Ecology, 77(6), 1996, pp. 1791–1807

PHENOTYPIC PLASTICITY FOR OFFSPRING TRAITS IN *POLYGONUM PERSICARIA*[1]

S. E. SULTAN[2]
Center for Population Biology, University of California, Davis, California 95616 USA

Abstract. This paper investigates the effects of parental environment and genotype on offspring provisioning, structure, and growth traits in the annual plant *Polygonum persicaria.* Replicate offspring were studied from cloned individuals of five parental genotypes grown in high vs. low light, soil moisture, and soil nutrients. Genotypic norms of reaction were determined for ecologically important offspring traits. The effects on those traits of parental genotype, parental environment, and their interaction were tested by analysis of variance. The results showed that parental genotypes altered offspring traits in response to particular resource limits, such that offspring quality was maintained or enhanced despite parental resource deprivation. By maximizing the probability of offspring success, resource-deprived parental plants may partly offset the reduction in their fitness due to lower offspring number. Although overall patterns of plasticity were common to all parents, even this small sample revealed differences among parental genotypes in their response to environment. This may reflect the degree to which variation in fitness-related offspring traits occurs within parents and hence is unavailable to selection.

Key words: *fitness*; *maternal effects*; *norm of reaction*; *offspring quality*; *parental investment*; *phenotypic plasticity*; Polygonum; *resource limitation*; *seed number*; *seed size.*

INTRODUCTION

A good deal is now known about the extent to which individual organisms respond phenotypically to their immediate environments, and in particular about the ways that trait- and resource-specific plasticity may maintain function and therefore reproductive fitness in unfavorable conditions (reviewed by Bradshaw 1965, Schlichting 1986, Sultan 1987, Bradshaw and Hardwick 1989, West-Eberhard 1989). It is also well known that a maternal individual's environment may affect not only the number but the size and properties of its offspring (Roach and Wulff 1987, Groeters and Dingle 1988, Sinervo 1991, Parichy and Kaplan 1992, and references therein). Yet only very recently has it been suggested that the ways that individuals alter their offspring in response to environmental circumstances may represent a further aspect of phenotypic plasticity, which by maximizing offspring success may enhance maternal fitness (Lacey 1991, Schmitt et al. 1992).

In plants, the effect of maternal environment on seed traits such as mass, chemical composition, viability, and germination have long been recognized by both agriculturists (Barton 1965, Koller 1972) and biologists (the extensive recent literature, primarily on cultivated species, is reviewed in Fenner 1985, Gutterman 1985, Roach and Wulff 1987, and Stratton 1989). The influence of maternal environment on seed mass and biochemistry reflects the fact that the mineral and carbohydrate resources on which initial seedling growth depends are provided by the maternal plant during seed maturation (Roach and Wulff 1987, Platenkamp and Shaw 1993). Thus, differences in seed provisioning will influence not only seed size and therefore dispersal (Harper et al. 1970, Morse and Schmitt 1985), but the growth rate, size, and competitive success of the emergent seedling (Stanton 1984*a, b,* Parrish and Bazzaz 1985). The seed coat and associated fruit tissues are genetically and developmentally tissues of the maternal plant and not the offspring (Westoby 1981). The thickness, structure, and chemistry of these tissues strongly affect both their permeability to oxygen and water, and their chemical inhibitory properties, and therefore determine germination response as well as seed longevity in the soil (Wareing 1982, Haig and Westoby 1988). In self-fertilizing plants, such effects are more precisely denoted as parental rather than maternal (Lacey 1991); the arguments here presented for parental effects would apply to maternal effects in other systems.

Clearly these environmentally labile traits are of key ecological importance, and are likely to strongly influence offspring success and therefore parental fitness. Although resource-deprived plants inevitably produce fewer seeds, parental fitness is determined by offspring quality as well as number (Lloyd 1987). For this reason, the evolutionary impact of this type of genotype-by-environment interaction will depend on the nature of the parental response to environment. If the effects of parental environment on offspring traits simply mirror the resource deficiencies of the parent, plants in unfavorable environments will produce lower quality as well as fewer offspring. Such parental response to en-

[1] Manuscript received 3 May 1995; revised 21 October 1995; accepted 22 November 1995; final version received 22 January 1996.

[2] Present address: Department of Biology, Wesleyan University, Middletown, Connecticut 06459-0170 USA.

vironment will therefore both magnify and temporally prolong the impact of environmental heterogeneity on individual fitness (Schaal 1984, Kirkpatrick and Lande 1989, Schmitt et al. 1992). However, if parental plants respond to resource-poor environments by altering progeny structure and provisioning so as to maintain or even enhance offspring quality (and hence the probability of each offspring's successful establishment), the reduction in fitness due to decreased offspring number may be partly offset. Because the developmental effects of resource limitation are an inextricable part of phenotypic response, it cannot be shown that the compensatory aspect of a particular response has evolved as a discrete target of natural selection apart from such effects. Nonetheless, phenotypic plasticity may be considered as functionally adaptive when it permits individuals to maximize fitness under environmental limits (Sultan and Bazzaz 1993*a*). By enhancing offspring quality, plasticity for offspring traits could mitigate environmentally induced variance in fitness, so that long-term genotypic fitness would be maintained (see Gillespie 1977; further references in Forbes 1991).

The purpose of this paper is to investigate the ways that parental environment affects offspring traits: specifically, to determine whether the responses of parental genotypes to unfavorable environments with respect to offspring structure and provisioning constitute phenotypic plasticity. I determine the norms of reaction in response to parental resource deprivation for seedling traits relevant to successful establishment in a well-studied model system, *Polygonum persicaria* (lady's thumb). The key advantage of this species for the study of parental effects is that unlike most annuals, genotypes can be clonally replicated. This permits use of a fully factorial design to estimate the relative variance contributions of parental environment and parental genotype. Because most previous studies cannot distinguish genetic from environmental parental effects (Lacey 1991), very little is known about the relative magnitudes of these effects or about genetic variation for parental response to environment (Roach and Wulff 1987, Platenkamp and Shaw 1993, Evans and Cabin 1995).

Although the seedling stage is recognized to be the primary determinant of plant mortality and competitive success (Harper 1977, Fenner 1987), this is one of very few studies to examine the effects of maternal environment on seedling traits in genotypes sampled from natural populations (Fenner 1985, Roach and Wulff 1987, Evans and Cabin 1995). Furthermore, despite a wealth of data on maternal effects due to complex field environments, very little is known about response to specific environmental factors (Roach and Wulff 1987, Platenkamp and Shaw 1993). Here I compare the effects of parental light, soil moisture, and nutrient deprivation on several offspring traits. These aspects of the plant environment are of particular interest for three reasons: (1) all are fundamental to plant growth; (2) they are likely to elicit qualitatively different responses; and (3) all are highly variable in nature, so that environmental maternal effects (like other aspects of genotype-by-environment interaction) are likely to be of evolutionary importance.

In this paper I address the following questions: (1) How are offspring traits of ecological importance affected by unfavorable parental environments; (2) to what extent are these effects resource-specific and/or trait-specific; and (3) do parental genotypes differ in their expression of these responses?

Materials and Methods

Study system

Polygonum persicaria L. is a widespread annual species of spatially and temporally variable habitats, with a mixed breeding system (Sultan 1990). Genotypes in this species express a wide range of functionally appropriate phenotypic plasticity in response to light, moisture, and nutrient conditions (Sultan and Bazzaz *a, b, c*). The *Polygonum* fruit is an achene: a seed, containing a small embryo embedded in starchy nutritive endosperm, enclosed in a hard, dry, pericarp (fruit wall). The achene constitutes a single offspring and can be considered as functionally equivalent to a seed (a "seed unit" sensu Harper et al. 1970).

Parental genotypes and environments

Genotypes were sampled from a natural population of *P. persicaria* in which light intensity, soil moisture, and soil nutrients are extremely variable (Great Brook Farm State Park, Carlisle, Massachusetts; see environmental data in Sultan and Bazzaz 1993*a, b, c*). Achenes were collected from several randomly chosen field plants, germinated, and grown under uniform greenhouse conditions for at least one generation before being cloned vegetatively (Fig. 1). The experiment was conducted on five families in which three offspring produced sufficient vegetative clones after losses to random experimental error. Clonal replicates of one offspring from each family were grown to maturity in each of three controlled greenhouse experiments (Fig. 1).

