

PHENOTYPIC PLASTICITY FOR FITNESS COMPONENTS IN *POLYGONUM* SPECIES OF CONTRASTING ECOLOGICAL BREADTH

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Abstract. The ecological distribution of species is influenced by individual patterns of response to environment for traits that contribute to fitness. Comparative data on fitness responses to complex environments are particularly valuable for understanding the relation of plasticity to ecological breadth. This study compares individual phenotypic plasticity for components of fitness in four congeneric annual plant species with contrasting ecological distributions (*Polygonum cespitosum*, *P. hydropiper*, *P. lapathifolium*, and *P. persicaria*). Replicate seedlings of 32 inbred lineages drawn from five natural populations per species were grown to maturity under controlled conditions in all 12 possible combinations of low and high light; dry, moist, and flooded soil; and poor vs. rich nutrients. Timing of reproduction, total reproductive output, offspring size, and allocation to reproduction were determined for each plant.

The data revealed highly complex differences among the species in patterns of plastic response for fitness traits (i.e., high-order species-by-environment interaction effects). These plasticity differences illuminate the species' known differences in ecological distribution. Individuals of the broad ecological generalist *P. persicaria* maintained fecundity and offspring size in poor conditions and also reproduced at extremely high levels when given plentiful resources. In contrast, *P. lapathifolium* plants showed high fitness in favorable treatments but sharply delayed and decreased reproduction as well as offspring size when deprived of light and other resources; this species is restricted in nature to high-light, moist sites. Conversely, *P. hydropiper* plants increased reproductive output relatively little in resource-rich environments, which may explain why this species is not an invasive colonizer. Although other factors evidently limit *P. cespitosum* to shaded habitats, the ability shown by plants in this species to maintain offspring size and output across a range of environments may be a factor in its extremely rapid spread. These results confirm that ecological breadth of distribution may reflect not an equable, constant pattern of fitness response, but rather the ability to both maintain fitness in resource-poor environments and opportunistically maximize fitness in favorable conditions. These results contribute three important insights to our understanding of the relation of phenotypic plasticity to ecological breadth: ecologically important species differences in fitness plasticity may entail (a) multiple environmental factors, as well as (b) a number of distinct fitness components; furthermore (c) neither reproductive plasticity nor constancy per se is necessarily associated with ecological breadth.

Key words: annual plants; ecological generalists; fitness components; maternal effects; niche breadth; phenotypic plasticity; *Polygonum*; reproduction, timing of.

INTRODUCTION

Although phenotypic plasticity is now widely recognized as a major source of variation in nature, the ecological significance of plasticity remains to be fully understood. How do individual patterns of response to environment influence the ecological distribution of taxa? Individuals of different taxa may show different patterns of plasticity for traits that contribute directly to fitness (Marshall et al. 1986, Bradshaw and Hardwick 1989, Ford and Seigel 1989, Travis 1994). These patterns of fitness response (along with the growth traits that underlie them) determine the range of con-

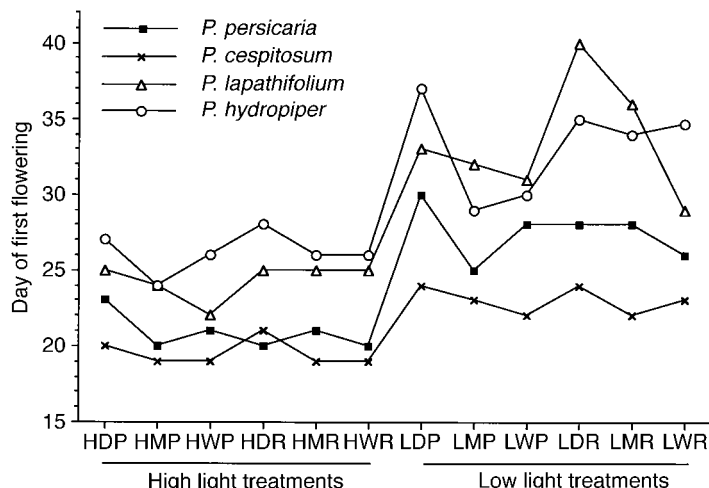
ditions in which species may survive and successfully reproduce, and hence their fundamental ecological breadth (sensu Futuyma and Moreno 1988). For instance, species may be excluded from certain environmental conditions in which their constituent individuals produce few, or poor-quality offspring, and hence fail to establish populations. Increasing our knowledge of phenotypic plasticity for fitness components is therefore essential to more fully understand ecological differences among species (Ford and Seigel 1989). However, relatively little is known about the nature of species differences in plasticity for fitness-related traits (Schlichting and Levin 1986, Roskam and Brakefield 1996), or about how such differences may affect ecological distribution (Travis 1994, Sultan 1995 and references therein).

Comparative information is also needed to clarify

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FIG. 1. Plasticity for time to reproduction (day of first flowering) in four *Polygonum* species grown in all combinations of high (H) vs. low (L) light; dry (D), moist (M), or wet (W) moisture conditions; and poor (P) vs. rich (R) nutrients. Means are shown for eight plants per multifactorial treatment per species; plants from the same set of eight inbred lineages are represented in every treatment (details in *Methods*).



the relation of ecological breadth to patterns of fitness plasticity in general (Sultan et al. 1998a). Species that are ecological generalists are thought to consist of individuals able to maintain fitness in a wide range of environments (Baker 1965, 1974; see Futuyma and Moreno 1988, Sultan 1992). Accordingly, one prevalent view holds that ecological generalists will be characterized by relatively constant or equable patterns of response across environments for fitness traits (Levins 1968, Lortie and Aarssen 1996). An alternative view predicts that the fitness response of generalist species will have two distinct aspects: maintaining reasonable levels of fitness in poor environments, and achieving

extremely high fitness in favorable, resource-rich conditions (Baker 1965, 1974, Noble 1989, Sultan 1995). Such a response pattern might be relatively constant for certain fitness traits, such as reproductive timing and offspring size, but markedly plastic for others such as total fecundity. To evaluate these general models regarding equability vs. plasticity of fitness traits and species distribution requires comparative plasticity data for species of contrasting ecological breadth.

The relative paucity of information on these critical issues may reflect the fact that appropriate studies are quite demanding in scope. First, studies designed to illuminate the ecological significance of fitness plas-

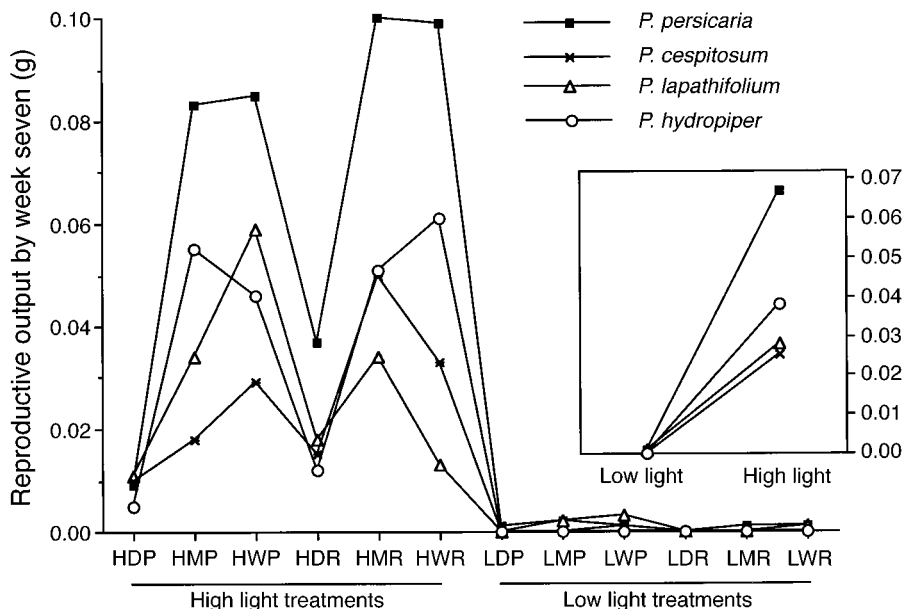


FIG. 2. Plasticity for early reproductive output in four *Polygonum* species grown in all combinations of high (H) vs. low (L) light; dry (D), moist (M), or wet (W) moisture conditions; and poor (P) vs. rich (R) nutrients. Means are shown for eight plants per multifactorial treatment per species; plants from the same set of eight inbred lineages are represented in every treatment (details in *Methods*). The inset shows species means for all plants in low and high light environments (averaged across moisture and nutrient treatments).

