. = 2, $P < 0.018$; Galloway, 2002). Seeds from flowers produced throughout the season did not differ in germination timing under controlled conditions (Galloway, 2002). Therefore the difference in season of germination of seeds from early and late flowers was not due to intrinsic factors. Greater fall germination of seeds from early season flowers was probably due to the longer period of time that seeds were available for germination before the onset of winter, and/or temperature and moisture conditions more

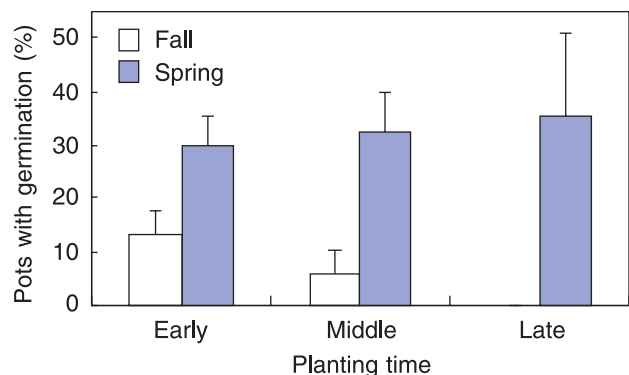


Fig. 3 The percentage of pots with seeds germinating in the fall and spring when seeds from plants in a natural *Campanula americana* population were planted as they matured. Because the time in the season that a flower is open is positively correlated with when it produces a mature fruit, early planted seeds are from early season flowers, while late-planted seeds are from late season flowers. Modified from Galloway (2002).

favorable for germination early in the fall. In summary, offspring life history schedule is determined in part by maternal flowering time with early flowering plants giving rise to more annual offspring than later flowering plants.

Flowering time exhibits plasticity in response to light availability. Plants in light gaps initiate flowering earlier than plants under the forest canopy. For example, the full-siblings discussed above flowered on average 10 d earlier when planted in the light gap than under the canopy ($t = 4.94$, d.f. = 123, $P < 0.001$; L. F. Galloway & J. R. Etterson, unpublished). Although this may result in some early season assortative mating, plants in both habitats largely overlap in their flowering phenology because the flowering season is 4–6 wk long (Galloway, 2002). Because flowering date is associated with the timing of fruit maturation and offspring germination season, maternal light environment may influence offspring life history schedule via its effect on maternal flowering time. Specifically, plants growing in light gaps will produce their seeds before plants growing under the forest canopy and these early produced seeds have a greater opportunity to germinate in the fall as annuals. Variation in flowering time is in part genetically controlled (L. F. Galloway, J. R. Etterson & K. S. Burgess, unpublished), and we are currently evaluating the potential for selection to mould life history schedule by acting directly on season of germination, a maternally inherited trait, as well as on the maternal trait, flowering time (e.g. Wolf *et al.*, 1998).

Our studies of the effect of maternal light environment on germination proportion and season reveal that a single environmental factor may create maternal effects through several mechanisms in *C. americana*. Fall germination was greater for seeds planted into their mother's light environment. In addition, fall germination was greatest for seeds produced on maternal plants grown in the sun, and spring germination greatest for seeds from shade-grown mothers. These maternal effects were all due to intrinsic differences in the seeds because all seeds were planted at the same time. Differences in phenology with earlier produced seeds in light gaps and later produced seeds under the canopy are likely to exacerbate the intrinsic differences in germination season between the seeds from the two maternal environments. Together the direct effects of the maternal light environment and the indirect effects, acting through flowering time, are expected to enhance the production of annual offspring in gap regions and biennials in the understory of the population. To understand the adaptive role of these maternal effects we must evaluate the fitness differences of annuals and biennials in each light habitat (e.g. Wardle, 1998). Other studies have shown that individuals of semelparous species with indeterminate life spans (i.e. facultative biennials) are typically longer lived under resource-limited conditions (e.g. Werner, 1975). If this is also true for *C. americana*, the fitness of biennials may be greater than that of annuals in the light-limited forest understory, matching the environments where they tend to be produced.