In each experiment a single environmental factor was varied. Experimental environments were: full vs. severely limited light (100% vs. 8% of full sun), abundant (field capacity) soil moisture vs. extremely dry soil (11% moisture by mass), and high vs. very low nutrient supplies (an inert medium containing either 0.42 g total nitrogen, 0.224 g total phosphorous, and 0.336 g total potassium per pot, or one-sixth of those levels). In each case, the low resource treatment corresponded to measured levels of that resource at the field site, and the high treatment matched the natural optimum for that resource (details in Sultan and Bazzaz 1993*a, b, c*). Each experiment consisted of 4–6 replicates of five

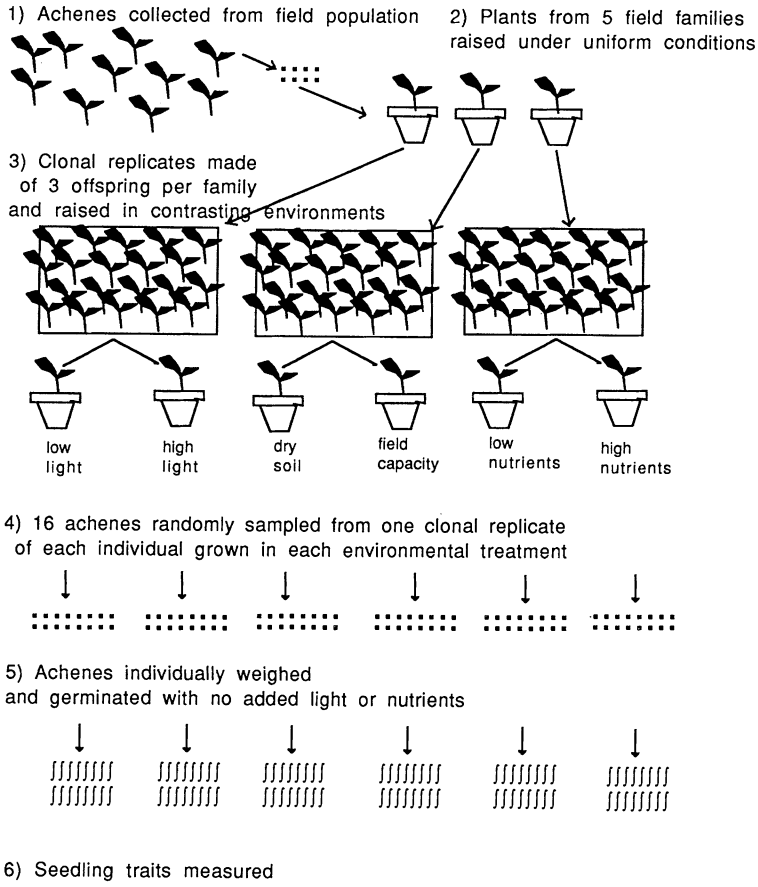

FIG. 1. Schematic of experimental protocol showing sampling of field families (steps 1–2), growth of parental generation in contrasting environments (step 3), and data collection on offspring (steps 4–6).

genotypes grown in each of two contrasting resource levels. Every replicate of each genotype in all six experimental environments produced mature, apparently viable, self-fertilized achenes. (The species is primarily selfing in nature and this population shows no inbreeding depression; Sultan 1990.)

Progeny sample

The study was performed on achenes collected from one randomly chosen clonal replicate of each of the 30 parent plants (five genotypes × two parental environments × three experiments; see Fig. 1). (In the case of the light experiment, which was a randomized complete block rather than a fully randomized design, all of the parent plants were drawn from a single randomly chosen block to avoid confounding block with other effects.) The progeny sample from parents grown at low light was drawn from more than one clonal replicate of each parent genotype when necessary to augment sample size. All achenes were air-dried on greenhouse benches for ≈1 wk and stored dry at 4°C for 45–51 mo. Moisture content (percent dry mass) was determined for a subsample of achenes from each of the six parental environments to verify that differences in initial achene mass were not due to differential drying of mature achenes at harvest (S.E. Sultan, *unpublished data*; cf. Wulff 1986*b*).

Experimental protocol

(See Fig. 1.) Sixteen randomly selected, mature achenes from each of the 30 parent plants were individually weighed on a Cahn model 25 analytical microbalance (Orion Research, Boston, Massachusetts). These achenes were cold-stratified at 3°C for 33 d in Corning 96-well tissue culture trays half-filled with distilled water, with a round of filter paper dropped into each well to hold the achene submerged. Achenes were manipulated with a dissecting probe tipped with a small piece of putty after I ascertained that the putty left no residue on the achene surface.

In order to compare strictly initial provisioning of achenes from the different parental genotypes and environments, seedlings were grown without added nutrients or light. Although this lack of added resources is a crucial part of the experimental design, it may have resulted in slower seedling growth than would occur in field conditions; note, however, that seedlings in nature may receive little light during the corresponding

stage in ontogeny. The weighed achenes were sown individually 0.5 cm deep in 2.5 × 2.5 × 11.4 cm cells of plastic Rootrainer containers (Spencer Lemaire Industries, Edmonton, Alberta, Canada) filled with sterile horticultural sand, and set in trays containing 1 cm of distilled water to bottom-saturate (sand was also misted with distilled water several times daily). Achenes were sown in a randomized complete block design, each block containing one replicate achene from each of the 30 parents. Blocks were re-randomized daily and showed no significant final effects. The containers were placed in a growth chamber set at 25°: 18°C in a 14: 10 h diurnal cycle and for the first 3 d given ≈180 μmol (of photons, fluorescent) daylight to cue germination (Justice 1941, Staniforth and Cavers 1979); starting 2 d prior to the first emergence, the chamber was kept dark 24 h a day (S.E. Sultan, *unpublished data*). Seedling emergence was censused daily between 1000 and 1200. The empty pericarp from each seedling was collected, air-dried, and weighed, and the seedling itself harvested 72 h after its emergence. Each root was washed and measured, and the seedling oven-dried (at 100°C for 1 h to prevent continued respiration and then at 65°C for ≥72 h) prior to weighing.

Due to relatively low germination of achenes from the moisture and nutrient experiments, the above protocol was repeated using additional randomly chosen achenes from the same progeny samples from these experiments (10 per parent and 16 per parent, respectively). The low germination was evidently due to the deep dormancy of 25–30% of the seeds (based on achene exhumations from a related greenhouse experiment, using the viability criterion of Hammerton and Jallocq 1970; S.E. Sultan, *unpublished manuscript*). This dormancy was likely due to prolonged dry storage, a possible brief exposure to high temperature during shipping, or parental environment effects (see *Results*). In this second sample, achenes were sown into individual wells of 24-well tissue culture trays lined with filter paper, moistened with distilled water, and harvested 96 h after radicle emergence.

Data analysis

Data on achenes produced at high vs. low light, moisture, and nutrients were examined separately since the parent plants had been grown in separate greenhouse experiments. Trait means for the progeny of each parent genotype grown in contrasting environments are presented graphically in norm of reaction plots. On average 8–10 replicate progeny were measured from each parent plant. The range depicted on the dependent-variable axis of each plot corresponds to the range of the raw data for that trait. "Emergence rate" is based on the day on which at least 50% of eventual germination had occurred (e.g., Shipley and Parent 1991), since means for emergence day are typically heavily influenced by one or two very late outliers.

Separate two-way analyses of variance (MGLH module, SYSTAT 3.1; Wilkinson and Bjerkness 1987) were used to test the effects of parent environment, parent genotype, and their interaction on initial achene mass, seedling biomass, seedling root length, pericarp mass, the proportion of achene mass due to pericarp, and the number of days to emergence. A sequential Bonferroni procedure was employed to protect the experimentwise alpha level for Type I error at <5% (Day and Quinn 1989, Rice 1989). Since the progeny were produced by selfing, the parent genotype effect includes both maternal and paternal nuclear genes as well as maternal cytoplasmic transmission. The effect of parent environment includes the influence of the maternal environment on ovule formation, seed provisioning and biochemistry, and achene structure, as well as any effects of the environment on pollen quality that might affect progeny.

Both parent environment and parent genotype were treated as fixed factors and tested over the error term (note that this sample of genotypes was chosen not on the basis of previous results for any of the variables of interest, but because the families to which they belonged were represented in all three experiments). Because the genotypic sample was not chosen at random from the population, I considered the fixed model to be most appropriate (Zar 1984). To ensure that this decision did not influence the results of the study, I repeated the 18 ANOVAs treating genotype as a random factor. The results of these significance tests were identical, with one exception noted in Table 3. The "error" term is of biological interest since it reflects variation among the 8–10 progeny measured from each individual parent plant (a single clonal replicate of a particular genotype and environment).

For the water and nutrient experiments, data from the original and repeated versions were combined by using experiment as a block effect, after verifying the absence of significant interactions between experiment and either parent genotype or parent environment (N. Willits, *personal communication*). One genotype was dropped from the analysis of the nutrient experiment due to the occurrence of an empty genotype × environment cell, to avoid confounding the genotype effect with the interaction of genotype and environment.

Although the fixed ANOVA model employed here is quite robust against both departures from normality and heteroscedasticity (Neter et al. 1990), residuals were examined to verify normality, and equality of variances was tested using Bartlett's test (Statistics module, SYSTAT 3.1). In most cases, the data met the assumptions of ANOVA without transformation. Emergence-day data (range, day 3–day 17) were transformed using the function $(\sqrt{x} + ½)$ appropriate for small numbers (Steel and Torrie 1960), which effectively reduced skewness of residuals. In 5 of the 18 analyses, variances among cells were unequal according to Bartlett's and Levene's tests (Levene 1960, Sachs 1984). In one case, the sample with greater variance had the

lower trait mean, which may cause the difference between the means to be underestimated (Snedecor and Cochran 1989); since the difference was detected at a probability of <0.001, this was not a problem. In the remaining cases variances were normalized either by a log-transformation of the data or by deleting a single high outlier; analyses of these transformed or reduced data sets yielded identical results. Since the actual scales of trait measurement are more biologically interesting than transformed scales, and since the outlying data points were valid measurements, in these cases the (robust) results of the original ANOVA are presented. Several seedlings noted during the experiment to have developed abnormally were omitted from analyses of seedling growth traits, and root length data were missing for eight seedlings. Outliers were deleted from analyses only in three cases where they appeared to be measurement errors, although the models were also tested on data sets from which valid outliers were deleted to know how strongly they influenced the results.

Nonsignificant effects of parental environment were examined using the power analysis method of Pearson and Hartley (Zar 1984) for determining the minimum detectable difference between levels of a factor in a two-way fixed ANOVA, using the harmonic mean in cases of unequal sample sizes. Pearson correlation coefficients were computed to examine possible relationships between pericarp proportion and days to emergence. The effects of parent genotype, environment, and interaction on the germination/nongermination response of each achene were tested using logistic regression (Brown et al. 1990; BMDP).