ticity depend critically upon a meaningful measurement of fitness (Reznick and Travis 1996 and references therein). Notwithstanding Darwin's elegantly simple concept of "success in leaving progeny" (1859: 62), this success is in fact difficult to measure because it depends on the production of offspring that themselves survive and reproduce (Slobodkin 1968, Pianka 1981, de Jong 1994). Although investigators often rely on reproductive output alone (or some proxy such as flower number), a complete evaluation of fitness must include, in addition, several traits that influence realized offspring success (Reznick and Travis 1996). In plants, offspring size and quality affect germination, emergence, and seedling growth rates; and hence survival, establishment, and fecundity of the offspring generation (Haig and Westoby 1988, Kalisz 1989, Farris and Lechowicz 1990, Sultan 1996, Donaghue and Schmitt 1998, Lloret et al. 1999). Developmental trajectories including reproductive allocation and timing may also influence adult success in leaving offspring, apart from total output (Marshall et al. 1986, Newman 1988, Sans and Masalles 1994, Galloway 1995). For instance, early flower and seed production may be essential in variable environments (Baker 1965, 1974, Meerts 1992, Zhang and Lechowicz 1994). Meaningful comparisons of fitness plasticity must therefore consider patterns of individual response for several traits likely to contribute to fitness in natural populations, including age at reproduction, number and size of offspring, and reproductive allocation (Marshall et al. 1986, Reznick and Travis 1996).

Second, in addition to considering multiple components of fitness, ecologically meaningful studies must examine plastic responses to environmental factors of known importance in the field (Marshall et al. 1986, Van Noordwijk 1989). Since environmental stresses as well as ecological differences between habitats are complex rather than single-factor in nature (Chapin et al. 1987, Bazzaz and Morse 1991, Chapin 1991), plasticity data for multifactorial environments offer greater insight into the nature of species differences in fitness response (Bazzaz 1996 and references therein, Tarasjev 1997). Environmental factors of interest must be varied under controlled conditions to accurately characterize and interpret patterns of plastic response (Travis 1994); responses to experimental environments can then be used to interpret known patterns of actual distribution (Trexler et al. 1990, Wesser and Armbruster 1991, Sultan et al. 1998a). Knowledge of field variability for key factors provides a particularly strong interpretive context for such response data (Zhang and Lechowicz 1994, Sultan 1995).

Finally, to investigate ecologically important species diversity in patterns of fitness response, closely related taxa must be compared that show contrasting ecological distributions in the absence of confounding phylogenetic or life-history differences (Marshall et al. 1986, Travis 1994). Robust species-level comparisons must

include individuals from several populations of each species (Colwell and Futuyma 1971, Quinn and Hodgkinson 1983, Bradshaw 1984).

Here I present the results of a comparative study designed to examine the relationship between phenotypic plasticity for fitness components and ecological breadth, using as a model system a group of four closely related plant species in the genus *Polygonum*. These species are colonizing annuals that inhabit significantly different ranges of light, soil moisture, and nutrient levels in the field (Sultan et al. 1998b). This model system affords marked contrasts in ecological breadth in the absence of confounding differences due to divergent evolutionary histories, life-cycle, breeding system, or general morphology (references in Sultan et al. 1998b; see Rabinowitz 1981, Kruckeberg and Rabinowitz 1985, and Harvey and Pagel 1991 on appropriate design of comparative studies). Using inbred lines drawn from several populations of each species, I determined patterns of individual plasticity for fitness components in response to controlled multifactorial light, moisture, and nutrient environments. In presenting the results, I address the following specific questions: (1) How do patterns of plasticity for fitness components differ among the *Polygonum* species? (2) Do species differences in patterns of fitness response explain known differences in their ecological distributions? (3) Does equability vs. plasticity for fitness traits correlate with ecological breadth?

METHODS

Study system

Polygonum persicaria, *P. lapathifolium*, *P. hydro-piper*, and *P. cespitosum* are closely related species within a strongly delineated monophyletic section of the genus (Löve and Löve 1956, Mitchell and Dean 1978, Weber and Wittman 1992). The species are extremely similar morphologically, and share an identical life history as obligately annual herbs of disturbed habitats (references in Sultan et al. 1998b). They also share a common breeding system consisting of predominant self-fertilization with a low proportion of outcrossing (Stanford 1925, Simmonds 1945a, b, Mulligan and Findlay 1970, Staniforth and Cavers 1979; S. E. Sultan, unpublished data). All four species reproduce by means of small, long-lived achenes (one-seeded fruits) produced in indeterminate spikes throughout the growth season. The species are all introduced in northeastern North America, where they occupy a common geographic range (Mitchell and Dean 1978, Gleason and Cronquist 1991, Hobbs 1992). Within this range, the species differ markedly in ecological breadth (Table 1; see Sultan et al. 1998b for environmental data and references). *P. persicaria* is an ecological generalist, excluded only from extremely low-light sites, while each of the remaining species is excluded from several low and/or high light, moisture, and nutrient habitats.

TABLE 1. Ecological distribution of *Polygonum* species and predicted patterns of plasticity for fitness components in corresponding experimental light, moisture, and nutrient treatments (details in *Methods*).

Species	Light		Moisture			Nutrients	
	Low	High	Dry	Moist	Wet	Poor	Rich
<i>P. persicaria</i>	≡		≡			≡	
Predicted plasticity	M	H	M	H	H	M	H
<i>P. lapathifolium</i>	≡		≡			≡	
Predicted plasticity	D/VL/R	H	D/VL/R	H	H	D/VL/R	H
<i>P. cespitosum</i>	≡		≡			≡	
Predicted plasticity	M	NH	D/VL/R	H	NH	M	NH
<i>P. hydropiper</i>	≡		≡			≡	
Predicted plasticity	D/VL/R	H	D/VL/R	H	H	D/VL/R	H

Notes: Triple lines (≡) denote the range of resource levels in which each species occurs in the field (based on environmental data of Sultan et al. [1998b]). Plasticity predictions are based on the view that species occurrence in resource-poor habitats requires maintaining reproduction and offspring quality despite low resource levels, while occurrence in resource-rich habitats requires achieving high reproductive output in favorable conditions (see *Introduction*). Prediction codes: M, species is predicted to maintain early flowering and fruiting, reproductive output, and achene mass in resource poor treatments (low light, dry, poor nutrients); D/VL/R, species predicted to show delayed flowering and fruiting and/or very low reproductive output and/or reduced achene mass in resource-poor treatments; H, prediction for species to achieve high reproductive output in favorable treatments (high light, moist, wet, rich nutrients); NH, prediction for species reproductive output in favorable treatments to be not high.