Conclusions

Environments within plant populations are often patchy and plants respond to this variation with plasticity. When the scale of seed dispersal is less than that of the habitat patches, offspring environments will be similar to maternal environments. These conditions favor the evolution of adaptive maternal effects. A review of our work on *C. americana* found that: first, offspring light environments are similar to maternal light environments; second, maternal light effects may enhance offspring fitness, both by increasing germination success of offspring when planted into their maternal environment and by influencing offspring season of germination and therefore life history schedule; and third, that these maternal effects are genetically variable. Although further data are required, these preliminary results support the idea that maternal effects enhance performance in habitat patches that their offspring are likely to experience. To understand the generality of these results it is necessary for future studies to consider the ecological context in which plasticity and maternal effects are expressed. This includes evaluating patterns of environmental heterogeneity in natural populations and intra- and intergenerational responses to this heterogeneity.

Acknowledgements

I thank Travis Brown for collecting the seed dispersal data; Julie Etterson for many discussions on maternal effects; Mountain Lake Biological Station for logistical support; and K. Donohue, E. Nagy, D. Roach, S. Sultan and two anonymous reviewers for comments on earlier versions of this manuscript. This work was funded by NSF DEB-9752947, DEB-9974126, DEB-0316298, and REU-sites grant DBI-0097249 to MLBS.

References

- Alexander HM, Wulff RD. 1985. Experimental ecological genetics in *Plantago*. X. The effects of maternal temperature on seed and seedling characters in *P. lanceolata*. *Journal of Ecology* 73: 271–282.
- Baskin JM, Baskin CC. 1984. The ecological life cycle of *Campanula americana* in northcentral Kentucky. *Bulletin of the Torrey Botanical Club* 111: 329–337.
- Björkman O. 1981. Responses to different quantum flux densities. In: Lange OL, Nobel PS, Osmond CB, Ziegler H, eds. *Encyclopedia of Plant Physiology*, Vol. 12A, Berlin, Germany: Springer, 57–107.
- Case AL, Lacey EP, Hopkins RG. 1996. Parental effects in *Plantago lanceolata* L. II. Manipulation of grandparental temperature and parental flowering time. *Heredity* 76: 287–295.
- Donohue K. 1999. Seed dispersal as a maternally influenced character: mechanistic basis of maternal effects and selection on maternal characters in an annual plant. *American Naturalist* 154: 674–689.
- Donohue K. 2002. Germination timing influences natural selection on life-history characters in *Arabidopsis thaliana*. *Ecology* 83: 1006–1016.
- Donohue K. 2003. Setting the stage: Phenotypic plasticity as habitat selection. *International Journal of Plant Science* 164: S79–S92.
- Donohue K, Schmitt J. 1998. Maternal environmental effects in plants: adaptive plasticity?. In: Mousseau TA, Fox CW, eds. *Maternal Effects as Adaptations*. Oxford, UK: Oxford University Press, 137–158.