Results

Progeny of plants grown at low vs. high light

Plants given only 8% of full sun produced achenes that were 25% smaller by mass than those produced by plants given full (100%) light (Fig. 2a; Table 1). The achenes produced by low-light-grown parents had higher final germination (68 vs. 52%; logistic regression $\chi^2 = 3.95$, $P \leq 0.047$, genotype and interaction effects not significant). Surprisingly, given the large effect of parent environment on achene mass, there was no significant effect of parent environment on seedling biomass (Fig. 2b; Table 1). This negative result was double-checked by a robust approximate t test, since the larger sample had larger variance (Sokal and Rohlf 1981); the treatment means did not differ significantly ($P \gg 0.05$). Note that almost all of the variation in seedling biomass occurred within parent plants (cf. model r^2, Table 1). The range within each parent was between 0.13 and 0.47 mg; according to a power analysis I could be 80% confident of detecting a difference as small as 0.063 mg ($\approx$7% of the mean) at a probability of $\leq$0.05. There was no significant effect of parent genotype on either initial achene mass or seedling biomass (Table 1).

The difference in mass between achenes produced in low vs. high light reflected a difference in achene structure. Parent plants grown in low light reduced the amount of pericarp tissue (fruit wall) surrounding each seed by >40% compared with achenes produced by plants of the same genotypes given full light (Fig. 2c; Table 1). Consequently, each seed was effectively surrounded by a thinner pericarp, shown by a significant reduction in the pericarp proportion of achene dry mass (pericarp proportion, Table 1; Fig. 2d). This structural difference was associated with a difference in emergence rate. Progeny of plants grown at low light emerged on average 1.6 d earlier than the progeny of plants grown at high light, so that at least 50% of low light progeny had emerged by days 6–8 of the experiment, whereas the high light progeny required 8–10 d to reach 50% germination (Fig. 2e). Variance in pericarp proportion explained nearly half of the variation in days to emergence (correlation coefficient for pericarp proportion and emergence day = 0.672; $P \ll 0.01$). The effect of reduced pericarp thickness on emergence rate was further supported by the fact that the two genotypes producing progeny that emerged significantly earlier (Table 1) also produced those with the thinnest pericarps (genotypes 8 and 9; Fig. 2d and e).

A second surprising result was that, although there was no effect of parental light deprivation on seedling biomass, the offspring of plants grown at low vs. high light did grow differently. The progeny of plants given reduced light produced roots that were $\approx$30% shorter than the progeny of the same genotypes given full sun (Fig. 2f). In the absence of differences in total biomass, the shorter roots of these seedlings indicate greater allocation of initial growth to shoot rather than root tissue. Note that in no case was the interaction of parent genotype and parent environment significant (Table 1). In other words, the differences between progeny produced by plants at high and low light were similar in all genotypes: when deprived of light, all genotypes produced achenes with a thinner pericarp, which germinated earlier and in higher numbers, and produced seedlings of equal biomass but with shorter roots.

Progeny of plants grown at low vs. high soil moisture

Plants of all genotypes grown in very dry soil produced achenes that were $\approx$16% larger (in dry mass) than the achenes of plants grown in a favorable (field capacity) moisture environment (Fig. 3a). The effect of genotype on achene mass was not significant (Table 2; Fig. 3a), as >80% of the variation in achene mass occurred within individual parent plants (Table 2). Achenes produced by water-deprived parent plants were not only heavier but also had higher total germination (60 vs. 26%; $\chi^2 = 39.05$, $P < 0.0001$), although the magnitude of this difference varied among

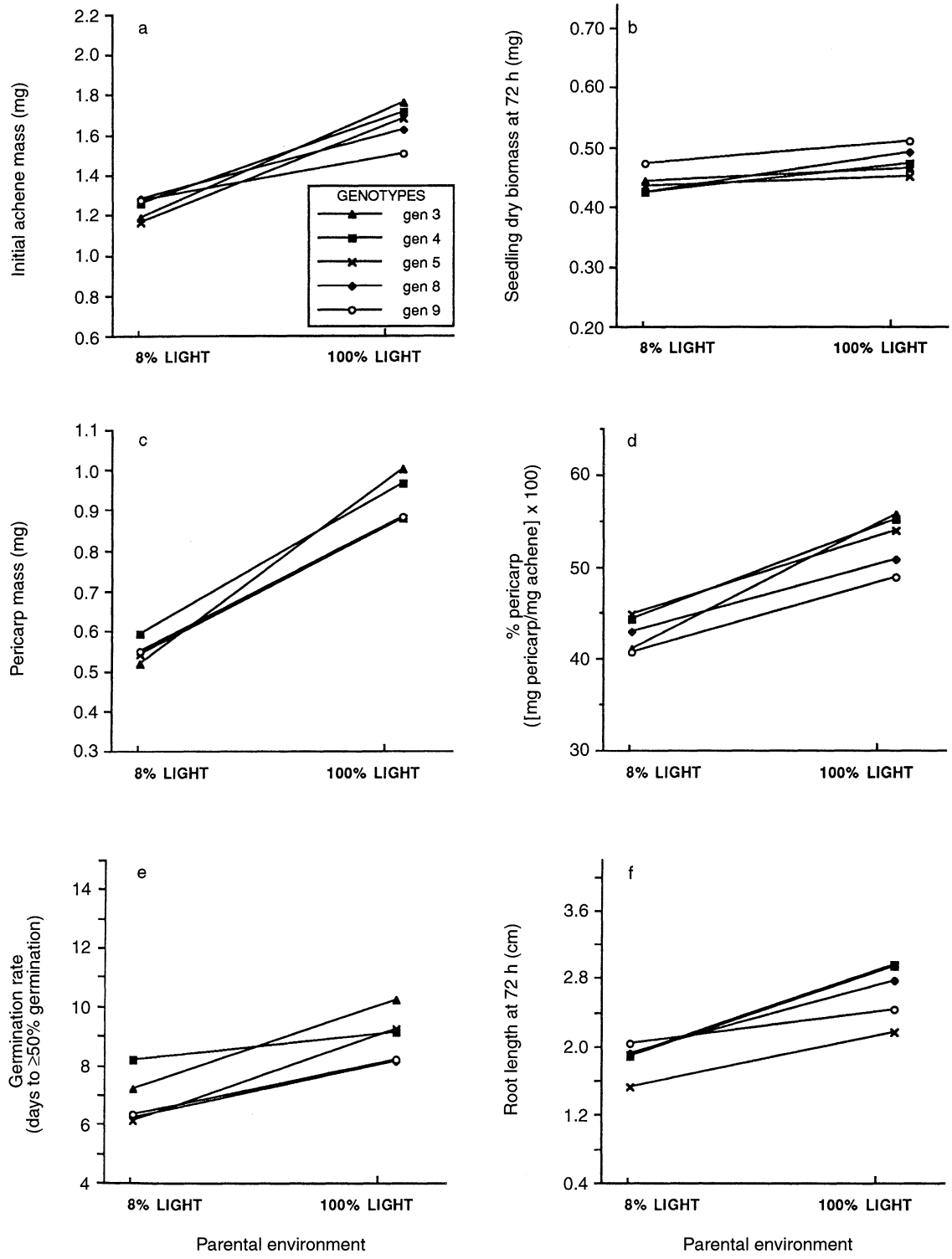

FIG. 2. Norms of reaction for five parental genotypes to low (8%) vs. high (100%) light (means of 8–10 replicate offspring). (a) initial achene mass; (b) seedling biomass; (c) pericarp mass; (d) pericarp proportion; (e) germination rate; (f) root length.

TABLE 1. Analyses of variance for traits of progeny from contrasting parental light environments.

Progeny trait	Source of variation	df	MS	F	P
Achene mass	Parental environment	1	6.495	68.622	.000*
(model $r^2 = 0.355$)	Parental genotype	4	0.022	0.232	.920
	Parental G × E	4	0.201	2.122	.081
	Error	154	0.095		
Seedling biomass	Parental environment	1	0.032	2.655	.107
(model $r^2 = 0.060$)	Parental genotype	4	0.006	0.511	.728
	Parental G × E	4	0.002	0.153	.961
	Error	90	0.012		
Pericarp mass	Parental environment	1	3.048	243.805	.000*
(model $r^2 = 0.769$)	Parental genotype	4	0.020	1.570	.190
	Parental G × E	4	0.022	1.771	.142
	Error	86	0.013		
Pericarp proportion	Parental environment	1	2140.455	70.107	.000*
(model $r^2 = 0.528$)	Parental genotype	4	65.432	2.143	.083
	Parental G × E	4	39.367	1.289	.281
	Error	84	30.531		
Emergence day	Parental environment	1	1.192	11.310	.001*
(model $r^2 = 0.298$)	Parental genotype	4	0.406	3.857	.006*
	Parental G × E	4	0.156	1.476	.216
	Error	89	0.105		
Root length	Parental environment	1	14.431	42.031	.000*
(model $r^2 = 0.024$)	Parental genotype	4	0.850	2.475	.050
	Parental G × E	4	0.403	1.172	.328
	Error	89	0.343		

* Effects marked with an asterisk are significant at an experiment-wide probability level of <0.050 according to sequential Bonferroni procedure (details in *Materials and methods: Data analysis*).

TABLE 2. Analyses of variance for traits of progeny from contrasting parental moisture environments.

