

Phenotypic Plasticity in Polygonum persicaria. II. Norms of Reaction to Soil Moisture and the Maintenance of Genetic Diversity Author(s): S. E. Sultan and F. A. Bazzaz Source: *Evolution*, Vol. 47, No. 4 (Aug., 1993), pp. 1032–1049 Published by: Society for the Study of Evolution Stable URL: http://www.jstor.org/stable/2409973 Accessed: 19-04-2016 18:17 UTC

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PHENOTYPIC PLASTICITY IN POLYGONUM PERSICARIA. IL NORMS OF REACTION TO SOIL MOISTURE AND THE MAINTENANCE OF GENETIC DIVERSITY

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Abstract. - Adaptive phenotypic plasticity is the predicted evolutionary response to fine-grained fluctuation in major environmental factors, such as soil moisture in plant habitats. This study examines genotypes from two natural populations of Polygonum persicaria, one from a relatively homogeneous, moderately moist site, and one from a site in which severe drought and root flooding occur within single growth seasons. Norms of reaction (phenotypic response curves) were determined for a random sample of eight and ten cloned genotypes, respectively, from each of the populations over a controlled moisture gradient ranging from drought to flooding.

Genotypes of both populations exhibited marked allocational and morphological plasticity in characters relating to plant function at both low moisture availability and flooded soil, including root characters that directly affect plant water status. Associated with this plasticity was the ability of all genotypes to survive and reproduce across the entire range of moisture conditions: individual genotypes possess a remarkable degree of ecological tolerance. This tolerance was equally broad in genotypes from both populations, although only one population encounters soil flooding in its native site.

Among the Polygonum genotypes studied, certain individuals exhibited relatively poor growth and reproductive output at several moisture levels. Although these genotypes thus showed significantly low average fitness, the magnitude and/or direction of the fitness differentials varied from one moisture treatment to another. The precise arrays of norm of reaction diversity among these genotypes, together with patterns of moisture variability at the field sites, indicate how genotype by environment interaction and environmental variability may lead to the maintenance of genetic diversity.

Key words.-Drought stress, flood tolerance, genetic variation, norms of reaction, phenotypic plasticity, Polygonum persicaria.

Received January 16, 1992. Accepted October 23, 1992.

The effectiveness of natural selection in shaping specially adapted populations and subpopulations depends in part on three aspects of genotype-by-environment interaction that determine the relative fitness of individuals under diverse conditions: the capacity for functionally adaptive phenotypic plasticity (and therefore environmental tolerance) inherent within genotypes; the pattern of diversity among genotypic norms of reaction within populations; and the distribution of environmental variability (Levins 1968; Sultan 1987). Although genotypes may differ in fitness in a particular environment, the magnitude and/or the direction of that difference may alter in another environment. If both environments occur within a population at a scale too fine to be tracked genetically, the genotypes may be maintained even if one expresses inferior fitness under certain conditions and, therefore, on the

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average (Via and Lande 1985; Mitchell-Olds and Rutledge 1986). Thus, one possible explanation for the maintenance of polygenic variation in natural populations-which never encounter constant environments-is that genotypes do not have consistent relative fitness in all environments (Barton and Turelli 1989; Gillespie and Turelli 1989). It is therefore of central importance to determine the patterns of diversity among genotypes in response to major environmental factors that vary at a fine scale in nature. However, few studies compare norms of reaction in reproductive fitness of genotypes from natural populations over the full range of relevant environmental variation (Sultan and Bazzaz 1993a).

Water availability is an aspect of the plant environment that is both essential to plant function and highly variable. Unlike certain constant environmental factors that have been directly implicated as agents of selective change within populations (reviewed in Bradshaw and Hardwick 1989), variability in soil moisture is, in most

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habitats, primarily temporal and short-term in nature. In general, evolutionary response to temporally variable aspects of environment is not well understood. Despite the central importance of soil moisture as an environmental and therefore an evolutionary factor (Bradford and Hsiao 1982), very little is known about either adaptive plasticity in response to soil moisture or about response diversity among naturally occurring genotypes and populations (Roy and Mooney 1982; Farris 1987).

This paper presents a study of norms of reaction in response to an extremely broad soil moisture gradient of genotypes from two natural populations of *Polygonum persicaria*. The data characterize (1) the range of appropriate phenotypic response to diverse soil-moisture conditions inherent within individual Polygonum genotypes, and (2) the precise distribution of genotypic differences in growth and reproduction across the range of moisture environments. The selective implications of these aspects of diversity are evaluated on the basis of actual patterns of moisture variability in the field. The two populations studied provide a salient contrast, as plants in one population experience uniformly moderate water availability, whereas those in the second may encounter both extreme drought and soil flooding within a single growth season.

MATERIALS AND METHODS

Study System. - Genotypes were studied from two genetically well differentiated populations (150 km apart) of the widespread annual species *Polygonum persicaria* L. (see Sultan and Bazzaz 1993a). The two populations occupy habitats that differ markedly in both the amount and variability of soil moisture. The soil at the hilltop Circle site consistently contains about 25% water at both surface and subsurface levels, approximately one-half of field capacity (the maximum amount of water the soil can hold against gravity; fig. 1A). Although the surface level occasionally dries slightly, there is little variation either among microsites within sampling days or over the growth season. Of 12 sampling dates over a 2-yr period, however, one occasion did occur (August 18, 1987) in which both soil levels throughout the site dried to about 10% soil moisture. Because the site's soil structure renders nearly 10% of the moisture present osmotically unavailable to P. persicaria roots (permanent wilting point, fig. 1A), at such conditions very little water is actually available to plants. Thus, plants at this

site experience consistent, moderately moist conditions but may rarely encounter drought at the end of the growth season.

