WILEY

Phenotypic Plasticity in Polygonum persicaria. III. The Evolution of Ecological Breadth for Nutrient Environment

Author(s): S. E. Sultan and F. A. Bazzaz

Source: *Evolution*, Vol. 47, No. 4 (Aug., 1993), pp. 1050-1071
Published by: Society for the Study of Evolution
Stable URL: http://www.jstor.org/stable/2409974
Accessed: 19-04-2016 18:21 UTC

Evolution, 47(4), 1993, pp. 1050–1071

PHENOTYPIC PLASTICITY IN *POLYGONUM PERSICARIA*. III. THE EVOLUTION OF ECOLOGICAL BREADTH FOR NUTRIENT ENVIRONMENT

S. E. SULTAN[1] AND F. A. BAZZAZ
Department of Organismic and Evolutionary Biology, Harvard University, 16 Divinity Avenue, Cambridge, Massachusetts 02138

Abstract.—Norms of reaction for a number of growth and reproductive characters were determined for 15 randomly sampled *Polygonum persicaria* genotypes, from two natural populations originating in sites with very different nutrient availabilities. Under severely limiting nutrient conditions, these genotypes shared not only plastic responses such as increased root-to-shoot ratio, but a surprising constancy in such functionally essential characters as leaf area ratio, leaf nitrogen concentration, and propagule nitrogen content. Because functional homeostasis depends on flexibility in underlying characters, similar homeostatic results can be achieved through different combinations of underlying plastic and fixed responses in genetically different entities. For example, plants in each population maintained a relatively constant propagule nitrogen content under extreme low-nitrogen conditions by varying either the size or the tissue nitrogen concentration of propagules. These genotypes also tolerated excessive nutrient levels toxic to many plants, evidently by storing excess nutrients in shoots. Although development was altered under such circumstances, reproductive fitness was maintained.

Genotypes of both populations thus were universally able to tolerate very limited as well as excessive nutrient supplies and to exploit favorable nutrient conditions. This capacity of individual genotypes to accommodate diverse nutrient environments reflects the specific nature of mineral resources and of plant physiology: because nutrient availability can be manipulated via root-system adjustments and facultative uptake mechanisms, and ions can be differentially allocated and translocated among plant parts, nutrient supply may be to a considerable extent mediated by the plant individual. The results further suggest that the response mechanisms conferring ecological breadth for nutrient environment may entail neither physiological costs nor fitness trade-offs, conditions favoring the evolution of plasticity rather than genetic specialization. The evolution of such plasticity also reflects the highly variable nutrient environment plants experience, because of fluctuations not only in soil minerals but in complex interacting factors such as moisture.

General conclusions based on the entire, three-part study follow the discussion.

Key words.—Homeostasis, nitrogen, norms of reaction, nutrient stress, phenotypic plasticity, *Polygonum persicaria*, specialization.

Received January 31, 1992. Accepted October 23, 1992.

The evolution of phenotypically plastic genomes has recently been described as an "alternative picture" to a conventional view of precise genotype-specific adaptations (Bradshaw and Hardwick 1989); in fact, the special implications of such systems for the action of natural selection have long been recognized (Wright 1931). The awakening of interest in this "alternative picture" in part reflects a sense that the paradigmatic cases of natural selection, such as industrial melanism in *Biston betularia* and heavy-metals tolerance in grass species, may not exemplify the process of evolution with respect to unexceptional environmental factors and less simply determined functional traits (Sultan 1987). If it is to be of adaptive value to the organism, plasticity must involve functionally appropriate adjustments in specific traits in response to particular environmental circumstances (Schmalhausen 1949; Bradshaw 1965). Clearly, the possibility that a particular environmental stress will be accommodated through the evolution of individual plasticity depends on both the distribution of its variability in the environment (Levins 1968) and on the possible means of tolerance and adjustment dictated by both the nature of the stress and the physiology of the organism. For this reason, our examination of plasticity in *Polygonum* has involved not a single, arbitrary environmental factor, but three fundamental aspects of the plant environment that vary at different temporal and spatial scales and demand different mechanisms of plant response. In related experiments (Sultan and Bazzaz 1993a,b), *Polygonum* genotypes were found to express a wide range of

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

adaptive plasticity to both light, which may vary at extremely fine temporal and spatial scales in plant habitats, and soil moisture, which generally varies temporally within the experience of individuals as well as on higher spatial and temporal scales. In this final paper, we examine plasticity in response to contrasting soil-nutrient conditions in order to consider the implications of such plasticity and the ecological breadth it affords for the evolution of genetic specialization for particular nutrient environments.

It is well known that genetic variation exists in the ability of plants to tolerate certain soil contaminants (Antonovics et al. 1971 and references), and it is often assumed that genotypes likewise vary in relative success at high versus low macronutrient levels (Snaydon 1970). Apart from data for artificially selected crop varieties, however, very little information is available regarding genetic diversity for response to soil nutrient supply (Crossley and Bradshaw 1968; Gerloff 1976; Marschner 1986). Indeed, in contrast to the case of heavy-metal tolerance, flexible norms of reaction in response to nutrient supply may be favored to evolve in plant genotypes for two reasons.