Experimental sample

To create robust samples for the species-level comparisons of interest, the study was designed to maximize the sample of populations within each species (Quinn and Hodgkinson 1983). Achenes were collected (September 1994) from five well-established populations of each species representing its range of habitats in northeastern North America (site details in Sultan et al. 1998b). Achenes collected from eight field parents per population were germinated and raised to maturity under uniform glasshouse conditions. Mature, inbred (selfed full-sib) achenes were collected from either one or two of these glasshouse-grown plants from each population, for a sample of eight randomly chosen inbred achene families per species representing five natural populations of that species (total experimental sample = 32 families). Achenes of each family were stratified in vials of distilled water for 6 wk at 4°C, and then sown into flats of moist vermiculite (18 March 1996). Flats were randomized on two glasshouse benches and maintained at 24°C day/20°C night until seedlings reached the first true-leaf stage. One seedling replicate from each family was randomly assigned to each of 12 multifactorial environmental treatments (see next paragraph), for an experimental sample of eight plants per species per treatment (1 plant per family per treatment × 12 treatments × 8 families per species × 4 species; total $N = 384$).

Environmental treatments

Treatments consisted of all possible combinations of high (H) vs. low (L) light; dry (D), moist (M), or wet (flooded, W) soil; and rich (R) vs. poor (P) nutrients, for a total of 12 multifactorial environments (e.g.,

HDR, HMR, etc.). Seedlings were transplanted into individual prefilled 0.8-L clay pots, set into randomly assigned positions and treatments in a random complete block design on eight glasshouse benches, and grown under natural photoperiod to senescence (11 April 1996–8 July 1996). Plants in low light were placed under frames covered in black plastic neutral-density shade cloth. They received ~15% of the photosynthetically active radiation reaching those in open plots (means ± 1 SD of 60 clear midday measurements per treatment = $185 \pm 40 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ [L] vs. $1239 \pm 108 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ [H]).

Moisture treatments were maintained by an automatic system that delivered reverse osmosis-filtered water to one (dry), two (moist), or four (wet) Chapin watering tubes per pot (Chapin Watermatics, Watertown, New York) via central feeder pipes on each bench plumbed to solenoid valves. All plants were kept evenly moist for the first 4 d of the experiment to insure establishment; on day five the system was programmed to release 10 mL of water per tube daily at 0700, 1100, and on H benches additionally at 1400. (The standard deviation among tubes was <5% of water volume, based on a random sample of 20 tubes per bench.) Watering volume on the H benches was increased from 30 to 40 mL/d on day 30. Plants in the W treatment were submerged in 1-gallon (3.79-L) white plastic tubs filled with water to within 2 cm of soil level; water levels were manually maintained as required. Mean soil moisture (percentage dry mass) in the D, M, and W treatments was $8.0 \pm 3.2\%$, $32.3 \pm 3.7\%$, and $49.2 \pm 2.6\%$ respectively (based on soil samples collected at 5 cm depth from one pot per species per multifactorial treatment; $N = 16$ pots per moisture treatment).

Nutrient treatments consisted of 800 mL per pot of a 1:1:1 mixture of sterilized sandy loam:coarse sand: Turface fritted clay (Profile Products, Buffalo Grove, Illinois), with either no added nutrients (P) or an addition of 2.5 g per pot of granular 15:8:12 NPK fertilizer (Agway Inc., Syracuse, New York; R). Soil macronutrient content (based on Morgan-extraction analyses [Lunt et al. 1950]) of mixed soil samples collected from three pots per nutrient treatment prior to planting (analyses performed by University of Massachusetts Soil Lab, Amherst, Massachusetts) was 2 mg/kg NH₄, 5 mg/kg P, and 118 mg/kg K in the poor treatment; compared with 46 mg/kg NH₄, 17 mg/kg P, and 310 mg/kg K in the rich treatment. These values correspond respectively to very low ammonium, low phosphorous, and moderate potassium levels for natural soils in the region (P); and high to extremely high levels for regional soils (R; Fellows 1981). Plants in all treatments were kept at 22°C day/19°C night (ranges 21–24°C and 18–21°C); daily mean relative humidity ranged from 52% to 82% and did not differ significantly among blocks (J. Tufts, *unpublished data*).

Data collection

Plants were monitored daily and the date of first flowering recorded for each plant. Mature achenes were collected from each plant at weekly intervals (starting at week five) by gently shaking infructescences into an envelope, to prevent possible loss of released achenes. Early reproduction was calculated for each plant as the cumulative air-dried mass of mature achenes produced by week seven. On days 71–75, the remaining achenes (mature and immature) were collected from all plants (along with vegetative tissues and roots, one block at a time), and air dried for one week on glasshouse benches. Total achene biomass (lifetime reproductive output) was computed as the summed air-dried mass of all achene collections for each plant. A random subsample of 20 mature achenes was taken from each plant's final achene collection and weighed to calculate the mean mass of individual achenes for each plant (= subsample mass/20). The total number of achenes produced by each plant was estimated as the total achene mass divided by the mean mass of individual achenes for that plant. The total biomass of plants was computed as the total achene biomass plus the summed masses of separately harvested leaves, stems, reproductive support, and washed roots, oven dried at 100°C for 1 h and subsequently dried to a constant mass at 65°C. Reproductive allocation (percentage biomass) was computed for each plant as $[(\text{total achene biomass} / \text{total plant biomass}) \times 100]$.

The final sample included 371 plants: 13 plants either died or were deleted from the data set due to treatment error. In addition, three very large outliers (>5 SE from the cell mean) were deleted for early reproduction and total achene biomass due to evident measurement error,

and first-flowering date information was missing for 13 plants.

Statistical analysis

Model I ANOVA (Systat 5.2.1; Wilkinson et al. 1992) was performed for first flowering date, early reproduction, total achene biomass, total achene number, and mean achene mass to test the (fixed) main effects of species, light, moisture, and nutrients and all two-way, three-way, and four-way interactions of these effects, as well as the (fixed) block effect, on each component of fitness. This univariate approach was appropriate because the specific effects on each variable were of primary interest (Scheiner 1993); experiment-wide probability levels for significance tests were protected by a sequential Bonferroni procedure (Rice 1989). All effects were tested against the error term representing variation among the sample of inbred families for each species; based on preliminary ANOVA showing no significant effect of population for any variable, the among-population source of variation was pooled rather than tested separately as a nested term (Sokal and Rohlf 1981). Variables were transformed as necessary to meet the ANOVA assumptions of homoscedasticity and normality: total achene and plant biomass were transformed as $\log_e(x+1)$ (Steele and Torrie 1980); first flowering date, early reproduction, and total achene number were transformed as $\sqrt{x}+0.5$ (Steele and Torrie 1980); mean achene mass required no transformation. Species-by-environment interactions of interest were examined in plots showing the appropriately calculated means for each species. For example, the species \times light figure for a given trait (e.g., Fig. 3a) shows the mean for each species of plants from eight inbred families grown at low light in all six moisture and nutrient combinations, and the mean of inbred replicates from the same eight families grown at high light in the six moisture and nutrient environments. Differences among species within particular treatments of interest were tested by post hoc Tukey's tests (Wilkinson et al. 1992).