In contrast, soil moisture varies enormously within the Pond site, a sand beach, at several temporal and spatial scales (fig. 1B). Soil moisture exceeds field capacity along the water's edge; plants in these locations experience root flooding. Because the water level itself recedes over the course of each growth season, Polygonum seedlings that emerge in damp sand experience increasing drought as the season progresses. The shore rises at an incline of about 15°, so that other microsites are well above the water table throughout the season. Extreme short-term fluctuation in moisture availability occurs at these locations. Because the Pond soil is nearly pure sand, it holds water very poorly: moisture content at the soil surface is not infrequently 1% or less (fig. 1B). When water is present, however (for instance, just after a rainfall), it is fully available to Polygonum plants (permanent wilting point, fig. 1B). Occasionally the site will remain largely submerged for most or all of the growing season, as occurred in 1987; this may occur once every several years (B. Sorrie, Massachusetts Natural Heritage Program pers. comm.). Individual Pond plants thus may encounter moisture conditions ranging from severe drought to flooding.

Experimental Plant Material. – Fruits were collected from 15 randomly chosen individuals ≥ 1 m apart in each field site, germinated, and grown under uniform glasshouse conditions for 6 wk. Vegetative cuttings were taken from each of 8 Circle and 10 Pond individuals, and placed in moist vermiculite in a warm growth chamber. After 9 d, 16 rooted cuttings of approximately uniform size were selected from each genotype and each randomly assigned a soil moisture treatment and a position on one of three glasshouse benches. Because winter-grown plants are less vigorous, fewer than 16 comparable cuttings were available for certain genotypes (propagation details in Sultan 1990).

Experimental Treatments.—We planted 280 rooted cuttings (8 Circle and 10 Pond genotypes \times 4 treatments \times 4 replicates, minus 8 missing cuttings) singly into 5-inch clay pots containing fertilized soil medium, placed them in plastic saucers, and set them in preassigned positions on three 420 \times 160 cm glasshouse benches in a completely randomized design. Plants were rerandomized over the three benches midway through the experiment. Plants were watered moderately for 14 d to insure uniform establishment, and then one of four watering regimes was imposed. These were designed to effect four physiologically distinct soil moisture treatments: Dry (causing midday wilting daily), Moist (50% of field capacity, and causing wilting only on unusually sunny days), Field Capacity (fully saturated yet aerated soil), and Wet (pot submerged and roots flooded). An automated watering system controlled by Rainmatic® computer-regulated valves supplied pots in each treatment twice daily with a specified amount of water, which was increased in constant proportion as the experiment progressed to maintain the physiological gradient described above. Wet-treatment pots were placed inside 1-gallon plastic containers that were kept filled with water to the soil level (± 2 cm) throughout the experiment. Gravimetric measurements (mean percentage of dry weight of samples from five pots \pm standard deviations) verified that the four treatments were both consistent and distinct: soil moisture was, respectively, $11.1 \pm 1.2\%$, $14.0 \pm 0.7\%$, $26.2 \pm 2.8\%$, and 74.0 \pm 6.3% in the Dry, Moist, Field Capacity, and Wet treatments (for full details, see Sultan 1990).

The experiment was designed to minimize confounding environmental effects: all plants were provided with ample nutrients, and closed systems prevented differential nutrient leaching as well as belowground interference. Aboveground interference was avoided by wide spacing of plants. Relative humidity fluctuated from 55% to 75% but was consistent throughout the glasshouse (as measured with a Licor 1600 steadystate porometer). Plants were grown under the four watering regimes for 63 days (January 23-March 27, 1987) at 26°C/22°C day/night temperature with a 14¹/₂-h daylength; when necessary ambient light was artificially supplemented in order to maintain moderate daytime light levels of approximately 600 $\mu E m^{-2} s^{-1}$. During the experiment, 19 plants died (from all 4 treatments).

Characters Measured.-Total plant biomass (dry weight) and proportional biomass allocation to root, stem, leaves, reproductive support and fruits (single-seeded achenes) were determined for each plant. Total live leaf area and number were determined; from these the mean size of individual leaves was calculated. The following ratios were also calculated: root-to-shoot (stem plus total leaf) biomass, leaf area ratio (live leaf



CIRCLE SITE

7/10

8/4 8/25

CLIFF POND

6/24

6/10

5/28

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60

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20 *

10

40

30

10

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10

*

7/9 8/18

7

9/18 5/14 molsture

8

area per unit of plant biomass), and specific leaf area (live leaf area per unit of live leaf biomass). For each plant, the mean weight of individual fruits was estimated based on random subsamples of 50 mature fruits, and fruit number was estimated by dividing the total fruit biomass by this mean weight. (Details of sampling methods and calculations in Sultan and Bazzaz, 1993a.)

Data Analysis. — The analytical approach taken is that of Sultan and Bazzaz (1993a). Overall treatment effects were further examined by performing a posteriori linear contrasts of treatment responses (i.e., Dry vs. Moist, Moist vs. Field, and Field vs. Wet; MGLH module, SYSTAT 3.0). These were treated as planned comparisons; contrasts with probabilities less than 0.05 were considered significant (F-ratios are given for characters of particular interest). In the majority of cases, neither initial nor final block was sta-

capaci field capacity 120 100 field 80 5 60 × 40 20 0 7/10 7/9 8/18 4/29 5/14 5/28 6/10 6/24 8/4 8/25 9/18 5/14 1987

Α. 180

160

140 capacity

120

100

80

20

0

160

140

4/29

field

2 60

* 40

B 180 field capacity

	Genotype	Moisture level	Genotype-by-moisture
	Circle Population	(N = 115)	
	df = 7	df = 3	df = 21
Multivariate F	3.110**	27.974**	1.191 NS
Univariate F			
Root proportion	1.090 NS	33.828***	1.000 NS
Stem proportion	4.567***	164.833***	1.377 NS
Leaf proportion	3.544**	8.515***	1.881*
Reproductive support	7.893***	54.628***	2.251**
Fruit proportion	1.873 NS	66.705***	1.447 NS
	Pond Population	(N = 146)	
	df = 9	df = 3	df = 27
Multivariate F	2.040**	29.305**	0.951 NS
Univariate F			
Root proportion	1.542 NS	5.748**	0.709 NS
Stem proportion	3.697***	226.813***	0.997 N S
Leaf proportion	1.031 NS	65.924***	0.802 NS
Reproductive support	2.693**	5.790**	1.240 NS
Fruit proportion	2.392*	46.690***	0.848 NS

TABLE 1. MANOVA for proportional components of biomass. Multivariate F-statistics based on Wilks's lambda shown with significance levels; details in *Methods* section.