First, unlike the physiological trade-offs inherent in heavy-metal tolerance (see Etherington 1982 and references), the nature of responses to limiting and excessive amounts of major nutrients may permit individual genotypes to succeed in a wide range of soil conditions. For instance, plasticity in characters important to nutrient uptake, such as allocation to root systems, may not entail physiological costs (Sultan 1992). Furthermore, the ability of plants to partition differentially mineral nutrients and to relocate them among plant parts throughout the life cycle suggests that plants may be particularly capable of flexible, homeostatic adjustments of tissue mineral concentrations. When phenotypic response mechanisms permit appropriate matching of phenotypes to environments and bear no inherent costs, plasticity rather than genetic specialization is selectively favored (Lewontin 1957; Levins 1968; Moran 1992).

Second, although general edaphic differences are indeed spatially distinct and consistent, soil macronutrients may vary at small spatial (Chapin 1980; Tilman 1982) as well as temporal scales (Robinson and Rorison 1983; Benner and Bazzaz 1988). Moreover, the availability of nutrients to plants depends on complex interactions between soil nutrient content and fluctuating environmental factors such as light intensity (Peace and Grubb 1982; Field and Mooney 1986; Evans 1989; Chapin 1989), soil moisture (Davidson 1969; Marschner 1986), neighbor density (Heywood and Levin 1986), and herbivory (Stafford 1989), as well as on interactions between specific mineral nutrients (Tilman 1982). Even in habitats with homogeneous substrates, then, nutrient availability will vary to some extent within populations and individuals, and therefore may not be subject to precise genetic tracking. For this reason, the ability to both maintain growth under conditions of low nutrient supply and exploit high nutrient supplies when available may be an important aspect of individual plant adjustment to environment (Bradshaw 1969; Epstein 1972; Chapin and van Cleve 1989; Jackson and Caldwell 1989).

Materials and Methods

Study System.—Genotypes were studied from two genetically differentiated natural populations of *Polygonum persicaria* located 150 km apart (see Sultan and Bazzaz 1993a). The Circle population occupies an abandoned agricultural field, and the Cliff Pond population, the bank of a freshwater pond. Soils at the two sites are quite different: the Circle site substrate is a sandy loam with about 7% organic matter and moderate nutrient-holding capacity, whereas the Pond site substrate is nearly pure ($\geq$98.8%) sand, with less than 0.2% organic matter and extremely low cation exchange capacity (details in Sultan 1990). These soils differ strongly in both content and variability of major nutrients (fig. 1). Nitrate and ammonium content of the Circle soil vary spatially and temporally from low to moderately high, whereas phosphorus, potassium, calcium, and magnesium content vary from moderate to high (based on ranges for Massachusetts soils). In contrast, the Pond substrate is consistently low in all of these major nutrients. Although spatial and temporal variability do occur at the Pond site within a much narrower range, even moderate levels of nutrients occur only rarely (fig. 1). The two populations are not compared directly, because of differences in their response to the cloning process and of the absence of comparative information on their genetic structure. Rather, they are considered separately, as self-contained examples of populations from variable and less variable nutrient environments.

Experimental Plant Material.—Mature fruits were collected from randomly chosen field par-