For each component of fitness, the phenotypic variability (plasticity) of each species in response to the range of multifactorial environments was assessed by calculating the species' coefficient of variation for that variable, computed as the standard deviation of the species' mean values in each of the 12 environments scaled by the overall mean of the 12 treatment means (Schlichting and Levin 1984). Species constancy (equability) for total achene biomass across the range of environments was also calculated, using as a performance index the proportion of the species' highest treatment mean that it produced in each environment, summed across the 12 environments (i.e., $\sum [(\bar{x}_{\text{env } 1} / \text{maximum } \bar{x}) + (\bar{x}_{\text{env } 2} / \text{maximum } \bar{x}) \dots + (\bar{x}_{\text{env } 12} / \text{maximum } \bar{x})]$; Adler's *F*; Sultan et al. 1998a). A relatively high level of Adler's *F* indicates that a species maintains close to its maximum reproductive output across

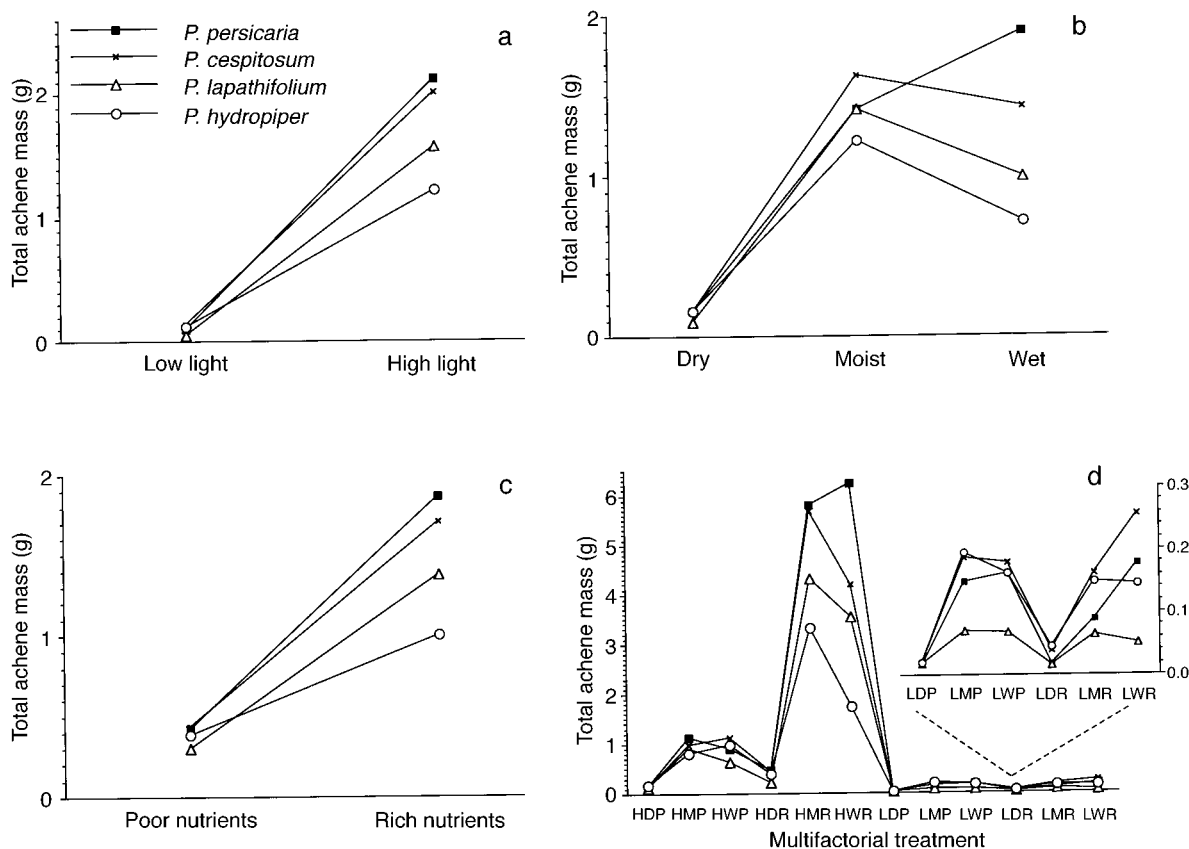


FIG. 3. Plasticity for lifetime reproductive output (total achene mass) in four *Polygonum* species. (a) Species means for plants in low and high light (averaged across moisture and nutrient treatments). (b) Species means for plants in dry, moist, and wet (flooded) soil (averaged across light and nutrient treatments). (c) Species means for plants in poor and rich nutrients (averaged across light and moisture treatments). (d) Complex environmental effects on reproductive output: species means for total achene mass produced in all combinations of high (H) vs. low (L) light; dry (D), moist (M), or wet (W) soil; and poor (P) vs. rich (R) nutrients. The inset shows achene mass of plants grown in low light treatments on an expanded scale. Means are shown for eight plants per multifactorial treatment per species; plants from the same set of eight inbred lineages are represented in every treatment (details in *Methods*).

the range of environments (in this case, an F of 12.0 would indicate equivalent, maximum output across all 12 treatments). This index is more straightforward to interpret in terms of actual fitness than alternative measures of performance equability such as Levins' β which differently weights treatment responses by squaring the adjusted means (Levins 1968; F. Adler, *personal communication*).

Reproductive allocation was analyzed based on MANOVA for proportional biomass allocation (percentage dry mass) to roots, leaves, stems, reproductive support, and achenes (SYSTAT 5.2.1). Univariate tests for effects of species, environmental factors, and their interactions specifically on reproductive allocation were examined only on effects for which the multivariate lambda was significant at a tablewide significance level of $P < 0.05$ after applying the conservative simultaneous Bonferroni correction (Rice 1989); significance levels of the univariate tests were protected using the same conservative procedure.

RESULTS

Environmental effects on fitness components were highly significant and showed complex differences among the *Polygonum* species in patterns of response. Total reproductive output (estimated as both number and total biomass of achenes) was significantly affected by all three environmental factors, their two- and three-way interactions, and the interactive effects of species by each factor and factor combination (Table 2). Although the *Polygonum* species differed on average in components of fitness (significant main effect of species), the main effect of light was the largest source of variation in all five traits (Table 2). In addition, the species \times light interaction was significant for all traits, indicating differences among the four species in the effect of light on every fitness component (Table 2). The main effect of moisture and/or the interaction effect of light \times moisture was also significant for all five traits (Table 2). Environmental effects on specific components of fitness are described below.

TABLE 2. ANOVA for effects of species and environmental factors on components of fitness.

Source of variation	df	First flowering date (model $r^2 = 0.597$)		Early reproduction (model $r^2 = 0.573$)		Total achene mass (model $r^2 = 0.933$)	
		MSE	<i>P</i>	MSE	<i>P</i>	MSE	<i>P</i>
Species	3	13.881	<0.001	30.06	0.002	0.413	<0.001
Light	1	33.990	<0.001	1635.54	<0.001	47.502	<0.001
Moisture	2	1.788	<0.001	98.44	<0.001	10.549	<0.001
Nutrients	1	0.480	0.123	0.65	0.740	10.984	<0.001
Block	7	0.388	0.064	24.15	<0.001	0.030	0.306
Species × Light	3	0.964	0.003	23.32	0.009	0.294	<0.001
Species × Moisture	6	0.108	0.778	4.02	0.663	0.105	<0.001
Species × Nutrients	3	0.298	0.219	8.54	0.228	0.224	<0.001
Light × Moisture	2	0.255	0.282	81.83	<0.001	6.645	<0.001
Light × Nutrients	1	0.138	0.407	6.90	0.280	11.221	<0.001
Moisture × Nutrients	2	0.226	0.326	8.65	0.232	1.527	<0.001
Light × Moisture × Nutrients	2	0.054	0.764	7.69	0.272	1.741	<0.001
Species × Light × Moisture	6	0.086	0.858	4.37	0.615	0.080	0.005
Species × Light × Nutrients	3	0.037	0.906	6.44	0.352	0.213	<0.001
Species × Moisture × Nutrients	6	0.225	0.351	5.04	0.527	0.101	0.001
Species × Light × Moisture × Nutrients	6	0.284	0.208	4.65	0.578	0.088	0.002
Error		0.201 (df = 304)		5.88 (df = 313)		0.025 (df = 313)	

Note: Bold-faced probability values are significant at a table-wide level of $P < 0.05$ (details in *Methods* section).