* P < 0.05; ** P < 0.01; *** P < 0.001; NS, $P \ge 0.05$.

tistically significant in ANOVA, indicating that the rerandomization performed half-way through the experiment successfully minimized bench effects.

RESULTS

Circle Population.-Circle genotypes shared similar, pronounced allocational responses to reduced soil moisture (treatment $P \leq 0.001$ for each biomass component; interaction nonsignificant; table 1): all significantly increased proportional allocation to root and fruit tissues, and decreased allocation to stem and reproductive support (fig. 2). In particular, root allocation increased significantly in the Moist treatment relative to Field Capacity (contrast F = 19.4) and at Dry relative to Moist soil (F = 16.6), but did not differ in the Field Capacity and Wet treatments. This response pattern was identical for all genotypes (table 1; nonsignificant genotype and interaction effects confirmed by ANOVA, P > 0.3). Circle genotypes also shared identical root-to-shoot biomass ratios within each moisture treatment, as well as common patterns of response (fig. 3I; table 2). All increased root biomass relative to shoots significantly from about 0.2 in both Field Capacity and Wet soils to 0.3-0.4 in Moist soil and to 0.4-0.5 in Dry soil. This two-and-one-half-fold change in root-to-shoot ratio was the most marked treatment effect of any character examined (table 2). Allocation to leaves was lowest in Wet treatment plants; high error may have obscured differences in leaf allocation among the remaining treatments.

Soil moisture level also significantly affected total biomass, total fruit biomass and number. mean fruit weight, total leaf area, leaf area ratio, and mean leaf size (table 2). Although the genotype term was significant for all of these characters, in no case was any genotype significantly different from others across the entire moisture gradient (table 3). Surprisingly, all Circle genotypes produced fruits of greater mean weight in response to reduced soil moisture (fig. 3J; Field vs. Moist contrast F = 32.7, Moist vs. Dry contrast F = 6.9). Total biomass, total fruit biomass, and fruit number were equally high at the Field and Wet treatments, but decreased significantly between Field and Moist and between Moist and Dry treatments (e.g., total biomass contrasts with respective F ratios of 1.6 (NS), 10.7, and 24.1; fig. 3A-C). The significant genotype and genotype-by-moisture interaction terms in these three characters (table 2) reflect the distinctive response patterns of two genotypes. Unlike the other six genotypes, Circle 9 and 12 did not increase total biomass and fruit production when grown at Field Capacity in comparison with their growth



FIG. 2. Proportional biomass allocation for eight Circle genotypes at four moisture levels. Root, stem, leaf, reproductive support, and fruit biomass presented as proportions of total plant biomass; means of four replicates.

at the drier treatments (fig. 3A–C), and therefore were significantly lower within this treatment (table 3). All genotypes produced fruits of equivalent mean weight at the Dry treatment. The significant genotype effect on fruit weight was due primarily to the heavier fruits produced by Circle 9 at the remaining three treatments, in which it also produced fewer fruits (table 3).

Leaf characters showed relatively slight soil moisture effects. All genotypes shared a similar, rather flat response norm in total leaf area, which decreased slightly but significantly at both the Dry and Wet treatments (fig. 3D). Again, differences among genotypes reflected the poor growth of Circle 9 and 12 at certain treatments. Although there was no effect of moisture treatment on leaf number (table 2), Circle plants produced slightly smaller and thinner leaves at the Dry treatment than at Field Capacity and Moist soils (fig. 3F,G). Leaves produced in Wet soil were also reduced in size (fig. 3F). The ratio of leaf area to plant biomass increased monotonically with decreasing moisture level (fig. 3H).

Pond Population.—Pond genotypes also expressed common, marked allocational changes in response to soil moisture level (table 1). Both



FIG. 3. Norms of reaction for eight Circle genotypes at four soil-moisture levels (means of four replicates). A, Total plant biomass; B, total fruit biomass; C, total fruit number; D, total plant leaf area; E, total leaf number; F, mean leaf size; G, specific leaf area; H, leaf area ratio; I, root-to-shoot ratio; J, mean fruit weight. Adjacent treatment contrasts that do not differ significantly at P < 0.05 are joined by a straight line; nonadjacent treatments that do not differ are shown with a dotted line.

	Ger	notype	Moist	ure level	Genotype × moisture		Error			
	MS	F	MS	F	MS	F	MS			
		(Circle Popula	tion						
	(df = 7) $(df = 3)$ $(df = 21)$ (
Total plant biomass	1.19	11.89***	2.56	13.82***	0.19	1.85*	0.10			
Root-to-shoot ratio	0.004	1.34 NS	0.424	125.50***	0.003	1.02 NS	0.003			
Leaf-area ratio	1.08	4.05**	13.56	29.76***	0.46	1.71*	0.27			
Total leaf area	33.99	8.67***	18.97	6.19**	3.06	0.78 NS	3.92			
Total leaf number	2.05	11.89***	0.28	1.06 NS	0.26	1.51 NS	0.17			
Mean leaf size	4.20	3.50**	8.19	3.30*	2.48	2.07*	1.20			
Specific leaf area	6697	7.59***	3198	2.09 NS	1531	1.73*	883			
Total fruit biomass	0.49	11.42***	0.48	5.03**	0.095	2.21**	0.043			
Total fruit number	1.32	12.44***	1.72	6.68**	0.26	2.43**	0.11			
Mean fruit weight	0.107	5.79***	0.714	36.89***	0.019	1.04 NS	0.019			
]	Pond Populat	tion						
	(di	f = 9	- (di	f = 3)	(df	(df = 102)				
Total plant biomass	0.55	5.77***	13.87	107.40***	0.13	1.36 NS	0.095			
Root-to-shoot ratio	0.004	1.22 NS	0.095	46.13***	0.002	1.59 NS	0.004			
Leaf-area ratio	0.44	2.71**	8.13	54.82***	0.15	0.91 NS	0.16			
Total leaf area	43.45	6.17***	497.6	47.37***	10.51	1.49 NS	7.04			
Total leaf number	0.74	4.78***	2.96	17.04***	0.17	1.12 NS	0.16			
Mean leaf size	1.25	1.92 NS	38.38	45.16***	0.85	1.31 NS	0.65			
Specific leaf area	2016	2.45*	14,310	12.78***	1120	1.36 NS	824			
Total fruit biomass	0.242	5.97***	4.755	73.24***	0.065	1.60*	0.040			
Total fruit number	0.65	7.33***	10.84	72.59***	0.15	1.69*	0.09			
Mean fruit weight	0.062	6.60***	0.220	12.79***	0.017	1.83*	0.009			

TABLE 2. Two-way plus block mixed ANOVA for growth and reproductive characters. Details of ANOVAs in Sultan (1990).