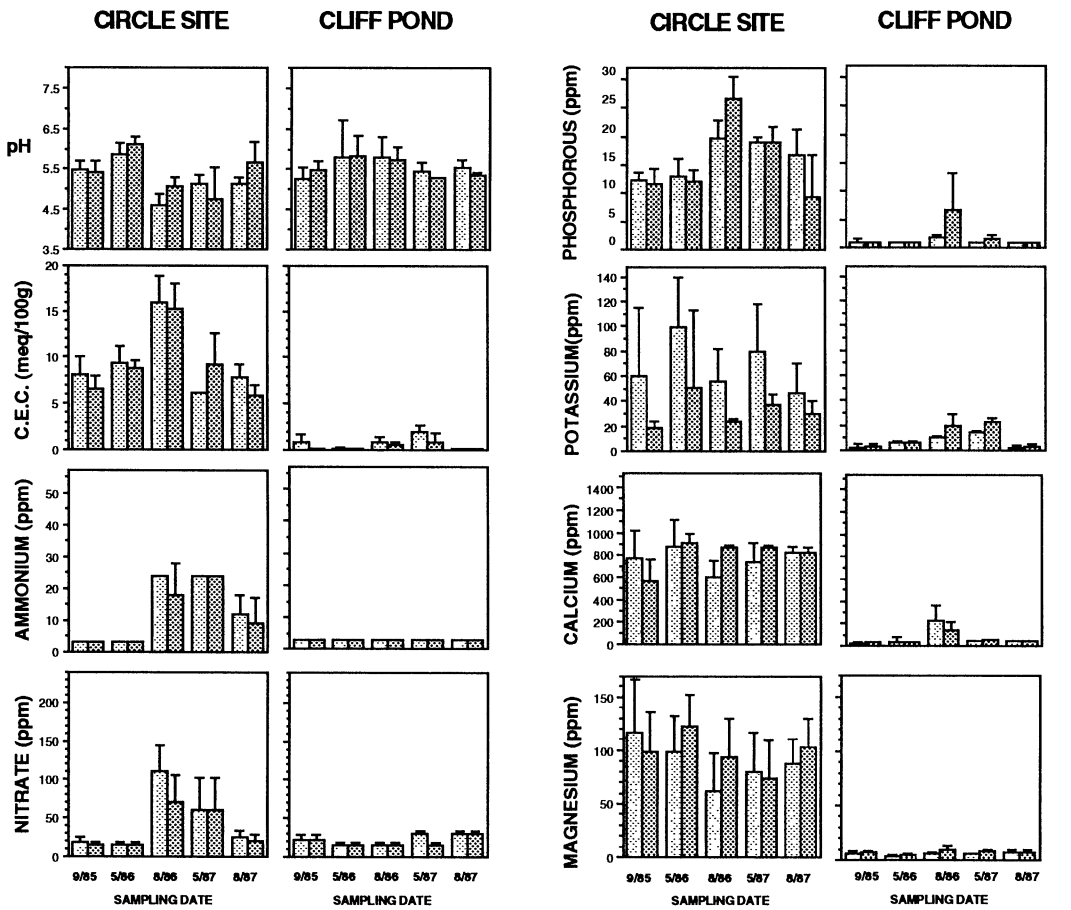

FIG. 1. Soil nutrient content at Circle Site and Cliff Pond, 1985–1987. Means ± standard deviations of 2–8 soil samples at surface (0–10 cm; light hatching) and subsurface (20–30 cm; dark hatching) levels, collected 9/15/85, 5/9/86, 8/25/86, 5/14/87, and 8/20/87; *y*-axis maxima are considered to be high for regional soils. (Soil tests performed by the University of Massachusetts Suburban Experiment Station Soil and Plant Tissue Lab, using the Morgan extraction system.)

ents growing 1 m or more apart, germinated, and grown under uniform glasshouse conditions for 6 wk. Vegetative cuttings were made from seven Circle and eight Pond individuals and placed in a warm growth chamber (27°/23°C) for 2 wk. Temperatures were lowered to 18°/18°C for a third week to slow development before the start of the experiment. Sixteen rooted cuttings of approximately uniform size were selected from each genotype and each randomly assigned a soil nutrient treatment and a bench position (propagation details in Sultan 1990).

Experimental Treatments.—We planted 238 rooted cuttings (2 populations × 7 or 8 genotypes × 4 treatments × 4 replicates, minus 2 missing cuttings) singly into 5-inch clay pots, placed them in plastic saucers, and set them on three 420 × 160 cm glasshouse benches in a completely randomized design. Each pot contained 1 liter of 2:1 sterile sand : Turface® fritted clay mixture, plus 1.2 g of Vitagran® micronutrient supplement and either 0.1 g, 1.0 g, 2.8 g, or 4.5 g of granular 15:8:12 nitrogen : phosporous : potassium fertilizer (Agway Co.), yielding 0.015 g, 0.150 g, 0.420 g, and 0.675 g total nitrogen per pot, respectively. For convenience, these treatments are referred to as $x/6$, $2x$, $5x$, and $8x$, respectively (based roughly on the recommended addition of x = 0.56g/liter soil; the $x/6$ and $8x$ treatments differ by a factor of exactly 45). The $x/6$ treatment was extremely low in nitrogen, phosphorus, and potassium, and is comparable in content of these

nutrients to soil at the Pond site. The $2x$ treatment contained moderately low nutrients, similar to average or high levels in Circle site soil. The $5x$ treatment corresponded to very high nutrient levels for natural soils, outside the range of both Circle and Pond population soils. Nutrient concentrations at the $8x$ treatment were more than double levels considered to be high for Massachusetts soils (Fellows 1981). Such excessive nutrient levels might occur in conjunction with human activity (e.g., fertilizer runoff or manure heaps). (Estimated concentrations of ammonium, nitrate, phosophorus, and potassium in the four experimental treatments are given in Sultan 1990).

Mean midday light intensity was maintained at about 600 $\mu E/m^2$ s throughout the experiment by the use of supplementary artificial light as required. Aboveground interference among plants was negligible. Plants in all nutrient treatments were kept at field capacity moisture. Relative humidity was consistent throughout the greenhouse module, varying from 50% to 75%. Plants were grown for 12 wk at 26°/22°C day/night temperature with a 13.5-h day length.

Characters Measured.—Total plant biomass and proportional biomass allocation to root, stem, leaves, reproductive support, and fruits were determined for each plant. Total live leaf area and total leaf number (live + senesced leaves) were determined at harvest, and mean leaf size calculated from the live-leaf area and number. The following ratios were calculated: root-to-shoot (stem plus total leaf) biomass, leaf area ratio (live leaf area per unit of plant biomass), and specific leaf area (live leaf area per unit of live leaf biomass). Mean fruit weight was estimated from 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.) In addition, the ratio of senesced leaf biomass to total leaf biomass at harvest was calculated in order to provide a description of leaf turnover patterns (senescent leaves do not abscise in this species).

Tissue nitrogen concentration was determined for leaves and fruits of a subset of plants using the Kjeldahl method (aluminum block digestion followed by steam distillation) in a semimicro Kjeltec® Auto 1030 Analyzer (Tecator, Inc.). Leaf samples consisted of 70–300 mg (dry weight) of fully expanded leaves chosen otherwise at random from leaves that had been harvested live. Oven-dried samples from 10 randomly selected plants per population per treatment were finely ground and redried at 50°C for 72 h before weighing and analysis. Population treatment means for leaf nitrogen concentration thus incorporate variation that is due to genotype, replicate, and leaf age. Fruit samples consisted of approximately 100 mature propagules (ca. 200 mg) from each of five randomly chosen plants per population per treatment, and, for those genotypes that produced distinctly large or small fruits at certain treatments, from three replicates per genotype at those treatments. Each sample thus incorporates variation among inbred fruits of a given plant as a result of position, time of development, etc.; treatment means additionally reflect both genotype and replicate sources of variation. Samples were redried at 50°C for 72 h before weighing; digestion and analysis were performed on entire fruits (seed plus pericarp).