First flowering date

In the high light environments, *P. cespitosum* and *P. persicaria* plants were the earliest to flower, and *P. hydropiper* the latest (Fig. 1). Although plants of all four species delayed flowering in low light, this delay was smallest in *P. cespitosum* (mean difference in L vs. H treatments of +3.3 d) and greatest in *P. lapathifolium* (mean difference + 9.1 d; cf. species × light effect, Table 2). Both the latter species and *P. hydropiper* required 29–40 d to flower in low light environments, compared with 25–30 d in *P. persicaria* and only 22–24 d in *P. cespitosum* (Fig. 1). *P. cespitosum* phenology was thus relatively constant across the range of environments (cv of treatment means = 0.09, compared with 0.15 in *P. persicaria* and *P. hydropiper*, and 0.19 in *P. lapathifolium*). Flowering was delayed in all species by ~2 d in dry compared with moist treatments, and there was no effect of nutrient level (Table 2).

Early reproduction

Reproductive output by week seven was influenced strongly by both light and moisture as well as their interactive effects (Table 2). Early reproduction in all four species was sharply reduced in low light environments and, to a lesser extent, in high light/dry treatments (HDP and HDR; Fig. 2). *P. persicaria* plants showed consistently higher early reproduction across the range of environments (cf. significant species effect, Table 2). Although all four species produced some early achenes in the high-light treatments, *P. persicaria* plants showed markedly higher early reproduction than the other species in these favorable environments (Fig. 2, inset). *P. persicaria* plants also had the highest early reproduction in the low light environments (cf. significant species × light effect, Table 2): by week seven, plants of this species had produced a mean of at least

one mature achene in five of the six factorial treatments, compared with three (*P. lapathifolium*), one (*P. cespitosum*), or zero (*P. hydropiper*) of the six low-light treatments.

Total achene biomass

Predictably, reproductive output in all four species decreased in low vs. high light, dry vs. moist soil, and poor vs. rich nutrients (Fig. 3a–c). Reproductive output was also significantly affected by interactive effects of resource levels (Table 2). Both simple and complex environmental effects differed significantly among species (two-, three-, and four-way species × treatment interactions; Table 2). As a result of these complex species differences in environmental fitness effects, both the magnitude and the rank order of species' fitness differences varied among particular combinations of light, moisture, and nutrient levels (Fig. 3d).

Generally, in resource-rich conditions *P. persicaria* produced the greatest total mass of achenes, and *P. hydropiper* the smallest (e.g., maximum treatment mean of *P. hydropiper* = 3.3 g, compared with maxima of 4.3 g, 5.7 g, and 6.2 g in *P. lapathifolium*, *P. cespitosum*, and *P. persicaria*). For example, although HMR and HWR were the most favorable experimental environments to all four species, *P. persicaria* had the highest reproductive output of any species in these resource-rich treatments (Fig. 3d; effect of species within HMR treatment significant at $P \leq 0.037$). In resource-deprived conditions (dry, poor, and/or low light treatments), *P. persicaria*, *P. cespitosum*, and *P. hydropiper* converged on extremely similar levels of reproductive output, while *P. lapathifolium* consistently produced the lowest total achene biomass (Fig. 3a–d). *P. lapathifolium* plants grown at low light produced significantly less reproductive biomass than did plants of all

TABLE 2. Extended.

Total achene number (model $r^2 = 0.920$)		Mean achene mass (model $r^2 = 0.815$)	
MSE	<i>P</i>	MSE	<i>P</i>
1 876.2	<0.001	17.060	<0.001
40 189.0	<0.001	21.074	<0.001
10 928.9	<0.001	0.124	0.155
9 002.9	<0.001	0.006	0.765
71.4	0.017	0.186	0.007
939.9	<0.001	1.890	<0.001
291.2	<0.001	0.411	<0.001
478.7	<0.001	0.270	0.007
4 143.9	<0.001	0.529	<0.001
8 629.6	<0.001	2.771	<0.001
1 050.8	<0.001	0.050	0.470
1 365.8	<0.001	0.013	0.821
171.6	<0.001	0.215	0.004
389.1	<0.001	0.305	0.003
118.7	0.001	0.054	0.556
100.6	0.002	0.008	0.994
28.8 (df = 316)		0.066 (df = 316)	

three other species ($0.000 \leq P < 0.05$ according to a post hoc Tukey's test), which did not differ ($P \geq 0.1$; cf. Fig. 3d). Post hoc tests of species differences within poor and dry treatments were nonsignificant due to very high variance among plants in high vs. low light. Although plants of all four species had extremely low achene production in the most unfavorable LDP environment, only *P. lapathifolium* plants failed to increase reproduction substantially when given more moisture and/or nutrients (e.g., LMP, LWR; Fig. 3d). The four species were quite similar in equability of reproductive output across the environmental range (Adler's $F = 2.44$ in both *P. persicaria* and *P. hydro-piper*, 2.35 in *P. cespitosum*, and 2.32 in *P. lapathi-folium*).

Total achene number

Due to characteristic species differences in achene size, the rank order of fitness differences estimated by achene number differed in two respects from those based on total achene biomass. First, although *P. persicaria* plants generally produced the greatest total mass of achenes, *P. cespitosum* plants consistently produced the highest number of (characteristically small) achenes (compare Figs. 3 and 4). These differences in achene number between the two top-ranked species were often nonsignificant (according to post hoc Tukey's tests). Second, *P. hydro-piper*, which produces much larger achenes than its congeners, produced the fewest achenes (though not the lowest biomass) in poor-nutrient treatments (compare Figs. 3c and 4c). *P. lapathifolium* had the lowest reproductive output in achene number as well as biomass in both low light and dry treatments (Fig. 4a, b).

Mean individual achene mass

Environmental effects on the mass of individual achenes were both highly significant and species spe-

cific (Table 2). Note that the species characteristically produced achenes that were either large (*P. hydro-piper*, overall mean 2.06 mg), intermediate (*P. persicaria* and *P. lapathifolium*, respective means of 1.39 mg and 1.29 mg), or small (*P. cespitosum*, mean 1.03 mg). To scale the environmental responses appropriately, they are presented relative to each species' mean achene mass in favorable conditions (Fig. 5a–c). Although plants of all four species produced smaller achenes in low light environments, this decrease was proportionately steeper in *P. hydro-piper* and *P. lapathifolium* (35% and 32% mean decrease from high to low light, compared with 21% and 19% respectively for *P. persicaria* and *P. cespitosum*; Fig. 5a). Species' responses to moisture and nutrient levels differed in direction as well as magnitude (cf. nonsignificant main effects of these factors due to significant species \times treatment interactions; Table 2). *P. persicaria*, *P. cespitosum*, and (to a lesser extent) *P. lapathifolium* produced larger achenes in dry than moist environments, while *P. hydro-piper* reduced achene mass in dry soil (Fig. 5b). *P. persicaria* and *P. cespitosum* also slightly increased offspring mass in wet compared with moist soil, while the remaining two species decreased achene mass under flooding (Fig. 5b). Finally, only *P. hydro-piper* plants reduced achene mass in poor-nutrient environments (Fig. 5c). As a result of these contrasting patterns of response, *P. cespitosum* and *P. persicaria* showed the greatest constancy in achene mass across the environmental range (respective coefficients of variation of 0.14 and 0.16, compared with 0.23 and 0.26 respectively for *P. lapathifolium* and *P. hydro-piper*; Fig. 5d).

Reproductive allocation

Proportional biomass allocation to achenes was significantly influenced by the following effects at a table-wide significance level of $P \leq 0.05$: species, light, moisture, nutrients, species \times light, and species \times moisture. Reproductive allocation was consistently high in *P. hydro-piper* (40–60% of total plant biomass in all 12 environments; Fig. 6). *P. hydro-piper* was the only species that increased reproductive allocation in low-light treatments (particularly LMP and LWP; Fig. 6). *P. persicaria* plants also maintained generally high reproductive allocation across the range of resource levels (Fig. 6). *P. cespitosum* and *P. lapathifolium* were less equable in reproductive allocation (coefficients of variation were 0.428 and 0.429, respectively, vs. 0.286 for *P. persicaria* and only 0.121 for *P. hydro-piper*).