Progeny trait	Source of variation	df	MS	F	P
Achene mass	Parental environment	1	5.369	38.652	.000*
(model $r^2 = 0.183$)	Parental genotype	4	0.403	2.903	.022
	Parental G × E	4	0.183	1.321	.263
	Block	1	0.017	0.124	.725
	Error	249	0.139		
Seedling biomass	Parental environment	1	0.088	8.171	.005*
(model $r^2 = 0.417$)	Parental genotype	4	0.001	0.111	.978
	Parental G × E	4	0.025	2.357	.061
	Block	1	0.445	41.321	.000
	Error	79	0.011		
Pericarp mass	Parental environment	1	0.027	1.011	.317
(model $r^2 = 0.223$)	Parental genotype	4	0.026	0.985	.420
	Parental G × E	4	0.067	2.520	.047
	Block	1	0.241	9.098	.003
	Error	90	0.027		
Pericarp proportion	Parental environment	1	77.308	4.757	.032
(model $r^2 = 0.266$)	Parental genotype	4	16.914	1.041	.391
	Parental G × E	4	31.147	1.917	.114
	Block	1	161.640	9.947	.002
	Error	90	16.250		
Emergence day	Parental environment	1	0.355	2.311	.132
(model $r^2 = 0.432$)	Parental genotype	4	0.519	3.383	.013
	Parental G × E	4	0.308	2.010	.100
	Block	1	4.892	31.886	.000
	Error	88	0.153		
Root length	Parental environment	1	0.009	0.014	.905
(model $r^2 = 0.244$)	Parental genotype	4	0.117	0.181	.948
	Parental G × E	4	2.552	3.944	.006*
	Block	1	1.100	1.699	.197
	Error	71	0.647		

* Effects marked with an asterisk are significant at an experiment-wide probability level of <0.050 according to sequential Bonferroni procedure (details in *Materials and methods: Data analysis*).

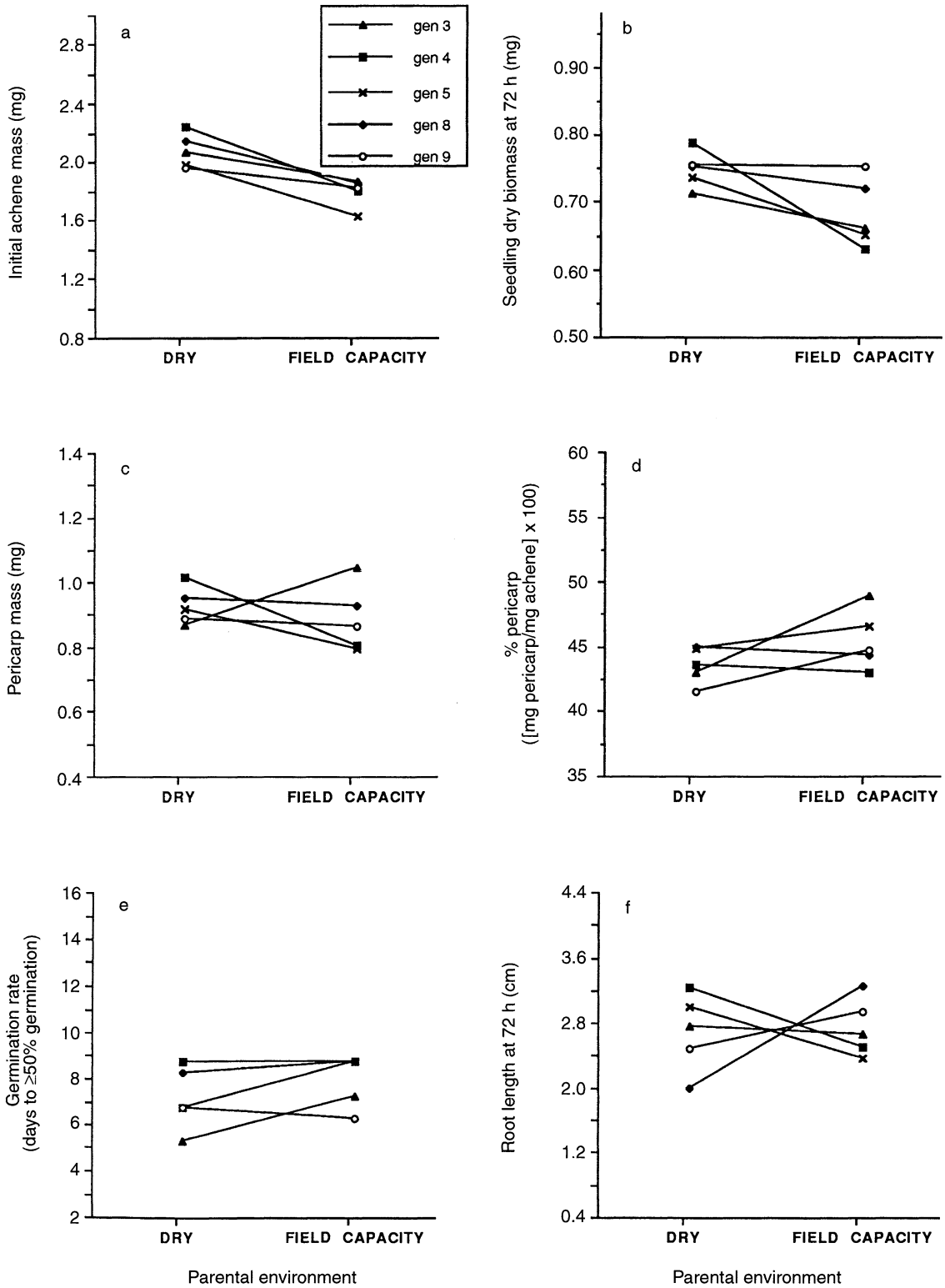

FIG. 3. Norms of reaction for five parental genotypes to dry vs. moist (field capacity) soil (means of 8–10 replicate offspring). (a) initial achene mass; (b) seedling biomass; (c) pericarp mass; (d) pericarp proportion; (e) germination rate; (f) root length.

genotypes and experimental blocks (three-way interaction $\chi^2 = 10.55$, $P \leq 0.032$).

The difference in the mass of achenes produced by plants in different soil moisture environments evidently resulted from increased provisioning to seeds by parents deprived of moisture: the seedling progeny of plants grown in dry soil had 10% greater biomass after 72 h of growth without added light or minerals (Fig. 3b; Table 2). Much of the variation in seedling biomass (≈60%, Table 2) occurred within parents. There was no average difference in the length of roots produced by the progeny of low- vs. high-moisture-grown parents (Fig. 3f), as parent genotypes varied significantly in the root length response of progeny to parental moisture environment (Table 2). Those parent genotypes which, when grown in moist soil, produced offspring with relatively short roots increased root length of offspring most sharply when deprived of soil moisture (Fig. 3f).

Unlike parental light environment, there was no average effect of soil moisture environment on the amount of pericarp tissue produced around each seed (pericarp mass, Table 2). Genotypes grown in dry soil either slightly increased or in one case decreased the amount of pericarp (Fig. 3c; cf. marginal but non-significant parent genotype × environment interaction, Table 2). This resulted in an unchanged pericarp proportion compared with high-moisture progeny (Fig. 3d; Table 2). In accordance with this very small effect of parental moisture environment on pericarp proportion, there was no significant effect of moisture environment on offspring emergence rate (Table 2; Fig. 3e), although the former did tend to germinate slightly earlier (mean time to emergence 7.4 ± 2.8 d vs. 8.1 ± 2.5 d). In this case, the correlation of pericarp proportion with emergence day was 0.388 ($P < 0.01$), indicating that ≈85% of the variation in emergence day was not explained by variation in pericarp proportion.

In summary, all genotypes when grown in dry as opposed to favorably moist soil produced heavier achenes, with a similar amount of pericarp tissue, that germinated at higher frequency and marginally earlier, and gave rise to larger seedlings with either longer or shorter roots. Although there was no main effect of genotype on achene mass, seedling biomass, root length, or amount or proportion of pericarp, parental genotypes differed in germination rate, and in their response to moisture environment with respect to root length and pericarp mass (Table 2).

Progeny of plants grown at low vs. high nutrient levels

The effect of low vs. high parental resource levels on offspring traits was smaller for nutrients (NPK) than for light and soil moisture, although still highly significant (Table 3). Achenes produced by parents deprived of nutrients weighed on average 9% less than those produced by parents given ample nutrients, although this response varied significantly among genotypes (Table 3; Fig. 4a). As in the previous experiments, most of the variation in achene mass occurred within individual parents (Table 3). Plants grown at the high nutrient treatment produced particularly variable achenes (range 0.924–3.492 mg for high nutrient parents vs. 0.961–2.743 mg for low nutrient parents). There was no main effect of parent nutrient environment on total germination ($\chi^2 = 0.05$, $P = 0.83$), but there was a significant genotype × environment interaction since genotypes deprived of nutrients produced achenes with either higher or lower percentage germination (interaction $\chi^2 = 29.16$, $P < 0.0001$). Total germination and achene mass were the only progeny traits with significant genotype × environment interaction effects.

Unlike the smaller achenes produced by light-deprived parents, the reduced mass of achenes produced by plants deprived of nutrients did reflect reduced seed provisioning. The seedlings of low-nutrient-grown parents had 7% less biomass than the progeny of plants given ample nutrients (Fig. 4b). In addition, this was the only experiment in which genotypes differed significantly in seedling biomass (Table 3). In accord with the within-parent variation in achene masses described above, seedlings from the two parent nutrient environments had similar minimum biomasses, but the high nutrient progeny had higher maxima.