* P < 0.05; ** P < 0.01; *** P < 0.001; NS, $P \ge 0.05$.

the patterns of response and the degree of genotypic uniformity mirror the results described above for the Circle population. Like Circle plants, they allocated proportionally more biomass to root and fruit and less to stem tissue in the Dry and Moist treatments than at Field Capacity (fig. 4), but unlike Circle plants, increased root allocation in Wet soil. This pattern of root allocation was uniform among genotypes (table 1: nonsignificant genotype and interaction terms confirmed by ANOVA, P > 0.3). Pond genotypes produced identical root-to-shoot biomass ratios within every moisture treatment, as did Circle plants (table 1). Root-to-shoot ratios were likewise equivalent in Field and Wet soils, and increased monotonically from Field to Dry soils (fig. 5I). Leaf allocation increased monotonically from Wet to Dry soil (fig. 4).

The effect of soil moisture was also highly significant for the remaining phenotypic characters examined (table 2). Patterns of treatment response in total biomass, total fruit biomass, fruit number, total leaf area, leaf number, and mean leaf size were extremely similar (cf. fig. 5A–F): all decreased monotonically from Field Capacity to Dry soils. However, plants grown at the Wet treatment did not differ in these growth and reproduction traits from those grown at Field Capacity, except for a slight decrease in total fruit biomass (fig. 5). The highly significant genotype terms for total and fruit biomass, fruit number, and leaf area and number (table 2) reflect correlated differences among genotypes in all five characters. These were slight but roughly consistent across the moisture gradient (table 4). For example, genotype P3 was relatively high, and P10 relatively low, in these characters at all moisture treatments (fig. 5B,C). However, as in the Circle plants, in no case did any genotype differ significantly from others at all treatments (table 4).

Like Circle plants, Pond plants produced fruits of greater mean weight in response to reduced water availability (fig. 5J). Mean fruit weight was slightly lower at the Wet treatment than at Field Capacity. At every treatment the genotypes which produced the fewest fruit also produced fruits of greatest mean weight (table 4). In particular, P3 TABLE 3. Circle population: genotypic differences within moisture treatments. Genotypes shown ranked by character value within each moisture treatment; those joined by a vertical line do not differ at a probability of < 0.05. Below these, F values and probability levels are given from ANOVA for genotype effect within each treatment; a boldface vertical line indicates that the genotype term is not significant ($P \ge 0.05$). Details are given in the *Methods* section.

TOTAL BIOMASS					тот	TAL FRU	IT BIO	FRUIT NUMBER				
	DRY	MOIST	FIELD	WET	DRY	MOIST	FIELD	WET	DRY	MOIST	FIELD	WET
	8 6 4 5 1 9 12	3 8 12 4 1 6 5 9	3 8 4 1 5 6 12 9	4 3 6 1 5 12 9	8 6 4 1 5 9 12	8 12 3 4 1 6 5 9	8 3 4 5 6 12 9	4 3 6 1 5 12 9	8 6 1 4 9 5 12	8 12 3 1 4 5 6 9	8 3 4 5 6 12 9	4 3 1 8 6 5 12 9
F P	2.97 .023	3.01 .022	6.63 .001	2.23 .076	2.84 .027	3.18 .018	6.12 .001	2.96 .027	3.05 .020	4.49 .003	6.98 .000	3.06 .023
	тс	TAL LE	EAF AR	EA		LEAF N	IUMBE	MEAN LEAF SIZE				
	DRY	MOIST	FIELD	WET	DRY	MOIST	FIELD	DRY	MOIST	FIELD	WET	
	8 3 4 6 1 5 9 12	3 8 12 6 1 5 9	4 8 3 1 5 6 12 9	4 8 3 5 6 1 12 9	4 3 8 1 5 6 9 12	3 12 4 1 8 6 5 9	3 8 4 5 1 6 9 12	3 4 1 6 5 12 9	6 5 8 12 9 3 1 4	9 6 4 5 8 3 12 1	12 4 8 1 3 9 6 5	9 4 3 8 6 5 1 3
F P	4.08 .005	2.08 .090	3.33 .019	2.13 .087	4.28 .004	3.90 .007	5.46 .002	3.56 .012	.028 .955	3.56 .010	3.42 .017	4.18 .006
	SPE	CIFIC L	EAF AR	EA	LF	AF ARF		Ю	RO	OT∙ SHO	OT RA	тю
	DRY	MOIST	FIELD	WET	DRY	MOIST	FIELD	WET	DRY	MOIST	FIELD	WET
	4 1 5 12 8 3 9	3 4 1 5 8 12 9	1 4 8 6 3 9 5 12	4 12 5 3 8 6 9	4 12 1 8 6 3 9 5	6 3 4 5 8 1 9 12	9 4 12 8 5 1 6 3	4 9 8 12 5 1 3 6	6 9 12 1 5 3 8 4	9 6 3 12 5 1 4	9 3 8 1 12 6 5 4	4 3 6 9 1 12 5
F P	2.74 .032	3.04 .022	4.00 .009	2.87 .030	4.08 .002	0.48 .841	3.50 .015	2.54 .048	0.51 .815	1.73 .154	2.30 .074	$0.47 \\ .844$
	ΜΕΔ	NERII	T WEIG	чт								
	DRY	MOIST	FIELD	WET								
	4 5 12 6 9 8 1 3	4 9 6 3 12 5 8 1	9 12 8 4 6 3 1 5	9 6 8 4 12 3 1 5								
F P	1.30 .300	2.87 .028	3.35 .018	3.52 .013								

consistently produced a large number of fruit (contrast vs. all other genotypes F = 29.9) but produced fruits of low mean weight (F = 16.3), and P10 produced relatively few fruits (F = 23.2) of larger mean size (F = 15.0) (all contrasts significant at P < 0.001 using Scheffe's test for unplanned comparisons).