DISCUSSION

Species differences in plasticity for fitness components

This study revealed dramatic and complex (interactive) effects of three environmental factors on all five components of fitness measured. These results confirm for fitness traits the fact that phenotypic response to

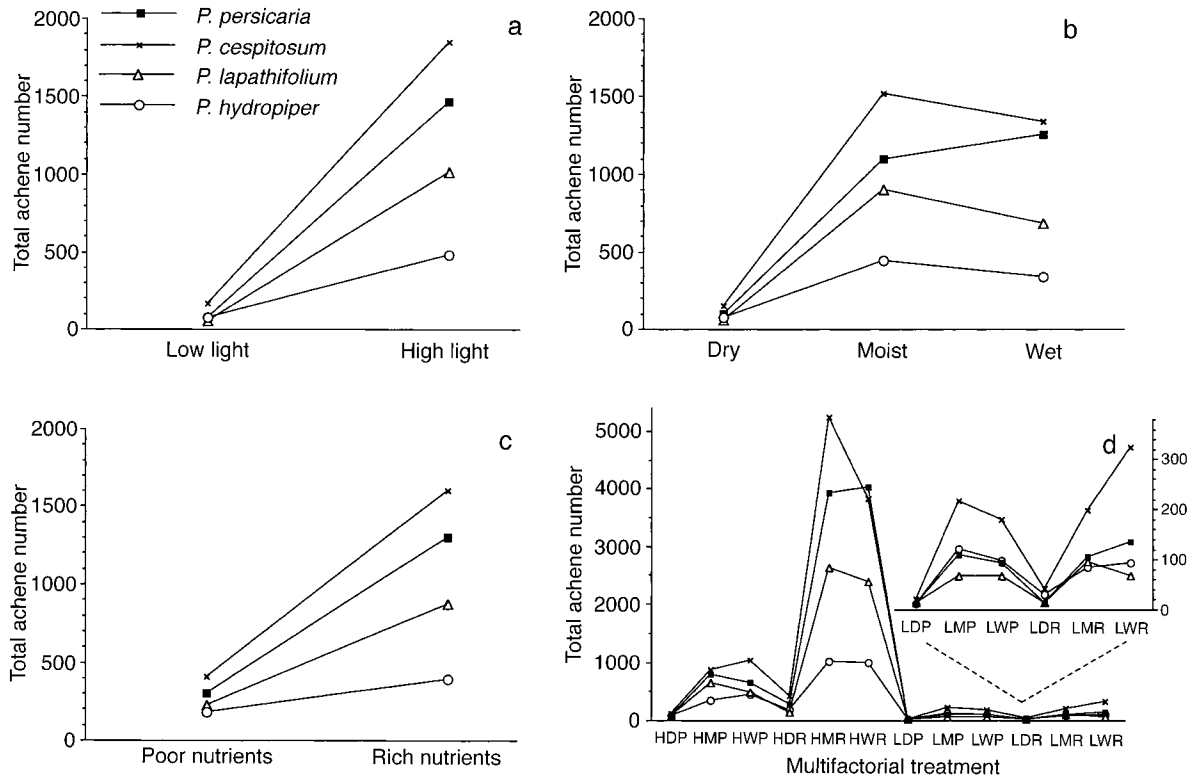


FIG. 4. Plasticity for lifetime reproductive output (total achene number) in four *Polygonum* species. (a) Species means for plants in low and high light (averaged across moisture and nutrient treatments). (b) Species means for plants in dry, moist, and wet soil (averaged across light and nutrient treatments). (c) Species means for plants in poor and rich nutrients (averaged across light and moisture treatments). (d) Complex environmental effects on reproductive output: species means for total achene number produced in all combinations of high (H) vs. low (L) light; dry (D), moist (M), or wet (W) soil; and poor (P) vs. rich (R) nutrients. The inset shows achene number of plants grown in low light treatments on an expanded scale. Means are shown for eight plants per multifactorial treatment per species; plants from the same set of eight inbred lineages are represented in every treatment (details in *Methods*).

environment may be extraordinarily specific with respect to levels of interacting resources, as well as the timing and duration of resource stress (Sultan 1995; e.g., Wayne and Bazzaz 1993, Novoplansky et al. 1994, Sultan et al. 1998a). Furthermore, these complex patterns of plasticity for fitness traits differed significantly among the four *Polygonum* species. For instance, total reproductive output (achene biomass and number) was significantly affected by all two-, three-, and four-way interactions of species by environmental factor. Although plant species generally have broadly overlapping resource requirements (Colwell and Futuyma 1971, Austin and Austin 1980, Bazzaz 1987), this dramatic result shows that closely related species may differ in characteristic and idiosyncratic ways in the magnitude and direction of environmental effects on individual fitness. Since organisms in nature encounter numerous interacting stresses (Bazzaz and Morse 1991 and references therein), these complex differences among species in individual fitness response may be an important, though often unrecognized, factor in ecological distribution.

These results strongly confirm the view that closely related species may differ in patterns of environmental sensitivity for life history traits (Marshall et al. 1986, Ford and Seigel 1989, Travis 1994). With respect to flowering time, early reproduction, and total reproductive output, the *Polygonum* species differed in the magnitude of environmental response: generally, all four species responded either positively or negatively to a given resource level, but differed in the slope of trait change among treatments. Such species differences in the magnitude of environmental effects on fitness components are known in animals (Ford and Seigel 1989) as well as plants (Battjes and Bachmann 1994). They may reflect different individual abilities to maintain fitness in stressful or resource-poor environments, and/or to maximize fitness in favorable conditions (see next section).

In other cases, the *Polygonum* species differed in the direction as well as the degree of environmental response. For instance, *P. persicaria* plants uniquely increased rather than decreased reproductive output in flooded compared with moist treatments (possibly due