Despite the reduction in seedling biomass, seedling root length was not significantly affected by parent nutrient deprivation. The absence of a significant effect is not the result of insufficient power to detect a decrease in root length, since the mean root length of the offspring of nutrient-deprived parents was actually 8% greater than that of the progeny of plants given ample nutrients (Fig. 3f; minimum detectable difference in root length given within-parent variability was 0.56 cm, or 22% of the mean root length of high nutrient progeny). Since the progeny of nutrient-deprived parents had less total biomass, the absence of a corresponding reduction in root length indicates greater proportional allocation of initial growth to elongating roots in these seedlings.

Parent nutrient environment did not affect the amount of pericarp tissue enclosing seeds (Table 3, Fig. 4c). Since the achenes produced by nutrient-deprived parents were reduced in mass by ≈9%, the effect of this constancy was to increase slightly the proportion of pericarp surrounding these achenes (cf. marginal significance, Table 3; Fig. 4d). Despite this slight difference in pericarp proportion, there was no effect of parent nutrient environment on rate of emergence (Table 3; Fig. 4e). In this case, the correlation of pericarp proportion to emergence day was only 0.134 ($P > 0.5$), so very little of the variation in time to emergence was related to variation in pericarp proportion.

To summarize, parent plants given very low compared with ample amounts of nutrients produced

TABLE 3. Analyses of variance for traits of progeny from contrasting parental nutrient environments.

Progeny trait	Source of variation	df	MS	*F*	*P*
Achene mass	Parental environment	1	1.970	16.151	.000*†
(model $r^2 = 0.206$)	Parental genotype	3	1.162	9.528	.000*
	Parental G × E	3	1.026	8.414	.000*
	Block	1	0.196	1.605	.206
	Error	276	0.122		
Seedling biomass	Parental environment	1	0.109	9.644	.003*
(model $r^2 = 0.558$)	Parental genotype	3	0.077	6.852	.001*
	Parental G × E	3	0.005	0.488	.692
	Block	1	0.209	18.538	.000
	Error	50	0.011		
Pericarp mass	Parental environment	1	0.000	0.001	.974
(model $r^2 = 0.114$)	Parental genotype	3	0.019	0.668	.575
	Parental G × E	3	0.019	0.654	.584
	Block	1	0.007	0.246	.622
	Error	54	0.029		
Pericarp proportion	Parental environment	1	106.449	5.445	.023
(model $r^2 = 0.241$)	Parental genotype	3	57.612	2.947	.041
	Parental G × E	3	19.160	0.980	.409
	Block	1	10.684	0.546	.463
	Error	54	19.550		
Emergence day	Parental environment	1	0.350	1.505	.225
(model $r^2 = 0.202$)	Parental genotype	3	0.553	2.379	.079
	Parental G × E	3	0.283	1.217	.311
	Block	1	0.606	2.608	.112
	Error	60	0.232		
Root length	Parental environment	1	0.003	0.005	.942
(model $r^2 = 0.193$)	Parental genotype	3	0.609	1.237	.306
	Parental G × E	3	0.439	0.892	.452
	Block	1	0.750	1.522	.223
	Error	49	0.493		

* Effects marked with an asterisk are significant at an experiment-wide probability level of <0.050 according to sequential Bonferroni procedure (details in *Materials and methods: Data analysis*).

† Note that the parental environment effect is not significant ($P > 0.050$) if the genotype factor is treated as random rather than fixed.

achenes that weighed less, contained the same amount and thus a slightly higher proportion of pericarp tissue, germinated at similar rates and either higher or lower total percentages depending on genotype, and gave rise to seedlings with less biomass but at least equally long roots.

DISCUSSION

Effects of parental environment on offspring traits

The major result of this study is that parental genotypes alter the structure, provisioning, and growth traits of their offspring in highly specific ways in response to resource limits (Table 4). This little-known dimension of environmental response has important implications for individual fitness, since resource-deprived plants inevitably produce fewer progeny than plants given ample resources. In this case, *P. persicaria* genotypes reduced offspring number sharply in response to limited moisture (42%), light (99%), and macronutrients (46%) (Sultan and Bazzaz 1993*a, b, c*). However, parental fitness is determined not by the total number of offspring but by the number that successfully reach reproductive maturity (Lloyd 1987 and references therein). Parental responses to environment that maximize the likelihood of each offspring's success may offset the fitness reduction in resource-limited parents due to decreased offspring number (Caspar 1990, Forbes 1991). Thus, to the extent that these parental responses maximize the probability of successful seedling establishment, they constitute phenotypic plasticity for offspring traits that may mitigate the negative fitness consequences of resource deprivation.

A particularly striking result was the high level of seed provisioning maintained by resource-deprived parents. The trade-off between provisioning and number of plant progeny has long been recognized as an important aspect of fitness homeostasis in resource-limited plants (Salisbury 1942, Haig and Westoby 1988). Such functional homeostasis can be defined as adaptive constancy of key traits achieved by means of plasticity in related traits (Sultan and Bazzaz 1993*c* and references therein). Parents in unfavorable environments are expected to regulate their commitment of resources to offspring largely by often drastic reductions in number, while maintaining relative constancy of offspring size and quality (Harper et al. 1970, Silvertown 1984, Forbes 1991, Stephenson 1992; e.g., Dolan 1984). *P. persicaria* genotypes grown in severely

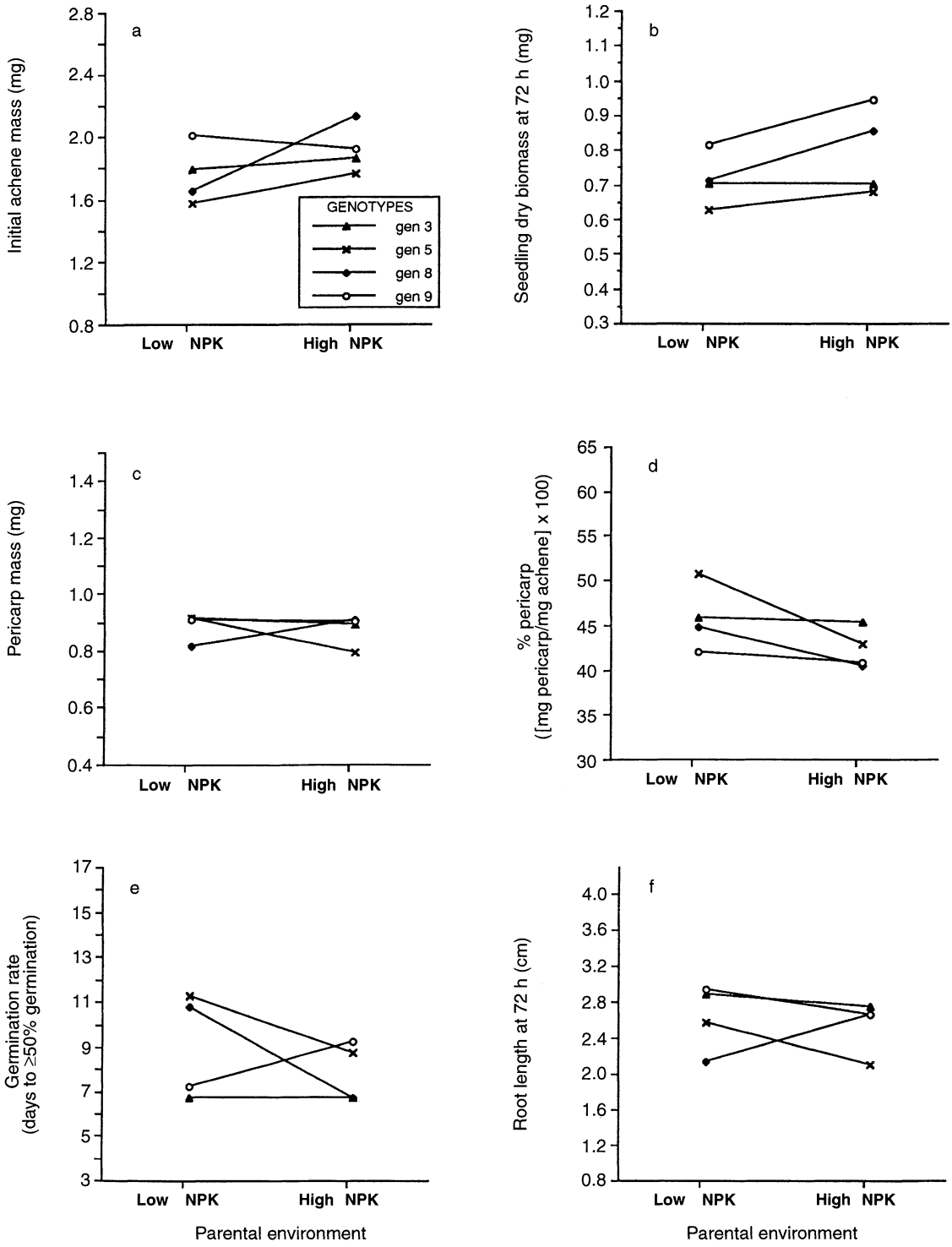

FIG. 4. Norms of reaction for four parental genotypes to low vs. high nutrients (means of 8–10 replicate offspring). (a) initial achene mass; (b) seedling biomass; (c) pericarp mass; (d) pericarp proportion; (e) germination rate; (f) root length.

TABLE 4. Summary of parental environment effects on progeny traits: progeny of resource-deprived compared with resource-rich parent plants.