In contrast to the Circle plants, Pond plants produced smaller but somewhat thicker leaves at both Moist and Dry treatments than at Field Capacity, and equally large but thinner leaves in Wet soil (fig. 5F,G). Because of increased allocation to leaf tissue, however, leaf area ratio was higher in plants grown at reduced moisture levels, as was the case for Circle plants (fig. 5H).

DISCUSSION

Phenotypic Plasticity in Response to Soil Moisture

Optimal plant-growth conditions occur when soil is at field capacity; the dry and wet ends of the moisture gradient pose distinct stresses, and are discussed separately.

Response to Drought.—The Moist and Dry treatments imposed continual mild and moderate drought stress, respectively, as indicated by the midday wilting of plants in the Dry but not the Moist treatment (Treshow 1970). Even mild drought stress, if prolonged, can have a deleterious effect on all major aspects of plant metabolism (reviewed in Gates 1968; Begg and Turner 1976; Levitt 1980; Bradford and Hsiao 1982; Kramer 1983). Overall plant growth is reduced both by biochemical disruptions and reduced cell enlargement, which leads to reduced leaf expansion and total leaf area, and therefore reduced whole-plant photosynthesis. Photosynthesis is further depressed at moderate drought stress because of the stomatal closure and inhibition of chloroplast activity that accompany wilting. As a result of these growth limits, drought-stressed plants generally produce fewer flowers and seeds (Slatyer 1969; Kaufmann 1972). In accordance with these physiological limits, plants of both populations produced lower total biomass, mean and total leaf area, and fruit biomass and number at the Moist and Dry treatments than at Field Capacity (figs. 3A-D,F; 5A-D,F).

Given these limits to plant growth and reproduction under reduced water availability, the salient question is whether *Polygonum* plants are capable of plastic adjustments that mitigate those limits. Appropriate plant responses to drought stress function to conserve tissue water and/or to reduce the stress itself by increasing the actual amount of water available to the plant. Because carbon gain and water loss are physically linked, responses to drought that conserve water by lowering transpiration (e.g., lower total and relative leaf area) necessarily reduce growth as well (Gates 1968; Bradford and Hsiao 1982; Kramer 1983). It is particularly advantageous for annual plants to maintain growth rates as high as possible, and therefore under drought stress to maximize water collection rather than reduce water use (Levitt 1980; shown empirically by Lechowicz and Blais 1988). In keeping with this prediction, plants of both *Polygonum* populations produced much higher ratios of root-to-shoot biomass in the Moist and Dry treatments than at Field capacity (figs. 3I, 5I), as a result of both increased proportional allocation to roots and reduced allocation to stem (but not leaf) tissue (figs. 2, 4). An increased root-to-shoot ratio makes more water available to aboveground tissues by allowing the plant to explore a greater soil volume as well as to present a larger absorptive root surface relative to its biomass. This is a common and welldocumented adaptive response to drought (e.g., Maximov 1929 cited in Levitt 1980; Mooney and Gulmon 1979; Meyer and Boyer 1981; additional references in Fitter and Hay 1981).

Surprisingly, in both populations, the ratio of leaf area to plant biomass was not only maintained but increased by approximately one-third at the two drier treatments, compared to Field Capacity (figs. 3H, 5H). These relatively slight changes in leaf area ratio (and specific leaf area) cannot be ascribed to a lack of phenotypic flexibility, since different light-intensity treatments elicited extremely dramatic changes in both of these characters from related genotypes (Sultan and Bazzaz 1993a). Rather, this suggests that, as expected, the primary plastic response to drought stress in these plants was an enhanced watercollecting capacity rather than conservation by means of reductions in relative photosynthetic surface area. Indeed, under conditions in which biomass is limited, it is particularly advantageous for plants to maintain as great a relative leaf area as is possible. The relatively large root systems of these smaller, droughted plants evidently provided adequate water to supply a high proportion of transpiring surface area. Similar results were obtained with Solanum genotypes grown in moist and dry soils: root-to-shoot ratios increased notably in dry soil, whereas leaf area ratio remained constant (Clough et al. 1979).

Polygonum plants also increased significantly proportional allocation to fruit at the Moist and Dry treatments relative to Field Capacity (figs. 2, 4). This developmental shift partially mitigated the reproductive consequences of the reduction in total plant biomass imposed by drought stress. Such an increase in fruit allocation has been found in several herbaceous crop plants exposed to drought (Kaufmann 1972). Al-



FIG. 4. Proportional biomass allocation for 10 Pond genotypes at four moisture levels. Root, stem, leaf, reproductive support, and fruit biomass presented as proportions of total plant biomass; means of four replicates.

though drought stress often results in smaller as well as fewer propagules (Slatyer 1969; Kramer 1983), *Polygonum* plants also produced fruit of *greater* mean weight at the two drier treatments than at Field Capacity (figs. 3J, 5J). Mean fruit weight decreased along with total biomass and fruit number in related genotypes grown at low light (Sultan and Bazzaz 1993a), so this is evidently not simply a consequence of fewer plant nutrient sinks. These heavier propagules possess



FIG. 5. Norms of reaction for 10 Pond genotypes at four soil moisture levels (means of four replicates). A, Total plant biomass; B, total fruit biomass; C, total fruit number; D, total plant leaf area; E, total leaf number; F, mean leaf size; G, specific leaf area; H, leaf area ratio; I, root-to-shoot ratio; J, mean fruit weight. Adjacent treatment contrasts that do not differ significantly at P < 0.05 are joined by a straight line; nonadjacent treatments that do not differ are shown with a dotted line.