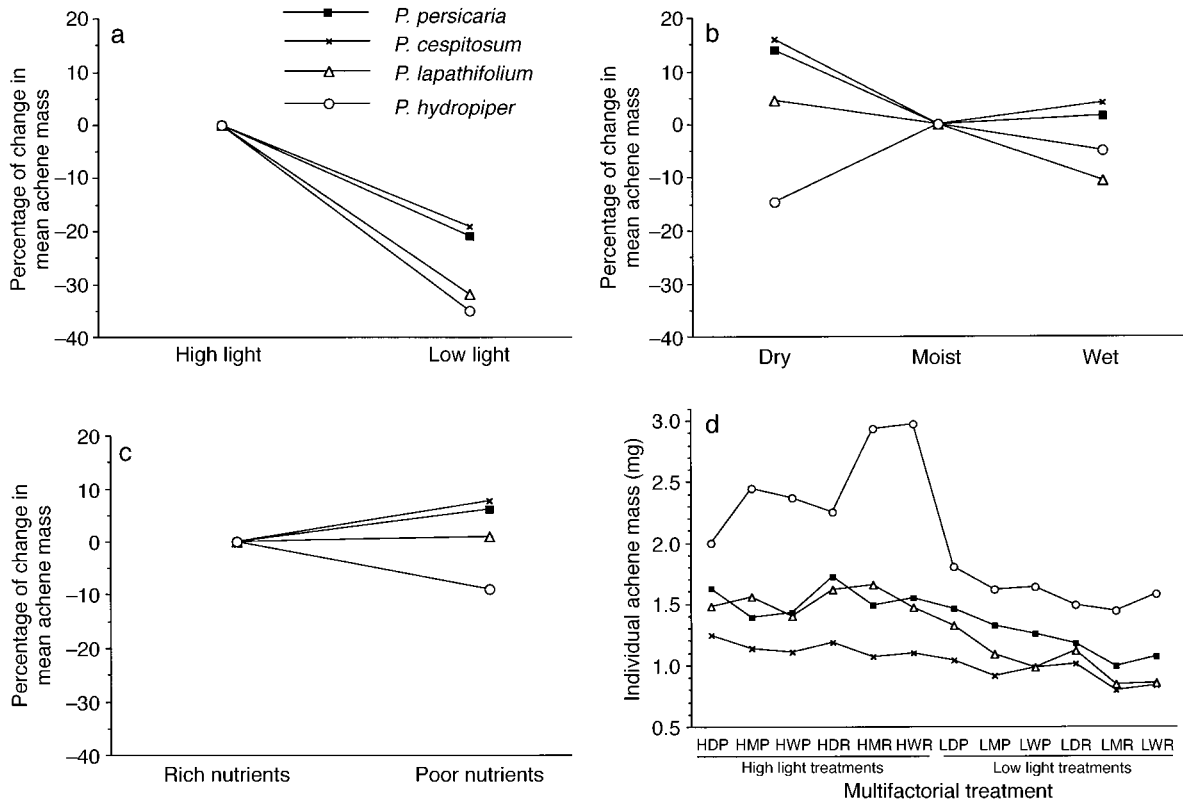
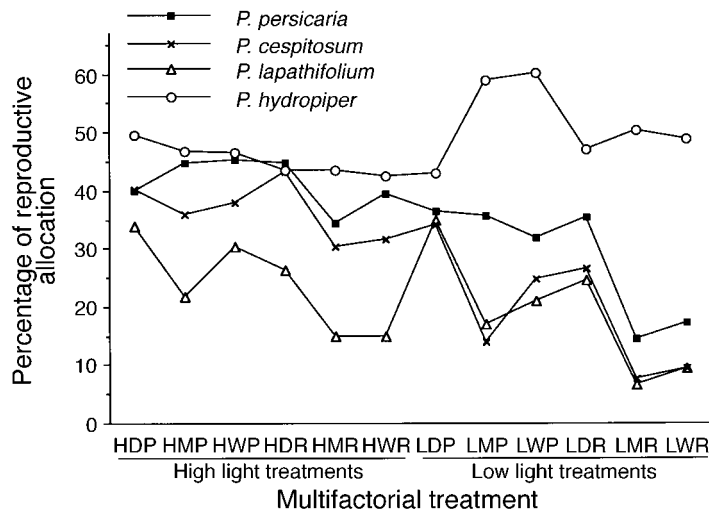


FIG. 5. Plasticity for individual offspring mass in four *Polygonum* species. (a) Percentage of change in mass of individual achenes: species means for plants in low relative to high light (averaged across moisture and nutrient treatments). (b) Percentage of change in mass of individual achenes: species means for plants in dry and wet soils relative to moist soil (averaged across light and nutrient treatments). (c) Percentage of change in mass of individual achenes: species means for plants in poor soil relative to rich soil (averaged across light and moisture treatments). (d) Mean absolute mass of individual achenes produced by plants in all combinations of high (H) vs. low (L) light; dry (D), moist (M), or wet (W) soil; and poor (P) vs. rich (R) nutrients. Means are shown for eight plants per multifactorial treatment; plants from the same set of eight inbred lineages are represented in every treatment (details in *Methods*).

FIG. 6. Plasticity for reproductive allocation (percentage total plant biomass) in four *Polygonum* species grown in all combinations of high (H) vs. low (L) light; dry (D), moist (M), or wet (W) soil; and poor (P) vs. rich (R) nutrients. Means are shown for eight plants per multifactorial treatment per species; plants from the same set of eight inbred lineages are represented in every treatment (details in *Methods*).



to functionally adaptive root plasticity in response to soil flooding; Bell and Sultan 1999). Environmental effects on offspring size also differed in direction as well as magnitude among the *Polygonum* species. For example, *P. persicaria*, *P. cespitosum*, and, to a lesser extent, *P. lapathifolium* plants increased achene mass when grown in dry soils, while plants of *P. hydropiper* decreased achene mass in dry compared with moist or flooded soils. Depending on the precise effects of these changes on seedling emergence and growth (S. El-mendorf and S. E. Sultan, *unpublished manuscript*), such species differences in plasticity for offspring mass may have significant effects on seedling establishment and competitive ability, and hence on species distribution (Sultan 1996, Thompson and Hodgkinson 1998).

Finally, the results show that, for a given fitness trait, related species may express similar response patterns to certain environments but diverge in others. For example, *P. lapathifolium* and *P. cespitosum* showed identical patterns of plasticity for reproductive allocation in low light environments, but differed markedly in the high light treatments.

Differences in patterns of environmental fitness response are well known at the level of genotype; this type of diversity is thought to contribute to the maintenance of genetic variation in natural populations where environments are inherently variable (Bazzaz and Sultan 1987, Mousseau and Roff 1987, Gillespie and Turelli 1989, Platenkamp and Foin 1990, Bell et al. 1991, Mazer and Schick 1991, Houle 1992, Sultan and Bazzaz 1993a, Stratton 1994, Galloway 1995, Bennington and McGraw 1996, Chippindale et al. 1996, Fry et al. 1996). At a higher level of evolutionary variation, complex species by environment differences in fitness response may likewise contribute to species coexistence in heterogeneous environments (cf. Wessler and Armbruster 1991).

Plasticity for fitness components and ecological distribution

Species' patterns of fitness response to environment obviously influence their realized ecological distributions. Two aspects of this response contribute to ecological breadth: the ability to produce at least some viable offspring in poor environments, and the ability to reproduce at high levels when conditions are favorable (Baker 1965, 1974). In other words, both tolerance or relative fitness constancy under stressful conditions, and effective exploitation of high resource levels ("environmental opportunism" sensu Zangerl and Bazzaz 1983) contribute to a species' success in maintaining populations across a range of environments (Baker 1965, Noble 1989, Sultan 1995). The *Polygonum* species differed in both of these aspects of fitness plasticity in ways consistent with several known differences in their realized ecological distributions (cf. predictions in Table 1). Note that both of these ecologically im-

portant aspects of fitness response reflect high underlying adaptive plasticity for growth and functional traits in response to different resource levels (Baker 1974, Brown and Marshall 1981, Sultan 1987, Jain 1990, Bell and Lechowicz 1994). In the *Polygonum* system, species differences in plasticity for physiological and morphological traits such as assimilation rate, leaf size, and root system deployment evidently underlie these differences in fitness response (Sultan et al. 1998a, Bell and Sultan 1999; S. E. Sultan, *unpublished data*).

P. persicaria, *P. cespitosum*, and *P. hydropiper* all maintained similar, modest levels of reproductive output in resource-poor environments, suggesting similar abilities to maintain fecundity at low resource levels or "make the best of a bad job" (Grafen 1988). In addition, resource-deprived plants of *P. persicaria* and *P. cespitosum* were able to maintain or increase the mass of individual achenes. Species that hold constant or increase offspring size in poor conditions may partially offset reduced fecundity by increasing the probability of each offspring's success (see discussion and references in Sultan 1996). *P. persicaria* plants also produced achenes of high germinability despite resource deprivation (achenes produced by *P. persicaria* plants in 11 of the 12 treatments germinated at rates of 50% or more, while in the other species plants from eight or fewer treatments produced achenes with comparable germination levels; C. Miller and S. E. Sultan, *unpublished data*). In contrast, *P. hydropiper* plants produced achenes of significantly lower mass in response to low light, moisture, and nutrients. Such reductions in offspring mass may exacerbate the effect of reduced achene number on realized fitness in environments where initial provisioning is critical to seedling survival and establishment, such as shaded or nutrient-poor habitats (Salisbury 1942, Lloyd 1987, McGinley et al. 1987, Mazer 1989, Thompson and Hodgkinson 1998). Note that unlike *P. persicaria* and *P. cespitosum*, *P. hydropiper* is excluded from such habitats (Sultan et al. 1998b and references therein). *P. lapathifolium* plants also decreased achene size sharply under low light; furthermore, plants of this species had consistently more delayed, as well as lower total, reproduction than its congeners when deprived of light, moisture, or nutrients. The relative inability of *P. lapathifolium* to maintain these various aspects of fitness in shaded and other resource-poor conditions may in part explain the restriction of this species to cultivated fields and other high-light, moist sites (Sultan et al. 1998b).