Progeny of light-deprived vs. light-rich parents	Progeny of moisture-deprived vs. moisture-rich parents	Progeny of nutrient-deprived vs. nutrient-rich parents
Equivalent seed provisioning†	Increased seed provisioning†	Reduced seed provisioning†
Thinner pericarp; earlier emergence	No difference in pericarp; marginally earlier emergence	Slightly thicker pericarp; no difference in emergence rate
Shorter roots; greater relative allocation to shoot growth	Root response depends on parent genotype	No difference in root length; greater relative allocation to root growth

† Seed provisioning based on seedling biomass. See *Results*.

light-limited conditions provisioned individual offspring equally well as did plants grown in full light. Light-deprived parents evidently economized on the carbon-based pericarp tissue, holding constant the nutrient supplies essential for initial seedling establishment, as shown by the equivalent seedling biomasses of low and high light offspring in the absence of added light or minerals. (Note that this result would not have been correctly interpreted in a study measuring achene mass rather than realized seedling biomass.) *P. persicaria* plants deprived of soil moisture not only maintained but actually increased provisioning to offspring: their seedlings had ≈10% greater biomass than the seedling progeny of well-watered parents. In contrast, parental plants deprived of nutrients reduced provisioning to offspring, such that the 96% reduction in parental NPK supply was reflected in a 7% decrease in initial seedling biomass. The reduced nitrogen content of these achenes (Sultan and Bazzaz 1993*c*) confirms that in the case of macronutrients, parental plants are evidently unable to fully buffer their offspring from their own resource limitations.

Because of the intense competitive pressures encountered by young seedlings, reduced initial provisioning is likely to prove disadvantageous in most circumstances (Harper et al. 1970, McGinley et al. 1987 and references therein). Adequate provisioning by parent plants may be particularly crucial in dry and low light conditions, since seedlings in such environments must produce more extensive root or shoot systems before they will receive enough water or light, respectively, to be self-supporting (Salisbury 1974, Silvertown 1984, Haig and Westoby 1988). Indeed, interspecific as well as intraspecific comparisons show that larger seeds are associated with both shaded and dry habitats (Salisbury 1942, Baker 1972, Schimpf 1977, Mazer 1989), presumably due to advantages in emergence, establishment, and competition under light and moisture limitation. In field tests of these putative advantages, *Panicum* seedlings from relatively heavy seeds had higher probabilities of both emergence and survival in dry plots than those from smaller seeds (Gross and Smith 1991), and only large seeds of *Prunella vulgaris* emerged successfully in microsites with plant cover (Winn 1985). Thus, the maintenance by light- and moisture-deprived parents of high levels of provisioning may maximize the per-offspring probability of successful establishment specifically in similar conditions. *P. persicaria* populations occur in patchy environments in which both light and soil moisture vary enormously among microsites (Sultan and Bazzaz 1993*a, b*). The achenes are gravity dispersed and hence are likely to germinate close to the parent plant's former site (S. Sultan, *personal observation*). These norms of reaction (Figs. 2b, 3b, 4b) may thus reflect selection for parents to equip offspring for the possibility of encountering like resource limitations.

As is the case with other aspects of phenotypic response to environment (Bradshaw 1965, Sultan 1987), the ability of *P. persicaria* genotypes to maintain or enhance seed provisioning under unfavorable conditions is resource specific. Like other aspects of plasticity, too, the extent of this homeostatic capacity, as well as the particular traits involved, will vary from one species to another. For instance, although moisture-deprived *P. persicaria* plants produced heavier achenes, in other species plants grown in dry conditions reduce the mean mass of seeds but increase the concentration of sucrose (Meckel et al. 1984) or proteins (Kaufmann 1977 and references). Similarly, nutrient deprivation leads to reduced propagule quality in some cases (e.g., Parrish and Bazzaz 1985, Boutin and Morisset 1988), while most species maintain constant or even increase seed mass (Haig and Westoby 1988, Arnold et al. 1992) or, like *P. persicaria,* show only slight effects of even severe mineral deficiency (Austin 1973, Gray and Thomas 1982, Fenner 1986*a, b*). Interestingly, artificially selected crop plants deprived of nutrients express less homeostasis for seed provisioning than do natural populations (Austin 1973, Roach and Wulff 1987), suggesting that the ability to maintain seed quality can be lost in the absence of natural selection.

In addition to effects on seed provisioning, resource limits to parental plants resulted in specific changes to offspring structure and germination behavior. As in other studies of phenotypic plasticity, evaluating the possible adaptive significance of these responses requires ecophysiological interpretation of particular traits and resources, since it is not possible to quantify the fitness contributions of single traits nor to operationally distinguish fitness decrements due to resource limitation from adaptive plasticity that mitigates such decrements

(Sultan and Bazzaz 1993*a*). The thinner pericarps produced by light-deprived parents resulted in earlier seed germination, which is likely to be advantageous in competitive situations (Fenner 1985). Studies in natural populations show that differences in emergence time of even 1–2 d can have enormous effects on seedling biomass (Morse and Schmitt 1985), survival (Howell 1981), and reproductive fitness (Kalisz 1986). Such a pre-emptive head start over competitors may be particularly critical to seedling success in light-limited microsites. Low light *P. persicaria* progeny emerged earlier from soil and consequently had a height and biomass advantage over the offspring of high-light-grown plants in both low and high light greenhouse plots (S. Sultan, *unpublished manuscript*). Note, however, that the early-emergence benefits of thinner pericarps probably entail reduced seed longevity in the seed bank as well as a greater risk of mortality due to late frost. The relative costs and benefits of this trade-off will obviously depend on seasonal conditions and will therefore vary even within local populations (Kalisz 1986). In addition, achenes of both light-deprived and moisture-deprived *P. persicaria* parents had greater total (immediate) germination than those produced by parents given ample resources. Again, this represents a trade-off between high immediate reproduction and spreading germination unevenly across a longer time period. Similar increases in immediate germination and reduced dormancy in the offspring of droughted plants have been noted in several species (Sawhney and Naylor 1982, Arnold et al. 1992), although other species respond to parental drought by producing *less* permeable seed coats, which result in longer dormancy (e.g., Nooden et al. 1985). The evolution of one plastic response or the other may reflect the degree to which drought conditions autocorrelate across growth seasons in conjunction with the strength of selection against germination in soil that is less than very moist. Note that in *P. persicaria,* the slightly earlier emergence of dry-produced achenes reflected not thinner pericarps (which would facilitate germination in relatively dry soil), but a faster initial growth rate due to enhanced seed provisioning.

Nutrient-deprived *P. persicaria* genotypes did not maintain or enhance offspring provisioning, nor did their progeny germinate faster or in higher proportions. Evidently, severe nutrient limitation does not allow for the homeostatic responses that occur under parental water and light deprivation. However, through plasticity in seedling growth patterns, these genotypes showed homeostasis under nutrient deprivation in another trait important to seedling fitness: although the offspring of nutrient-deprived plants were slightly (7%) smaller in total biomass than the progeny of well-nourished parents, their roots were at least equally long (Fig. 4f). These seedlings thus were either allocating relatively more of their biomass to root growth, or were producing finer roots with a given amount of tissue. Parental nutrient deprivation thus influences the precise pattern of seedling development in a way that may be particularly valuable under similar conditions of offspring growth, since allocation to root growth relative to shoots is particularly critical to seedling fitness in low nutrient environments (Wulff 1986*a*). A similar root response to parental environment was found in a study of *Erodium* in which the offspring of plants grown in a simulated dry season produced significantly longer roots upon germination in uniform conditions but no difference in biomass compared with offspring of well-watered plants (A. Dowd-White and K.J. Rice, *unpublished data*). Similarly, the offspring of light-deprived parents produced shorter roots, evidently allocating more of their initial biomass to shoot growth. This pattern of development could be advantageous in a light-limited environment, where the surface layers of soil are likely to be moist, so that initial root elongation may be a lower priority for the seedling than maximizing shoot height and surface area for light interception. The mechanism for these remarkably specific effects of parental environment on seedling growth pattern may be found in the fact that the content and balance of growth hormones in seeds is affected by many aspects of parental environment, including drought, mineral nutrient supply, light quality and duration, and temperature (Gray and Thomas 1982, Gutterman 1982, Khan 1982, King 1982, Arnold et al. 1991). Although the precise role of hormones in seed germination and seedling growth is not fully understood (Gray and Thomas 1982), these growth substances are known to regulate germination, cell division, seedling root and hypocotyl elongation, and source–sink relations of the developing seedling (King 1982, van Staden et al. 1982), and thus provide a plausible mechanism for the effects of parental environment on seedling growth patterns.

Other sources of variation for offspring traits

Although the patterns of response discussed above were common to all genotypes, *P. persicaria* genotypes differed significantly in their patterns of response to parental environment in 5 of the 21 analyses performed on traits of ecological importance. For example, when deprived of soil moisture, certain genotypes produced offspring with longer roots, and others produced offspring with similar or shorter roots (Fig. 3f). Little is known about the generality of parental genotype-by-environment interaction for offspring traits (Schmitt et al. 1992), although significant interaction has been found in other plant species for temperature and drought effects on seed dry mass and dormancy (Sawhney and Naylor 1982 and references therein).