TABLE 4. Pond population: genotypic differences within moisture treatments. Genotypes shown ranked by character value within each moisture treatment; those joined by a vertical line do not differ at a probability of < 0.05. Below these, F values and probability levels are given from ANOVA for genotype effect within treatment; a boldface vertical line indicates that the genotype term is not significant ($P \ge 0.05$). Details are given in the *Methods* section.

	TOTAL BIOMASS					TOTAL FRUIT BIOMASS					FRUIT NUMBER					
	DRY MOIST FIELD WET					<u>Y</u>	MOIST	FIELD	WET		DRY	MOIST	FIELD	WET		
	3 19 9 8 7 6 10 14 5 11	5 7 3 11 9 8 6 19 14 10	3 6 5 9 7 11 8 14 19 10	3 8 9 7 5 10 19 11	1 1 1 1	3 9 7 9 5 1 0 5 1	3 5 7 9 11 8 14 6 19 10	6 3 9 5 7 11 8 14 19 10	8 3 7 9 5 19 10 14 11		3 19 7 9 8 6 14 5 10 11	3 5 7 8 9 6 11 14 19 10	6 3 9 5 7 11 14 19 8 10	3 8 6 9 7 10 5 19 14 11		
F P	2.23 .050	1.20 .338	3.22	3.37 .007	2.4	1	1.59 .171	3.47 .007	1.89 .097		3.35 .007	1.82 .113	3.63 .005	2.43 .036		
	TC	TAL LE	AF AR	EA		LEAF NUMBER						MEAN LEAF SIZE				
	DRY	MOIST	FIELD	WET	DRY	<u>.</u>	MOIST	FIELD	WET		DRY	MOIST	FIELD	WET		
	3 8 9 19 7 6 14 10 5 11	7 3 8 5 9 11 19 6 14 10	6 3 9 7 8 11 14 19 10	3 8 6 9 7 10 5 19 11 14			5 7 3 8 9 11 19 6 14 10	3 6 5 9 7 11 14 19 8 10	3 8 6 7 9 5 10 11 14 19		19 6 11 10 5 3 9 8 14 7	14 7 10 11 19 6 8 3 9 5	8 6 19 3 5 7 14 9 10 11	19 10 14 6 5 11 9 7 3		
F P	2.90 .015	1.33 .269	3.53 .006	2.66 .024	2.4 .03	1 7	1.41 .237	1.70 .141	2.71 .022		1.52 .189	0.77 .642	$\substack{1.71\\.143}$	1.52 .193		
	SPE	CIFIC L	EAF AF	REA		LE	AF ARE	EA RAT	'IO		RO	OT: SHO)OT RA	TIO		
	DRY	MOIST	FIELD	WET	DR	<u> </u>	MOIST	FIELD	WET		DRY	MOIST	FIELD	WET		
	6 7 14 3 8 10 9 19 11 5	7 3 14 8 6 5 11 19 9 10	14 19 11 7 6 5 10 9 8 3	14 7 11 6 10 5 8 19 9 3	1 1 1 1	1 5 7 0) 3 9 9 1 5	7 8 3 9 14 19 6 10 11 5	5 10 6 14 9 3 8 19 7 11	10 7 9 14 6 19 8 3 5 11		7 3 8 11 9 10 14 5 19 6	8 14 19 11 7 3 9 10 5 6	8 19 9 14 11 3 6 7 10 5	9 6 19 7 14 3 5 8 11 10		
F P	1.98 .082	$0.97 \\ .487$	2.63 .027	1.31 .276	2.0	2 4	$1.07 \\ .414$	2.11 .068	$1.42 \\ .229$		0.84 .588	0.47 .878	1.30 .288	0.77 .649		
	MEAN FRUIT WEIGHT															
F P	DRY 10 11 5 19 3 14 7 8 9 6 3.91 .003	MOIST 10 11 9 14 5 6 7 3 19 8 2.92 .016	FIELD 10 8 11 7 5 9 14 19 6 3 2.72 .023	WET 11 5 19 8 6 14 9 7 10 3 4.51 .001												

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thicker pericarps and/or greater nutrient reserves than those produced at more favorable soil moisture conditions (S. E. Sultan unpubl. ms). Such differences could benefit the subsequent generation by protecting the dormant embryo from desiccation, preventing germination in insufficiently moist soil, and making possible rapid initial root growth in a drought-prone environment (Baker 1972). The functional trade-off between propagule number and size is well known (Jain 1979; Morse and Schmitt 1985; Venable and Brown 1986); greater size may be of particular advantage to a propagule encountering dry conditions (Salisbury 1942). This plasticity in individual fruit weight may therefore enhance the reproductive fitness of plants limited in fruit number as a result of drought, and indeed is analogous to the correlation found among herbaceous California species between individual seed weight and increasingly xeric habitats (Baker 1972).

Two additional mechanisms may have contributed to the maintenance of growth in these plants under drought stress. (These are mentioned only as possibilities, since the relevant physiological data were not collected in this study.) Polygonum persicaria may be capable of maintaining metabolically favorable leaf water potentials under drought stress by virtue of exceptionally sensitive stomatal control, as is the closely related P. pensylvanicum (Wieland and Bazzaz 1975). Polygonum persicaria may also be among those herbaceous species that respond to drought by means of osmotic adjustment that permits the extraction of water from soil at very low water potentials (Meyer and Boyer 1981). That the norms of reaction for root-to-shoot ratio are flatter in Pond than in Circle genotypes (cf. figs. 3I and 5I) suggests that such physiological mechanisms may be particularly important to drought tolerance in these plants. Because this experiment involved only reduced soil moisture and not the entire field "syndrome" of drought stress (Begg and Turner 1976), these plants were not expected to respond by increased cuticle thickness (Fitter and Hay 1981) or leaf parahelionasty (Begg 1980), although such responses might be elicited from these genotypes under excessive transpirational demand. Indeed, Polygonum plants orient leaves vertically at the Pond site, where they experience an extremely high energy load (Sultan 1990).