Data Analysis.—The analytical methodology is that of Sultan and Bazzaz (1993a). Because the block term explained only a negligible amount of the experimental error (see Sultan 1990) it was not included in the ANOVA models. One outlier for mean fruit weight was deleted. For several characters, variance was somewhat greater (according to Bartlett's test) within the $8x$ and, in Circle plants, the $5x$ treatments. However, omission of the $8x$ treatment reduced the error mean squares by only about 10%, and the results of significance tests were unchanged, indicating that the ANOVA results were robust. This greater among-replicate variation in high nutrient treatments was interpreted as the interaction of nutrient availability with variation in cutting vigor (e.g., meristem number) and/or proximity to artificial light sources. Overall treatment effects were further examined by performing a posteriori linear contrasts of treatment responses (i.e., $x/6$ vs. $2x$, $2x$ vs. $5x$, and $5x$ vs. $8x$; for details, see Sultan and Bazzaz 1993b).

The effect of nutrient treatment on tissue nitrogen concentration was estimated by one-way ANOVA for nutrient treatment on randomly subsampled plants from each population. Differences among treatment means were tested using Student-Newman-Keuls. Because fruit nitrogen means were based on only five plants per treatment, differences were considered to be significant at a probability level less than or equal to 0.10. Linear regression of fruit nitrogen concentration on nutrient treatment was estimated (MGLH module, SYSTAT 3.0) following the hy-

TABLE 1. Two-way mixed ANOVA for growth and reproductive characters.

	Genotype		Nutrient level		Genotype-by-nutrient		Error
	MS	*F*	MS	*F*	MS	*F*	MS
Circle Population							
	(df = 6)		(df = 3)		(df = 18)		(df = 72)
Total plant biomass	0.242	1.10 NS	3.176	18.04***	0.176	0.80 NS	0.219
Root-to-shoot ratio	0.015	4.13**	0.111	25.55***	0.004	1.22 NS	0.004
Leaf area ratio	55.52	2.10 NS	59.10	2.79 NS	21.21	0.80 NS	26.50
Senesced leaf proportion	0.088	3.57**	0.052	1.15 NS	0.045	1.82*	0.025
Total leaf area	21.75	1.82 NS	163.4	27.13***	6.02	0.50 NS	11.98
Total leaf number	0.72	1.89 NS	3.20	9.72***	0.33	0.87 NS	0.38
Mean leaf size	9.63	6.35***	17.56	7.81**	2.25	1.48 NS	1.52
Specific leaf area	8816	4.58**	5605	4.36*	1286	0.67 NS	1926
Total fruit biomass	0.242	1.29 NS	1.671	11.31***	0.148	0.79 NS	0.187
Total fruit number	0.309	0.87 NS	3.186	10.53***	0.303	0.85 NS	0.355
Mean fruit weight	0.188	7.80***	0.031	0.70 NS	0.044	1.84*	0.024
Pond Population							
	(df = 7)		(df = 3)		(df = 21)		(df = 85)
Total plant biomass	0.473	1.69 NS	18.367	44.80***	0.410	1.47 NS	0.279
Root-to-shoot ratio	0.003	0.61 NS	0.124	18.10***	0.007	1.37 NS	0.005
Leaf area ratio	129.5	1.85 NS	207.3	2.21 NS	93.64	1.34 NS	70.04
Senesced leaf proportion	0.024	1.23 NS	0.008	0.34 NS	0.023	1.18 NS	0.020
Total leaf area	59.66	1.72 NS	1718.7	37.28***	46.11	1.33 NS	34.72
Total leaf number	0.541	1.52 NS	12.25	24.47***	0.500	1.40 NS	0.357
Mean leaf size	3.66	2.50*	75.71	35.46***	2.13	1.46 NS	1.47
Specific leaf area	3940	1.68 NS	20,436	7.53**	2716	1.16 NS	2343
Total fruit biomass	0.396	1.74 NS	12.353	40.10***	0.308	1.35 NS	0.228
Total fruit number	1.02	2.13*	23.45	30.36***	0.77	1.61 NS	0.36
Mean fruit weight	0.084	6.18***	0.714	33.09***	0.022	1.59 NS	0.014

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

pothesis that tissue concentration would increase with soil nitrogen content. Independent *t*-tests based on three replicates per group (STATISTICS module, SYSTAT 3.0) were used to compare specified genotype means for fruit nitrogen concentration; differences at a probability level of $P \leq 0.10$ were considered significant.

RESULTS

Circle Population.—Total plant biomass, fruit biomass, fruit number, leaf area, and leaf number all decreased monotonically from the favorable $5x$ treatment to the nutrient-poor $x/6$ treatment, but did not differ between the $5x$ and excessive $8x$ treatments (contrasts nonsignificant, $P \geq 0.35$; cf. fig. 2A–D). Norms of reaction in these growth and reproductive characters did not differ significantly among Circle genotypes (cf. nonsignificant genotype and genotype-by-nutrient terms, table 1). Although genotypes differed on average in several traits, in no case did any genotype differ from others at all nutrient treatments (table 2). Because of substantial among-replicate variation in leaf number at higher nutrient levels (Methods section), genotypes did not differ significantly despite the apparently distinct response of Circle 10 (fig. 2E). In general, genotypic variance was greater at higher nutrient levels; genotypes did not differ significantly within the $x/6$ treatment in any of 11 phenotypic characters examined (table 2).