The existence of significant genotype and genotype-by-environment variation in even this quite small sample of genotypes (Tables 1–3) suggests that natural populations may harbor a good deal of genetic variation for parental effects on fitness-related offspring traits

such as those measured in this experiment. The existence of such genetic variation may in part be explained by its magnitude relative to sources of variation unavailable to natural selection. In this and other studies (e.g., Schmitt et al. 1992), the effects of parental environment are typically far greater in magnitude than those of parental genotype, particularly under competitive or other naturalistic conditions (Stratton 1989). Mazer (1987) determined that in wild radish, the effect of the offspring's nuclear genotype on seed mass (which correlates strongly with fitness in this system) was 18 times weaker than the effect of maternal environment and cytoplasm (the latter of which was negligible), so that selection would be unable to effect phenotypic change despite the strong fitness effects of seed size variation. In general, additive genetic variation for a trait contributing to individual fitness can persist in populations if the expression of that trait is simultaneously influenced by environmental factors (Price et al. 1988, Alatalo et al. 1990, Sultan and Bazzaz 1993*a*). Since offspring traits such as size, provisioning, and emergence time are strongly affected by parental environment, response to selection on those traits may be slowed or prevented (Howell 1981, Roach and Wulff 1987, Kirkpatrick and Lande 1989). Note that the offspring's own immediate environment will also affect its expression of these traits and their impact on fitness (Haig and Westoby 1988, Venable 1992). Thus, like other aspects of genotype-by-environment interaction for traits important to fitness, environment-specific parental effects on offspring traits can obscure average differences among genotypes and thus act to maintain genetic variation (Via 1987, Sultan 1987).

Finally, there is great variation within *P. persicaria* parents for the size and provisioning of individual offspring, probably as a result of position and timing effects on maturing achenes. Seedling biomass varied 2–3 fold within parent plants of a given genotype and environment (cf. dependent-variable ranges, Figs. 2b, 3b, 4b). This is ecologically important variation that is inherently unavailable to selection; indeed much of the seed-size variation that has been found to correlate with offspring success originates within parent individuals (e.g., Carleton and Cooper 1972). Seed mass generally varies from 5–10 fold within parent plants (Stanton 1984*b*, Fenner 1985, Gross and Smith 1991). In addition to size and provisioning effects, variation among offspring of a plant in position and time of development can lead to variability in germination behavior, longevity, and seedling growth rate (Wulff 1973, Gray and Thomas 1982, Gutterman 1982, Silvertown 1984). This within-parent variability can be viewed as an adaptive solution to environmental unpredictability (Kaplan and Cooper 1984), although it may simply represent parental inability to produce uniform offspring given position effects on development and temporal changes in parental resource status (McGinley et al. 1987). In either case, because the expression of genetic variation for offspring traits is strongly influenced by parental environment, and substantial variation in fitness-related traits occurs within parental genotypes, genetic variation among parents for these traits is likely to be largely unavailable to selection.

Conclusions

It has often been assumed (based on seed mass changes) that plants in unfavorable circumstances inevitably produce poorly provisioned offspring that will carry the parent's environmental disadvantage into the subsequent generation. Detailed study of *P. persicaria* achene and seedling traits revealed that parental genotypes alter the provisioning, structure, and growth traits of offspring specifically in response to parental conditions in ways likely to maintain or enhance the probability of successful establishment. These trait- and resource-specific responses thus constitute an aspect of phenotypic plasticity, the capacity of individual organisms to appropriately change and/or hold constant functionally important traits in response to environmental limits. The results make clear that it may not be possible to correctly assess the effects of parental environment on offspring fitness based on propagule mass alone, as changes in size may not reflect effects on propagule structure and composition that influence germination and performance (Marshall et al. 1985, Benner and Bazzaz 1988, McGinley and Charnov 1988, Lacey 1991).

Acknowledgments

This research was fully supported by a Center for Population Biology Post-Doctoral Fellowship from the University of California at Davis. I thank Maureen L. Stanton and Kevin J. Rice for generously making growth chamber, greenhouse, and laboratory facilities available. I am also indebted to them and to the members of their lab groups for valuable discussion of experimental design and analysis. Staci Markos provided capable technical assistance. I thank F. A. Bazzaz for providing growth facilities for the parental generation, Marc Mangel for the use of computing facilities, and Neil Willits of the U.C. Davis Statistics Lab for statistical consultation. The manuscript was improved by the comments of David Ackerly, Richard Grosberg, Bob Lalonde, and David Parichy, as well as those of Diane Marshall, Massimo Pigliucci, and three anonymous reviewers.

Literature Cited

Alatalo, R. V., L. Gustaffson, and A. Lundberg. 1990. Phenotypic selection on heritable size traits: environmental variance and genetic response. American Naturalist **135**: 464–471.

Arnold, R. L. B., M. Fenner, and P. J. Edwards. 1991. Changes in germinability, ABA content and ABA embryonic sensitivity in developing seeds of *Sorghum bicolor* induced by water stress. New Phytologist **118**:339–347.

Arnold, R. L. B., M. Fenner, and P. J. Edwards. 1992. Mineral allocation to reproduction in *Sorghum bicolor* and *S. halapense* in relation to parental nutrient supply. Oecologia **92**:138–144.

Austin, R. B. 1973. Effects of environment before harvesting on viability. Pages 114–148 *in* E. H. Roberts, editor. Viability of seeds. Chapman and Hall, London, UK.

Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. Ecology **53**:997–1010.

Barton, L. V. 1965. Seed dormancy: general survey of dormancy types in seeds, and dormancy imposed by external agents. Encyclopedia der Pflanzenphysiologie: 699–720.

Benner, B. L., and F. A. Bazzaz. 1988. Carbon and mineral element accumulation and allocation in two annual plant species in response to timing of nutrient addition. Journal of Ecology **76**:19–40.

Boutin, C., and P. Morisset. 1988. Etude de la plasticité phénotypique chez le *Chrysanthemum leucanthemum.* I. Croissance, allocation de la biomasse et reproduction. Canadian Journal of Botany **66**:2285–2298.

Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics **13**:115–155.

Bradshaw, A. D., and K. Hardwick. 1989. Evolution and stress—genotypic and phenotypic components. Biological Journal of the Linnean Society **37**:137–155.

Brown, M. B., L. Engelman and R. I. Jennrich. 1990. BMDP. University California Press, Berkeley, California, WA.

Carleton, A. E., and C. S. Cooper. 1972. Seed size effects upon seedling vigor of three forage legumes. Crop Science **12**:183–186.

Casper, B. B. 1990. Seedling establishment from one- and two-seeded fruits of *Cryptantha flava*: a test of parent–offspring conflict. American Naturalist **136**:167–177.

Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs **59**:433–463.

Dolan, R. W. 1984. The effect of seed size and maternal source on individual size in a population of *Ludwigia leptocarpa.* American Journal of Botany **71**:1302–1307.

Evans, A. S., and R. J. Cabin. 1995. Can dormancy affect the evolution of post-germination traits? The case of *Lesquerella fendleri.* Ecology **76**:344–356.

Fenner, M. 1985. Seed ecology. Chapman and Hall, London, UK.

———. 1986*a*. The allocation of minerals to seeds in *Senecio vulgaris* plants subjected to nutrient shortage. Journal of Ecology **74**:385–392.

———. 1986b. A bioassay to determine the limiting minerals for seeds from nutrient-deprived *Senecio vulgaris* plants. Journal of Ecology **74**:497–505.

———. 1987. Seedlings. New Phytologist **106** (supplement): 35–47.

Forbes, L. S. 1991. Optimal size and number of offspring in a variable environment. Journal of Theoretical Biology **150**:299–304.

Gillespie, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. American Naturalist **111**:1010–1014.

Gray, D., and T. H. Thomas. 1982. Seed germination and seedling emergence as influenced by the position of development of the seed on, and chemical applications to, the parent plant. Chapter 4 *in* A. A. Khan, editor. Physiology and biochemistry of seed development, dormancy, and germination. Elsevier Biomedical, New York, New York, USA.

Groeters, F. R., and H. Dingle. 1988. Genetic and maternal influences on life history plasticity in milkweed bugs: response to temperature. Journal of Evolutionary Biology **1**: 317–333.

Gross, K. L., and A. D. Smith. 1991. Seed mass and emergence time effects on performance of *Panicum dichotomiflorum* Michx. across environments. Oecologia **87**:270–278.

Gutterman, Y. 1982. Phenotypic maternal effect of photoperiod on seed germination. Pages 67–80 *in* A. A. Khan, editor. Physiology and biochemistry of seed development, dormancy, and germination. Elsevier Biomedical, New York, New York, USA.

———. 1985. Flowering, seed development, and the influences during seed maturation on seed germination of annual weeds. Pages 1–25 *in* S. O. Duke, editor. Weed physiology. CRC, Boca Raton, Florida, USA.

Haig, D. and M. Westoby. 1988. Inclusive fitness, seed resources, and maternal care. Pages 60–79 *in* J. and L. Lovett-Doust, editors. Plant reproductive ecology. Oxford University Press, Oxford, UK.

Hammerton, J. L., and M. Jalloq. 1970. Environmental effects on seed weight, seed polymorphism, and germination behavior in *Polygonum lapathifolium* and *P. persicaria.* Weed Research **10**:204–217.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.

Harper, J. L., P. H. Lovell, and K. G. Moore. 1970. The shapes and sizes of seeds. Annual Review of Ecology and Systematics **1**:327–356.

Howell, N. 1981. The effect of seed size and relative emergence time on fitness in a natural population of *Impatiens capensis.* American Midland Naturalist **105**:312–320.

Justice, O. L. 1941. A study of dormancy in seed of *Polygonum.* Memoirs of the Cornell Agricultural Experiment Station Number **235**.

Kalisz, S. 1986. Variable selection on the timing of germination in *Collinsia verna.* Evolution **40**:479–491.

Kaplan, R. H., and W. S. Cooper. 1984. The evolution of developmental plasticity in reproductive characteristics: an application of the "adaptive coin-flipping" principle. American Naturalist **123**:393–410.