Response to Flooding.-Flood stress such as that imposed at the Wet treatment consists of primarily of a root oxygen deficit, which causes reduced plant growth or death because of the lower energy efficiency and phytotoxic end products of anaerobic fermentation as compared with aerobic respiration (Levitt 1980; Fitter and Hay 1981). Plants in flooded soil may also experience nutrient or even water deficiency from reduced uptake capacity or root death (Kramer 1983; Schülze et al. 1987). In many annual species, total and reproductive biomass are reduced as much in flooded as in extremely dry soil (e.g., Pickett and Bazzaz 1978). Surprisingly, the total biomass and fruit number of Polygonum plants from both populations were equally high at the Wet treatment and at Field Capacity (figs. 3A,C; 5A,C) (although mean fruit weight and therefore total fruit biomass was slightly reduced in Pond plants; fig. 5H,B). Polygonum genotypes thus successfully avoided the deleterious effects of oxygen deficits on plant growth. This success may be largely due to the dense mats of finely branched superficial and adventitious roots produced by all genotypes when grown in the Wet treatment. This remarkable plastic change in root-system morphology and deployment was not observed at any other experimental moisture, light, or nutrient treatment. Similarly, total plant biomass was equally high at flooded conditions and at field capacity in Carex flacca, which also facultatively produces adventitious roots in response to flooding (Heathcote et al. 1987). Perturbation experiments have directly implicated such roots in individual flood tolerance (Etherington 1984).

Consistent with the reduced capacity for water uptake in flooded conditions, allocation to leaves decreased at the Wet treatment in both populations (figs. 2, 4), such that leaf-area ratio was either as low or lower than at Field Capacity (figs. 3H, 5H). Such an allocational shift was predicted as an adaptive response in flood-stressed plants by Schülze et al. (1987) using a carbohydrate partitioning model based on optimal trade-offs between water uptake and photosynthetic capacity.

Environmental Tolerance.—A striking result of this study was the ability of all genotypes of both populations to survive and reproduce amply at soil-moisture conditions ranging from extremely dry to flooded. The constancy of both the drought and flood stresses imposed in this experiment renders them particularly severe compared with field moisture conditions, in which periods of moisture recovery and aeration would occur (Begg and Turner 1976). Even at the Dry treatment, in which soil water potentials were so low that plants wilted virtually every day, every genotype produced a mean of over 500 fruits (figs. 2C, 3C). Furthermore, growth and reproduction were maintained at close to maximum levels at the flooded treatment, although such flooding constitutes an extreme plant environment, and one often limited to specialized wetland species (Kramer 1983; Heathcote et al. 1987; Carter and Grace 1990).

The *Polygonum* genotypes studied thus universally possess extremely broad environmental tolerance with respect to soil moisture. Such ecological breadth (i.e., the ability to survive and reproduce in a broad range of environmental conditions) may be common among weedy annuals (Bazzaz 1979, 1987), although in general its within-genotype basis remains to be established.

Patterns of Genetic Diversity, Environmental Variability, and the Maintenance of Variation

Apart from convergent responses in root-toshoot ratio, in both populations genotypes differed significantly on average in nearly all characters measured (table 2). Yet, as a result of changes in genetic variance and rank order from one moisture treatment to another, in no trait did any two genotypes differ significantly from each other across the entire environmental gradient, nor did any genotype rank highest or lowest in fitness across the gradient (total fruit weight; tables 3, 4). Despite the existence of average differences among genotypes, such differences in genetic variance and correlation between environments can operate to obstruct selection for particular norms of reaction (Via 1987; Van Tienderen 1991; for discussion of "antagonistic pleiotropy" or genetic correlations of disadvantageous and advantageous responses to alternative environments, see Moran 1991 and Via 1991). Genetic variation will be maintained when there is genotype-by-environment interaction in populations that encounter spatial or temporal variability in the relevant aspects of environment (Via and Lande 1985; Mitchell-Olds and Rutledge 1986); in other words, when the same genotypes do not have higher relative fitness in all environments that occur (Gillespie and Turelli 1989). The results of this norm of reaction study demonstrate that patterns of genotypic diversity in natural populations may lead to the maintenance of genetic variation rather than reveal fitness differences upon which selection might readily act. As described below, the precise patterns of diversity may prevent the elimination from the population of genotypes with significantly low average reproduction. (Since *P. persicaria* is a sexual, though largely inbreeding, species, we do not argue that particular genotypes will persist, but rather consider the variation expressed in each population within a single generation as a case study of the availability of variation to selection).

The fitness differences of greatest magnitude arose from the strikingly different norms of reaction of genotypes 9 and 12 in comparison with the other Circle plants (fig. 3B). In Circle 12, significantly low reproductive output at both Dry and Field Capacity soils was joined by high output relative to other genotypes at the Moist treatment (total fruit biomass, table 3). This norm of reaction thus exemplifies "crossover interaction" (Baker 1988), defined as reversals in relative rank among genotypes at different states on an environmental range. Because of their particular selective implications, the identification of such crossing patterns is a major goal of normof-reaction studies. If norms cross, a significant genotype main effect does not necessarily signify the presence of genetic differences available to natural selection (Gupta and Lewontin 1982). If genotypes reverse relative phenotypic rank in environments that are consistently distinct, selection will favor different genotypes in each environmental state and thus may (depending on the relative magnitudes of selection and migration) produce environmentally specialized populations (Wade 1990). Where environmental variation is fine-grained, however, crossing norms may render average differences among genotypes unavailable to selection (Gupta and Lewontin 1982; Via and Lande 1985; Sultan 1987; Via 1987; Gillespie and Turelli 1989; Stratton 1992). Because soil water potential at the Circle site is generally similar to that at the Moist treatment, this genotype may remain in the population despite its relatively poor performance at other moisture levels within the range of variation at this site. Similarly, genetic diversity for phosphoglucoisomerase is apparently maintained in populations of Amaranthus retroflexus by the conjunction of crossing norms of reaction and within-site soil moisture variation (Zangerl and Bazzaz 1984). ANOVA cannot suggest evolutionary consequences precisely because of its inability to distinguish crossover interaction from

patterns of genotype by environment interaction that do not involve rank reversals (Via 1987). [No statistical method is available that adequately distinguishes these patterns (Baker 1988), although it is possible to test whether at least one crossover occurs between two treatments (Azzalini and Cox 1983)].