Nutrient treatment also had a highly significant effect on proportional biomass allocation to root, leaf, reproductive support, and fruit tissues (table 3). With decreasing nutrient supply, allocation to roots and fruits increased, whereas allocation to leaves and reproductive support declined (fig. 3). In contrast, allocation to stem tissue did not vary with nutrient treatment (table 3). These allocational adjustments were common to all genotypes (cf. nonsignificant genotype-by-nutrient interaction terms; table 3). In accordance with these allocational changes, root-to-shoot ratio increased significantly with reduced nutrient levels, from about 1:5 at the $5x$ treatment to approximately 1:3 at the low extreme of the gra-

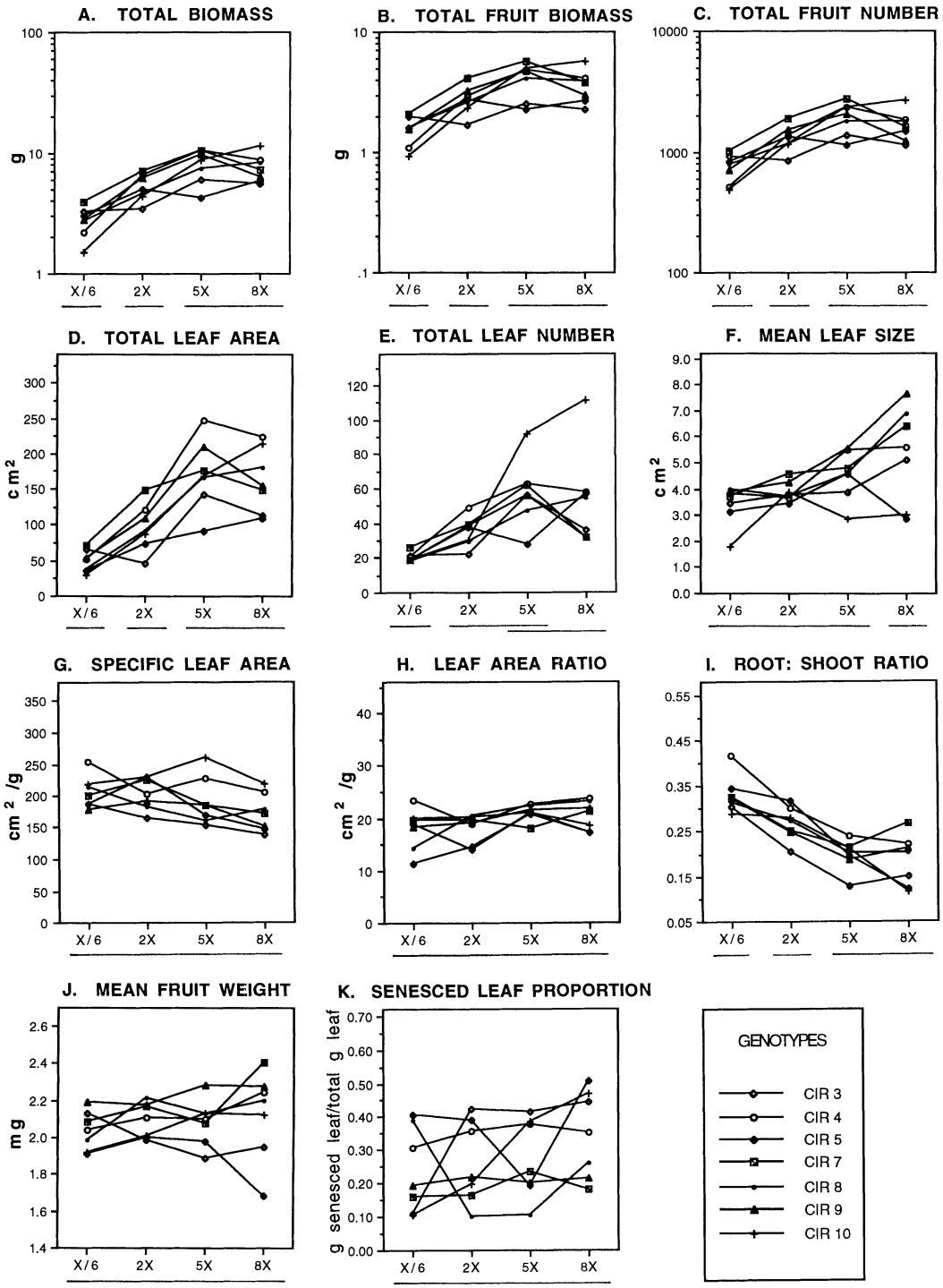

FIG. 2. Norms of reaction for seven Circle genotypes at four nutrient levels (means of four replicates). A, Total plant biomass; B, total fruit biomass; C, total fruit number; D, total plant leaf area; E, total leaf number; F, mean leaf size; G, specific leaf area; H, leaf area ratio; I, root-to-shoot ratio; J, mean fruit weight; K, senesced leaf proportion. Adjacent treatment contrasts that do not differ significantly at $P < 0.05$ are joined by a straight line.