- Dudley SA, Schmitt J. 1996. Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *American Naturalist* 147: 445–465.
- Etterson JR, Galloway LF. 2002. The influence of light on paternal plants in *Campanula americana* (Campanulaceae): pollen characteristics and offspring traits. *American Journal of Botany* 89: 1899–1906.
- Galloway LF. 1995. Response to natural environmental heterogeneity: maternal effects and selection on life-history characters and plasticities in *Mimulus guttatus*. *Evolution* 49: 1095–1107.
- Galloway LF. 2001a. The effect of maternal and paternal environments on seed characters in the herbaceous plant, *Campanula americana* (Campanulaceae). *American Journal of Botany* 88: 832–840.
- Galloway LF. 2001b. Parental environmental effects on life history in the herbaceous plant *Campanula americana*. *Ecology* 82: 2781–2789.
- Galloway LF. 2002. The effect of maternal phenology on offspring life history in the herbaceous plant *Campanula americana*. *Journal of Ecology* 90: 851–858.
- Galloway LF, Etterson JR, Hamrick JL. 2003. Outcrossing rates and inbreeding depression in the herbaceous autotetraploid *Campanula americana*. *Heredity* 90: 308–315.
- Hangelbroek HH, Santamaria L, de Boer T. 2003. Local adaptation of the pondweed *Potamogeton pectinatus* to contrasting substrate types mediated by changes in propagule provisioning. *Journal of Ecology* 91: 1081–1092.
- Lacey EP. 1996. Parental effects in *Plantago lanceolata* L. I. A growth chamber experiment to examine pre- and postzygotic temperature effects. *Evolution* 50: 865–878.
- Lacey EP, Herr D. 2000. Parental effects in *Plantago lanceolata* L. III. Measuring parental temperature effects in the field. *Evolution* 54: 1207–1217.
- Lechowicz MJ, Bell G. 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. *Journal of Ecology* 79: 687–696.
- Levin DA, Kerster HW. 1974. Gene flow in seed plants. *Evolutionary Biology* 7: 139–220.
- Linhart YB, Grant MC. 1996. Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27: 237–277.
- McCauley DE. 1994. Contrasting the distribution of chloroplast DNA and allozyme polymorphism among local populations of *Silene alba*: implications for studies of gene flow in plants. *Proceedings of the National Academy of Science, USA* 91: 8127–8131.
- Miao SL, Bazzaz FA, Primack RB. 1991. Persistence of maternal nutrient effects in *Plantago major*: the third generation. *Ecology* 72: 1634–1642.
- Mousseau TA, Fox CW. 1998. *Maternal Effects as Adaptations*. Oxford UK: Oxford University Press.
- Munir J, Dorn L, Donohue K, Schmitt J. 2001. The effect of maternal photoperiod on seasonal dormancy in *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany* 88: 1240–1249.
- Roach DA, Wulff RD. 1987. Maternal effects in plants. *Annual Review of Ecology and Systematics* 18: 209–235.
- Rossiter MC. 1998. The role of environmental variation in parental effects expression. In: Mousseau TA, Fox CW, eds. *Maternal Effects as Adaptations*. Oxford, UK: Oxford University Press, 112–134.
- Schmid B, Dolt C. 1994. Effects of maternal and paternal environment and genotype on offspring phenotype in *Solidago altissima*. *Evolution* 48: 1525–1549.
- Schmitt J, Gamble SE. 1990. The effect of distance from the parental site on offspring performance and inbreeding depression in *Impatiens capensis*: a test of the local adaptation hypothesis. *Evolution* 44: 2022–2030.
- Schmitt J, Niles J, Wulff RD. 1992. Norms of reaction of seed traits to maternal environments in *Plantago lanceolata*. *American Naturalist* 139: 451–466.
- 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.
- Smith H. 1982. Light quality, photoreception, and plant strategy. *Annual Review of Plant Physiology* 33: 481–518.
- Steinger T, Roy BA, Stanton ML. 2003. Evolution in stressful environments II. Adaptive value and costs of plasticity in response to low light in *Sinapis arvensis*. *Journal of Evolutionary Biology* 16: 313–323.
- Stratton DA, Bennington CC. 1998. Fine-grained spatial and temporal variation in selection does not maintain genetic variation in *Erigeron annuus*. *Evolution* 52: 678–691.
- Sultan SE. 1996. Phenotypic plasticity for offspring traits in *Polygonum persicaria*. *Ecology* 77: 1791–1807.
- Sultan SE, Spencer HG. 2002. Metapopulation structure favors plasticity over local adaptation. *American Naturalist* 160: 271–283.
- 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.
- Van Kleunen M, Fischer M. 2003. Effects of four generations of density-dependent selection on life history traits and their plasticity in a clonally propagated plant. *Journal of Evolutionary Biology* 16: 474–484.
- Wardle GM. 1998. A graph theory approach to demographic loop analysis. *Ecology* 79: 2539–2549.
- Weinig C. 2000. Differing selection in alternative competitive environments: Shade-avoidance responses and germination timing. *Evolution* 54: 124–136.
- Werner PA. 1975. Predictions of fate from rosette size in Teasal (*Dipsacus fullonum* L.). *Oecologia* 20: 197–201.
- Wolf JB, Brodie ED, III, Cheverud JM, Moore AJ, Wade MJ. 1998. Evolutionary consequences of indirect genetic effects. *Trends in Ecology and Evolution* 13: 64–69.



About *New Phytologist*

- *New Phytologist* is owned by a non-profit-making **charitable trust** dedicated to the promotion of plant science, facilitating projects from symposia to open access for our Tansley reviews. Complete information is available at www.newphytologist.org.
- Regular papers, Letters, Research reviews, Rapid reports and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as-ready' via *OnlineEarly* – the 2003 average submission to decision time was just 35 days. Online-only colour is **free**, and essential print colour costs will be met if necessary. We also provide 25 offprints as well as a PDF for each article.
- For online summaries and ToC alerts, go to the website and click on 'Journal online'. You can take out a **personal subscription** to the journal for a fraction of the institutional price. Rates start at £109 in Europe/\$202 in the USA & Canada for the online edition (click on 'Subscribe' at the website).
- If you have any questions, do get in touch with Central Office (newphytol@lancaster.ac.uk; tel +44 1524 592918) or, for a local contact in North America, the USA Office (newphytol@ornl.gov; tel 865 576 5261).