When grown in resource-rich conditions, plants of *P. lapathifolium* and especially *P. persicaria* and *P. cespitosum* increased reproductive output sharply. In contrast, *P. hydropiper* plants increased reproduction relatively modestly even in the most favorable experimental treatments. This response pattern may in part explain the fact that this species is neither an invasive

colonizer nor an agricultural weed (Muenscher 1955, Staniforth and Bergeron 1990). Indeed *P. hydropiper* has a narrow realized distribution relative to its congeners, being restricted to bright, wet, highly organic sites where seedling flood tolerance may grant a competitive advantage (Sultan et al. 1998b; C. Miller and S. E. Sultan, unpublished data).

The species differences in fitness response revealed in this study support the view that certain species may be ecological generalists compared with more narrowly restricted congeners, without the inherent fitness trade-off implied by the notion that the "Jack of all trades" is necessarily the "master of none" (critiqued by Futuyma and Moreno 1988, Greene 1982, Sultan 1992, Whitlock 1996). In other words, species considered ecological "specialists" may simply be limited to certain habitats, while "generalist" species may be equally successful in those habitats and in others as well. *P. persicaria* plants maintained fecundity and offspring quality in poor conditions, and also reproduced at extremely high levels when resources were plentiful. This pattern of fitness response has been described by Baker (1965, 1974) as characteristic of aggressively colonizing generalist species (see also Noble 1989). Indeed, compared with *P. lapathifolium*, *P. hydropiper*, and *P. cespitosum*, this widespread species establishes populations in a very broad range of field environments (Sultan et al. 1998b), and is a serious agricultural weed in many temperate regions (Muenscher 1955, Mitchell and Dean 1978, Holm et al. 1979, Staniforth and Cavers 1979, Preston and Whitehouse 1986). *P. persicaria* plants also had much higher early reproduction than congeners in both favorable and resource-poor treatments, possibly an aspect of fitness response that promotes persistence by avoiding the possibility of zero offspring (see Gillespie 1977 on the theoretical advantages of such a fitness strategy). Note that the fitness impact of rapid vs. delayed reproduction may be trivial in some environments but profound in others (Kalisz 1986, Stewart and Schoen 1987, Newman 1988), for example in sites or years with an early onset of frost or drought.

Similarly, *P. cespitosum* plants maintained fitness in poor environments and also expressed high fecundity under favorable greenhouse treatments. The high output by *P. cespitosum* plants of consistently well-provisioned achenes across a range of environments may be a factor in the rapid geographical spread of this species within its habitat range (Mitchell and Dean 1978). However, this species presents a less straightforward situation since it is an aggressive and rapid colonizer, but only of shaded sites (Sultan et al. 1998b and references therein). *P. cespitosum* may be excluded from high-light habitats despite its high fitness under like experimental conditions due to a competitive disadvantage arising from its characteristically low stature (J. Schmitt, personal communication) or due to other biotic interactions.

In comparison with the latter two species, *P. hydropiper* and particularly *P. lapathifolium* showed relatively low fitness with respect to fecundity and/or offspring quality in resource-poor environments. This pattern of fitness response may partly explain the restriction of these species to habitats with high available light and other key resources.

Fitness equability vs. plasticity in relation to ecological breadth

Depending on the trait, functionally adaptive response to a range of environments may be associated with phenotypic adjustment or *plasticity*, or with phenotypic constancy or *equability* (Thoday 1953, Lacey et al. 1983, Van Tienderen 1991, Sultan and Bazzaz 1993b, c). This apparent paradox is one reason that patterns of plasticity and in particular life history plasticity may be problematic to interpret (see Grafen 1988, Bell and Lechowicz 1994, Travis 1994, Gottard and Nylin 1995, Sultan 1995, and Pigliucci and Schlichting 1996 on these interpretive issues). For components of fitness such as reproductive output, one prevalent view (e.g., Lortie and Aarssen 1996) is that the greatest degree of equability across environments indicates the greatest ecological breadth, while narrowly adapted species will show the greatest performance reduction in stressful conditions and hence the greatest variability (i.e., nonadaptive plasticity). This view is the basis of using response equability measures such as Levins' β as performance-scaled indicators of ecological breadth (Levins 1968).

However, equability vs. plasticity may be a misleading index of reproductive response, since equability is maximized by both relatively high performance in poor environments and relatively low performance in rich environments (Falconer 1990). Hence, equability alone does not distinguish a consistently low fecundity response, such as that of *P. hydropiper*, from a species that opportunistically increases reproduction in favorable environments, such as *P. persicaria* (note that the two species shared identical Adler's F equability values of 2.44 for total reproductive output). The same interpretive ambiguity arises with coefficients of variation, which scale phenotypic variation to the mean response: a high CV may indicate a steep drop in poor environments (e.g., *P. lapathifolium*, CV for total achene biomass = 1.78) or a sharp increase in resource-rich conditions (e.g., *P. persicaria*, CV = 1.80). Since both maintaining reproduction in poor environments and maximizing it in rich environments are important components of ecological breadth, measures of either equability or plasticity per se across environments may not describe fecundity responses in meaningful terms. Possibly models relating fitness plasticity to ecological performance can be designed to take into account these two distinct aspects of environmental response.

Plasticity and equability per se may also provide inadequate information regarding response patterns for

other components of fitness. For example, species able to flower and fruit rapidly even when deprived of resources (e.g., *P. persicaria* and *P. cespitosum*) may be more likely to complete their life cycle in poor habitats than those which respond to environmental stress by delaying reproduction (e.g., *P. lapathifolium*). Such equability for early reproduction may constitute adaptive homeostasis (Baker 1965), possibly due to plastic adjustment of other traits such as threshold reproductive size (Clauss and Aarssen 1994) or biomass allocation (see Galloway 1995). However, equability measures do not distinguish this ecologically adaptive response pattern from a consistently slow and therefore inherently high-risk phenology, such as that of *P. hydropiper*. These comparative fitness data make clear the fundamental point that in interpreting phenotypic response to environment, the degree of plastic variability or constancy per se is ecologically uninformative in the absence of actual trait values evaluated in their specific environmental context (Via 1994, Sultan 1995, see Sultan et al. 1998a for discussion of equability vs. plasticity for physiological response).

Fitness components and ecological distribution

Powerful correlative methods to compare adaptations generally estimate fitness in different environments using a single major reproductive trait such as total fecundity (reviewed in Wade and Kalisz 1990). Although investigators often rely on total fecundity as a single estimate of fitness, this "short-sighted" emphasis on reproductive output (Beatty 1992, De Jong 1994) may give only limited insight to the realized fitness that is the basis of ecological establishment: the number of offspring that actually survive and reproduce in successive generations (Thoday 1953, Slobodkin 1968, Calow 1981, Pianka 1981, Primack and Kang 1989, Biere 1995). Hence, to understand how patterns of plastic response to environment influence the ecological distribution of taxa, it is essential to consider several traits that contribute to fitness in different ways, such as age at reproduction and size as well as number of offspring (Reznick and Travis 1996 and references therein; cf. Kalisz 1986, Marshall et al. 1986, Newman 1988, Galloway 1995). As demonstrated in the *Polygonum* system, diverse fitness components may show highly species-specific patterns of plasticity in response to multiple interacting environmental factors. To more fully understand the basis of species differences in ecological distribution, we must expand our investigations to consider the fascinating interplay of diverse aspects of fitness in complex environments.

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