TABLE 2. Circle population: genotypic differences within nutrient treatments. Genotypes shown ranked by character value within each nutrient 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; boldface vertical line indicates that the genotype term is not significant ($P \geq 0.05$). Details in the *Methods* section.

TOTAL BIOMASS

X/6	2X	5X	8X
7	7	4	10
3	4	10	4
5	9	9	7
9	5	7	8
8	8	8	5
4	10	3	9
10	3	5	3
F 1.36	1.12	0.73	0.81
P .282	.385	.634	.576

TOTAL FRUIT BIOMASS

X/6	2X	5X	8X
7	7	10	10
3	4	4	4
9	9	7	7
8	5	9	8
5	8	8	5
4	10	5	9
10	3	3	3
1.48	1.01	0.84	0.89
.239	.448	.555	.522

TOTAL FRUIT NUMBER

X/6	2X	5X	8X
7	7	10	10
3	4	4	4
8	5	7	5
5	9	9	7
9	10	8	3
10	8	5	8
4	3	3	9
1.76	0.82	0.65	0.95
.164	.565	.687	.548

TOTAL LEAF AREA

X/6	2X	5X	8X
7	7	4	10
3	4	9	4
9	9	10	8
4	8	7	7
8	10	8	9
5	5	3	5
10	3	5	3
F 1.13	1.94	0.66	0.65
P .385	.123	.680	.691

TOTAL LEAF NUMBER

X/6	2X	5X	8X
7	4	10	10
3	5	4	5
10	7	9	4
5	9	7	3
4	10	3	8
8	8	8	7
9	3	5	9
0.76	1.13	0.78	1.86
.608	.382	.597	.143

MEAN LEAF SIZE

X/6	2X	5X	8X
8	7	9	9
9	9	4	8
4	10	7	7
7	3	8	4
3	8	5	3
5	4	3	10
10	5	10	5
1.33	0.81	1.78	4.28
.295	.574	.163	.007

SPECIFIC LEAF AREA

X/6	2X	5X	8X
4	5	10	10
10	10	4	4
8	7	9	8
7	4	7	7
3	9	5	9
5	8	8	5
9	3	3	3
1.89	1.06	2.58	1.53
.137	.416	.058	.223

LEAF AREA RATIO

X/6	2X	5X	8X
4	8	4	4
10	10	8	8
7	7	9	9
3	9	3	7
9	4	10	10
8	5	5	5
5	3	7	3
2.64	1.53	0.24	0.76
.052	.218	.957	.612

ROOT: SHOOT RATIO

X/6	2X	5X	8X
4	5	4	7
5	4	7	4
7	10	10	9
9	8	8	8
8	7	5	3
3	9	9	5
10	3	3	10
1.07	1.22	2.86	4.75
.415	.338	.041	.005

MEAN FRUIT WEIGHT

X/6	2X	5X	8X
9	8	9	7
3	9	8	9
7	7	10	4
4	4	4	8
8	10	7	10
10	5	5	3
5	3	3	5
2.14	1.17	3.17	3.50
.099	.359	.028	.018

SENESCED LEAF PROPORTION

X/6	2X	5X	8X
5	3	3	5
8	5	10	10
4	4	4	3
9	9	7	4
7	10	9	8
3	7	5	9
10	8	8	7
1.38	3.28	2.69	1.84
.154	.021	.051	.147

dient (contrasts significant at $P \leq 0.001$; fig. 2I). Although genotypes shared identical root-to-shoot ratios within the two low nutrient treatments, genotypes differed significantly in the $5x$ and $8x$ treatments (table 2).

Unlike the characters discussed thus far, mean leaf size decreased only slightly at the $x/6$ treatment compared with the $5x$ treatment, and increased significantly in the $8x$ treatment (fig. 2F). This increase in leaf size was particularly pronounced in those genotypes that produced fewer leaves in the $8x$ treatment (Pearson correlation coefficient of genotype means for leaf size and number at this treatment = -0.82; cf. table 2).

TABLE 3. MANOVA for proportional components of biomass. Multivariate and univariate *F*-statistic shown with significance levels; details in the *Methods* section.

	Genotype	Nutrient level	Genotype-by-nutrient
	Circle Population ($N = 101$)		
	df = 6	df = 3	df = 18
Multivariate *F*	4.048**	6.436**	0.869 NS
Univariate *F*			
Root proportion	11.437***	20.050***	1.187 NS
Stem proportion	1.098 NS	1.940 NS	0.768 NS
Leaf proportion	5.177***	16.143***	1.346 NS
Reproductive support	2.804*	9.236***	0.749 NS
Fruit proportion	4.338**	10.264***	1.400 NS
	Pond Population ($N = 117$)		
	df = 7	df = 3	df = 21
Multivariate *F*	1.130 NS	8.153**	1.053 NS
Univariate *F*			
Root proportion	1.626 NS	13.951***	1.111 NS
Stem proportion	1.247 NS	18.277***	0.960 NS
Leaf proportion	1.280 NS	3.557*	1.665 NS
Reproductive support	0.790 NS	1.599 NS	0.568 NS
Fruit proportion	2.431*	1.358 NS	1.322 NS

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

Unlike the characters described previously, mean leaf size differed significantly among genotypes (table 1). Genotypes produced slightly thinner as well as smaller leaves in response to decreased nutrient levels (fig. 2G). Leaves of plants in the $8x$ treatment were thus both thicker and larger than those produced at less than excessive nutrient levels. These leaves also had significantly higher concentrations of nitrogen (per unit of dry weight), whereas leaf nitrogen concentration did not differ significantly among plants from the $5x$, $2x$, and $x/6$ treatments (fig. 4A). The increase in specific leaf area with decreasing nutrients offset the concomitant decrease in leaf biomass allocation, so that leaf area ratio remained constant across the nutrient gradient (fig. 2H; table 1). Patterns of leaf biomass turnover (senesced leaf proportion) were also unaffected by nutrient treatment (table 1; fig. 2K).