Because the plant environment is defined by myriad influences which may vary independently (Bazzaz 1987), such crossover interactions may also occur among different environmental factors. For instance, genotype Pond 19, which had relatively low reproductive fitness in nutrient-rich Field Capacity and Moist soils and across a broad gradient of nutrient levels in which soils were at field capacity, had high reproductive output relative to other genotypes in dry, nutrient-rich soil and in moist, rich soil at very low light (Sultan and Bazzaz 1993a,b). Both the crossing patterns among genotypic norms of reaction for fitness, and the environmental variation that thereby prevents selective elimination of particular genotypes, must therefore be conceived to operate in many dimensions rather than on a single axis. Because of the extreme variability of soil moisture, light, and other aspects of the plant environment at disturbed sites (Bazzaz 1987), crossover interaction may be particularly important in maintaining genetic diversity in populations of colonizing species such as P. persicaria.

In contrast, genotype Circle 9 has relatively low reproductive output at every treatment on the moisture gradient (fig. 3B). However, since it is statistically indistinguishable from most or all other genotypes at several moisture treatments (total fruit biomass, table 3), it is not at a consistent selective disadvantage. Depending on the distribution of environments, such differences in genetic variance from one environment to another can obstruct selection (Via 1987). Genotypes with relatively poor growth in certain environments may be shielded from selection in a population which encounters other environments to which genotypes respond similarly (e.g., Clough et al. 1980). This explanation also holds for genotypes Pond 10 and 11, which are each significantly low in fitness at only one point on the moisture gradient (table 4). Similarly, two Pond genotypes produced significantly less fruit biomass than others at a moderate nutrient treatment, but all genotypes reproduced equally at a very low nutrient level similar to usual conditions at the Pond site (Sultan and Bazzaz 1993b).

A second possible factor in the maintenance of the consistently poor Circle 9 genotype may be its ability to produce relatively large fruits at favorable soil conditions in which it produces fewer fruits than other genotypes (fig. 3J): if fruit weight is an important determinant of propagule success, this would constitute a crossover interaction for an important component of fitness.

In both populations, the greatest genetic variance occurred not at the environmental extremes, but at the favorable Field Capacity treatment (e.g., figs. 2A-C, 3A-C). (This does not refer to larger absolute variance associated with larger means, but to significant differences among genotypes within each treatment.) Although all genotypes were able to tolerate the entire range of moisture conditions, some evidently exploited the optimal treatment more fully. Greater variance among genotypes at favorable than unfavorable growth conditions has also been found for total biomass in Solanum (Clough et al. 1980) and for susceptibility to insect herbivory in Solidago (Maddox and Cappuccino 1986). Laboratory lineages of Tribolium beetles differed most strongly under optimal population growth conditions (Wade 1990). At the population level, Phlox drummondii populations of diverse habitats differed in response to favorable light, water, and nutrient conditions but did not differ significantly at unfavorable response states (Schwaegerle and Bazzaz 1987). With respect to light, however, Polygonum genotypes differed more markedly in morphology at suboptimal than at optimal conditions (Sultan and Bazzaz 1993a). The latter result supports the contrary view that genetic variance tends to increase at the extreme end of an environmental range (Lewontin 1974). These opposite results for closely related genotypes from the same populations suggest strongly that the degree of genotypic spread does not correspond to "stress" in some abstract sense, but rather depends on specific environmental factors and the responses they elicit.

Soil moisture strongly affected the reproductive fitness of *P. persicaria* genotypes: the mean reduction in total fruit biomass within genotypes at Dry soil compared with Field Capacity was 50%–70%. Because soil moisture can vary dramatically among microsites within a plant population (Bazzaz 1987; e.g., fig. 1B), and because such variation is randomly distributed with respect to genotype, it can alter the magnitude and/ or direction of fitness differentials among individuals with nonparallel norms of reaction, and therefore promote the maintenance of genetic diversity (Bazzaz and Sultan 1987). This argument also applies to soil macronutrient content, which likewise varies spatially and temporally within populations and strongly affects reproductive output (Sultan and Bazzaz 1993b). Thus the absence of parallel reaction norms may explain the maintenance of genetic variation in natural populations, which necessarily experience inconstant environments (Barton and Turelli 1989). The effect of moisture on relative fitness is particularly complex because the larger propagules produced by drought-stressed plants may be overrepresented in the next generation, again depending on the distribution of environmental variability (S. E. Sultan unpubl. ms).

CONCLUSIONS

Genotypes from two natural populations of *Polygonum persicaria* demonstrated specific, functionally adaptive allocational and morphological responses to an extreme range of soil moisture conditions. This repertoire of plastic expression confers upon individual genotypes remarkable ecological breadth: environmental extremes typically associated with specialized species, such as soil flooding, may be accommodated within single genotypes.

Genotypes within populations were not consistently superior and inferior in reproductive output across the moisture gradient. Although certain genotypes showed significantly low average fitness, either the magnitude or the direction of differences in relative fitness varied among soil moisture treatments. As a result of these nonparallel norms of reaction for reproductive fitness, temporal variation in soil moisture in these populations may explain the maintenance of genetic variation, despite average fitness differences. In natural systems, the environment consists of complex combinations of many independently varying factors, so that selection always operates in the context of environmental variability. Because of this joint effect of genotype-by-environment interaction and environmental variability in opposing selection, to better understand natural selection and its limits it is essential to know the extent to which natural populations are characterized by parallel or nonparallel norms of reaction.

ACKNOWLEDGMENTS

We thank R. Lewontin for valuable discussion, and E. Fajer, A. Knoll, S. Morse, R. Tryon, and two anonymous reviewers for critical comments on the manuscript. We also thank K. Mc-Connaughay and E. G. Reekie for practical advice, and C. Johnston for greenhouse and lab assistance. This work was partially supported by National Science Foundation grant BSR-8414355 to F.A.B. and by a research grant from the Department of Organismic and Evolutionary Biology to S.E.S.

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Corresponding Editor: T. Meagher