Kaufmann, M. R. 1977. Water deficits and reproductive growth. Pages 91–124 *in* T. T. Kozlowski, editor. Plant responses and control of water balance. Volume III. Academic Press, New York, New York, USA.

Khan, A. A. 1982. Giberellins and seed development. Chapter 5 *in* A. A. Kahn, editor. Physiology and biochemistry of seed development, dormancy, and germination. Elsevier Biomedical, New York, New York, USA.

King, R. W. 1982. Abscisic acid in seed development. Chapter 7 *in* A. A. Kahn, editor. Physiology and biochemistry of seed development, dormancy, and germination. Elsevier Biomedical, New York, New York, USA.

Kirkpatrick, M., and R. Lande. 1989. The evolution of maternal characters. Evolution **43**:485–503.

Koller, D. 1972. Environmental control of seed germination. Pages 2–102 *in* T. T. Kozlowski, editor. Seed biology. Volume II. Academic Press, New York, New York, USA.

Lacey, E. 1991. Parental effects on life-history traits in plants. Pages 735–744 *in* E. C. Dudley, editor. The unity of evolutionary biology. Volume II. International Congress of Systematic and Evolutionary Biology IV. Dioscorides, Portland, Oregon, USA.

Levene, H. 1960. Robust tests for equality of variance. Pages 278–292 *in* I. Olkin, editor. Contributions to probability and statistics. Stanford University Press, Stanford, California, USA.

Lloyd, D. G. 1987. Selection of offspring size at independence and other size-versus-number strategies. American Naturalist **129**:800–817.

Marshall, D. L., N. L. Fowler, and D. A. Levin. 1985. Plasticity in yield components in natural populations of 3 species of *Sesbania.* Ecology **66**:753–761.

Mazer, S. J. 1987. Quantitative genetics of life history and fitness components in *Raphanus raphanistrum*: ecological and evolutionary consequences of seed-weight variation. American Naturalist **130**:891–914.

———. 1989. Ecological, taxonomic, and life-history correlates of seed mass among Indiana dune angiosperms. Ecological Monographs **59**:153–175.

McGinley, M. A., D. H. Temme, and M. A. Geber. 1987.

Parental investment in offspring in variable environments. American Naturalist **130**:370–398.
McGinley, M. A., and E. C. Charnov. 1988. Multiple resources and the optimal balance between size and number of offspring. Evolutionary Ecology **2**:77–84.
Meckel, L., D. B. Egli, R. E. Phillips, D. Radcliffe, and J. E. Leggett. 1984. Agronomy Journal **76**:647–650.
Morse, D. H., and J. Schmitt. 1985. Propagule size, dispersal ability, and seedling performance in *Asclepias syriaca*. Oecologia **67**:372–379.
Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models. Third edition. Richard D. Irwin, Boston, Massachusetts, USA.
Nooden, L. D., K. A. Blakley, and J. M. Grzybowski. 1985. Control of seed coat thickness and permeability in soybean: a possible adaptation to stress. Plant Physiology **79**:543–545.
Parichy, D. M., and R. H. Kaplan. 1992. Maternal effects on offspring growth and development depend on environmental quality in the frog *Bombina orientalis*. Oecologia **91**:579–586.
Parrish, J. A. D., and F. A. Bazzaz. 1985. Nutrient content of *Abutilon theophrasti* seeds and the competitive ability of the resulting plants. Oecologia **65**:247–251.
Platenkamp, G. A. J., and R. G. Shaw. 1993. Environmental and genetic maternal effects on seed characters in *Nemophila menziesii*. Evolution **47**:540–555.
Price, T., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. Science **240**:798–799.
Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution **43**:223–225.
Roach, D. A., and R. D. Wulff. 1987. Maternal effects in plants. Annual Review of Ecology and Systematics **18**: 209–235.
Sachs, L. 1984. Applied statistics. Second edition. Springer-Verlag, Berlin, Germany.
Salisbury, E. J. 1942. The reproductive capacity of plants. Bell, London, UK.
———. 1974. Seed size and mass in relation to environment. Proceedings of the Royal Society of London, Series **B 186**: 83–88.
Sawhney, R., and J. M. Naylor. 1982. Influence of drought stress during seed development on duration of seed dormancy. Canadian Journal of Botany **60**:1016–1020.
Schaal, B. A. 1984. Life-history variation, natural selection, and maternal effects in plant populations. Pages 188–206 *in* R. Dirzo and J. Sarukhán, editors. Perspectives on plant population ecology. Sinauer, Sunderland, Massachusetts, USA.
Schimpf, D. 1977. Seed weight of *Amaranthus retroflexus* in relation to moisture and length of growing season. Ecology **58**:450–453.
Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. Annual Review of Ecology and Systematics **17**:667–693.
Schmitt, J., J. Niles, and R. D. Wulff. 1992. Norms of reaction of seed traits to maternal environments in *Plantago lanceolata*. American Naturalist **139**:451–466.
Shipley, B., and M. Parent. 1991. Germination responses of 64 wetland species in relation to seed size, minimum time to reproduction and seedling relative growth rate. Functional Ecology **5**:111–118.
Silvertown, J. W. 1984. Phenotypic variety in seed germination behavior: the ontogeny and evolution of somatic polymorphism in seeds. American Naturalist **124**:1–16.
Sinervo, B. 1991. Experimental and comparative analysis of egg size in lizards: constraints on the adaptive evolution of maternal investment per offspring. Pages 725–734 *in* E. C. Dudley, editor. The unity of evolutionary biology. Volume II. International Congress of Systematic and Evolutionary Biology IV. Dioscorides, Portland, Oregon, USA.
Snedecor, G. W., and W. G. Cochran. 1989. Statistical methods. Eighth edition. Iowa State University Press, Ames, Iowa, USA.
Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman, New York, New York, USA.
Staniforth, R. J., and P. B. Cavers. 1979. Field and laboratory germination responses of achenes of *Polygonum lapathifolium, P. pensylvanicum,* and *P. persicaria*. Canadian Journal of Botany **57**:877–885.
Stanton, M. L. 1984*a*. Seed size variation in wild radish: effect of seed size on components of seedling and adult fitness. Ecology **65**:1105–1112.
———. 1984*b*. Developmental and genetic sources of seed weight variation in *Raphanus raphanistrum*. American Journal of Botany **71**:1090–1098.
Steele, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, New York, New York, USA.
Stephenson, A. G. 1992. The regulation of maternal investment in plants. Pages 151–172 *in* C. Marshall and J. Grace, editors. Fruit and seed production: aspects of development, environmental physiology and ecology. Cambridge University Press, Cambridge, UK.
Stratton, D. J. 1989. Competition prolongs expression of maternal effects in seedlings of *Erigeron annuus* (Asteraceae). American Journal of Botany **76**:1646–1653.
Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. Evolutionary Biology **21**:127–176.
———. 1990. Evolutionary implications of phenotypic plasticity: genetic diversity for norms of reaction to resource gradients in *Polygonum persicaria* L. Dissertation. Harvard University, Cambridge, Massachusetts, USA.
Sultan, S. E., and F. A. Bazzaz. 1993*a*. Phenotypic plasticity in *Polygonum persicaria*. I. Diversity and uniformity in genotypic norms of reaction to light. Evolution **47**:1009–1031.
Sultan, S. E., and F. A. Bazzaz. 1993*b*. Phenotypic plasticity in *Polygonum persicaria*. II. Norms of reaction to soil moisture, ecological breadth, and the maintenance of genetic diversity. Evolution **47**:1032–1049.
Sultan, S. E., and F. A. Bazzaz. 1993*c*. Phenotypic plasticity in *Polygonum persicaria*. III. The evolution of ecological breadth for nutrient environment. Evolution **47**:1050–1071.
van Staden, J., J. E. Davey, and N. A. Brown. 1982. Cytokinins in seed development and germination. Chapter 6 *in* A. A. Kahn, editor. Physiology and biochemistry of seed development, dormancy, and germination. Elsevier Biomedical, New York, New York, USA.
Venable, D. L. 1992. Size–number tradeoffs and the variation of seed size with plant resource status. American Naturalist **140**:287–304.
Via, S. 1987. Genetic constraints on the evolution of phenotypic plasticity. Pages 47–71 *in* V. Loeschcke, editor. Genetic constraints on adaptive evolution. Springer-Verlag, Berlin, Germany.
Wareing, P. F. 1982. Hormonal regulation of seed dormancy. Chapter 8 *in* A. A. Kahn, editor. Physiology and biochemistry of seed development, dormancy, and germination. Elsevier Biomedical, New York, New York, USA.
West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics **20**:249–270.
Westoby, M. 1981. How diversified seed germination behavior is selected. American Naturalist **118**:882–885.
Wilkinson, L., and M. Bjerknes. 1987. SYSTAT version 3.1 for Macintosh. SYSTAT, Evanston, Illinois, USA.
Winn, A. A. 1985. Effects of seed size and microsite on seedling emergence of *Prunella vulgaris*. Journal of Ecology **73**:831–840.

Wulff, R. 1973. Intrapopulational variation in the germination of seeds in *Hyptis suaveolens*. Ecology **54**:646–649.

———. 1986*a*. Seed size variation in *Desmodium paniculatum*. II. Effects on seedling growth and physiological performance. Journal of Ecology **74**:99–114.

———. 1986*b*. Seed size variation in *Desmodium paniculatum*. III. Effects on reproductive yield and competitive ability. Journal of Ecology **74**:115–121.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.