Mean fruit weight did not change significantly in response to nutrient treatment (table 1; cf. fig. 2J). However, fruit nitrogen concentration decreased slightly at lower nutrient levels (fig. 4B; linear regression of nitrogen concentration on treatment significant at $P = 0.035$). Genotypes differed in mean fruit weight only within the high ($5x$ and $8x$) nutrient levels (table 2). Although Circle 5 fruits were significantly smaller than those of all but one other genotype at the $8x$ treatment (table 2), they contained a significantly higher tissue nitrogen concentration (*t*-test of 3 Circle 5 fruit samples versus 3 other randomly chosen $8x$ plants significant at $P \leq 0.044$). The highly significant genotype effect on mean fruit weight (table 1) largely reflects the relatively small fruits produced by this genotype at all treatments (contrast with all other genotypes significant at $P < 0.001$ according to Scheffé's test).

Pond Population.—As in the Circle plants, total biomass, fruit number and biomass, and leaf number and area, all decreased monotonically from the high nutrient treatment ($5x$) to the very low ($x/6$) treatment (fig. 5A–E). Values for these traits were equally high or nonsignificantly higher at the excessive $8x$ treatment as at $5x$ (fig. 5A–E). This pattern of response to the nutrient gradient was common to all Pond genotypes (table 1). Patterns of biomass allocation in response to nutrient treatment were also uniform among Pond genotypes (cf. nonsignificant genotype and genotype-by-nutrient interaction terms; table 3). As in the Circle population, Pond plants grown at moderately and extremely low nutrient levels produced proportionately more root biomass, but unlike Circle plants, they reduced stem rather than leaf allocation as well (fig. 6). As a result of these allocational changes, root-to-shoot ratio increased significantly with decreasing nutrient

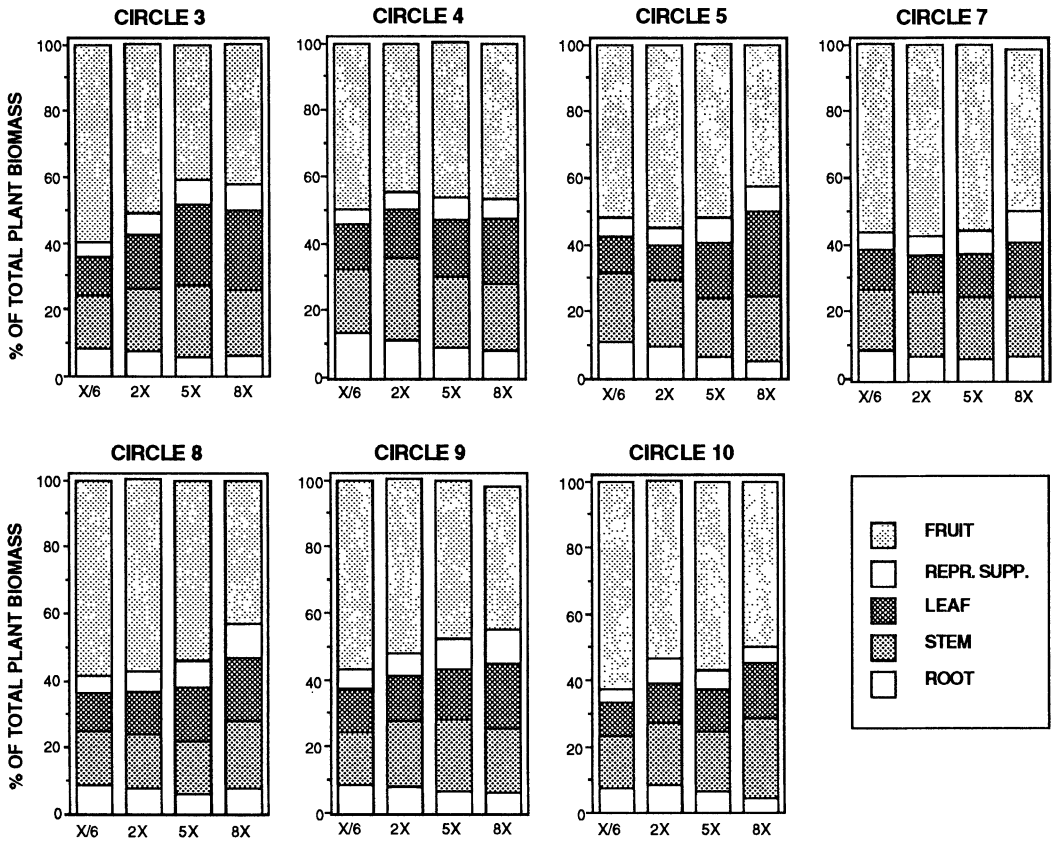

FIG. 3. Proportional biomass allocation for seven Circle genotypes at four nutrient levels. Root, stem, leaf, reproductive support, and fruit biomass presented as proportions of total plant biomass; means of four replicates.

supply in all genotypes (table 1), from nearly 1:4 at the ample $5x$ treatment to more than 1:3 at the extreme low treatment (adjacent treatment contrasts significant at $P \leq 0.01$; cf. fig. 5I). Allocation to fruit did not vary in response to nutrient treatment.

Leaves produced at low nutrient levels ($2x$ and $x/6$) were fewer in number, smaller, and (unlike Circle plants) slightly thicker than those produced at the ample $5x$ treatment (fig. 5E–G). However, as in the Circle plants, leaf nitrogen concentration remained constant across all three treatments (fig. 4A). Furthermore, the slight decrease in specific leaf area at low nutrient levels was offset by an increase in allocation to leaf tissue such that, as in the Circle plants, leaf area ratio remained constant across the entire range of nutrient treatments (table 1, fig. 5H). Senesced leaf proportion was also constant across the gradient (table 1; fig. 5K). Leaves produced at the $8x$ treatment did not differ in size or specific area from those at the $5x$ treatment, but their nitrogen concentration was nearly double that of leaves from any other treatment (fig. 4A).

Along with reduced fruit number, the mean weight of individual fruits decreased significantly in Pond plants at lower nutrient treatments relative to the $5x$ treatment (adjacent contrasts significant at $P \leq 0.001$; cf. fig. 5J), but did not differ in the $5x$ and $8x$ treatments (contrast $F = 0.2$, NS). The concentration of nitrogen in fruit tissue varied in an opposite pattern: concentration increased as nutrient treatment declined from excessive to moderately low, and then decreased at the very low nutrient treatment to a level equivalent to that at the $8x$ treatment (fig. 4B). Mean fruit weight also differed significantly among genotypes (table 1), reflecting the consistently smaller fruits produced by genotypes Pond 7 and Pond 19 (table 4; contrasts of each of these genotypes versus all others significant at $P \leq 0.001$ using Scheffé's test). Although nitrogen

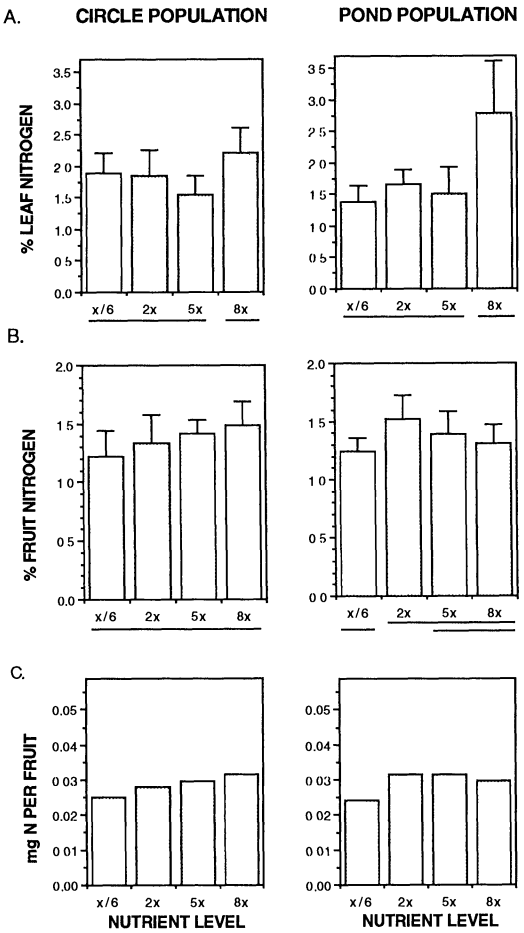

FIG. 4. Tissue nitrogen concentration of Circle and Pond population plants at four nutrient levels. A, Leaf nitrogen concentration: means ± standard deviations of 10 random plants per treatment per population; results shown of Student-Newman-Keuls tests at $P \leq 0.05$. B, Fruit nitrogen concentration: means ± standard deviations of five random plants per treatment per population; results shown of Student-Newman-Keuls tests at $P \leq 0.10$. C, Estimated fruit nitrogen content (mg N per individual fruit, calculated from treatment mean fruit weight × mean fruit nitrogen concentration).

concentration was measured in only a small subsample of genotypes and treatments, those cases examined do reveal negatively correlated genotypic differences in fruit nitrogen concentration. Specifically, the fruits produced by Pond 19 at the $5x$ treatment were significantly smaller than those of Pond 11 but higher (at borderline significance) in nitrogen concentration (t-test $P \leq 0.11$; $n = 3$).

Although Pond genotypes differed significantly in mean fruit weight, total fruit number, and mean leaf size (table 1), genetic diversity varied from treatment to treatment (table 4). For example, genotypic ranking for mean fruit weight was roughly parallel across the nutrient gradient, but genotypes diverged sufficiently to differ significantly only at two treatments (table 4). Genotypes were statistically indistinguishable in most growth and reproductive characters within three of the four nutrient levels, but at the moderate $2x$ treatment, two genotypes were markedly lower than others (fig. 5A–F). No genotype was the highest or lowest in rank across the entire gradient in any character (table 4).

DISCUSSION

Homeostatic Response to Low Nutrient Conditions

Plant responses to low nutrient availability reflect a complex interplay of growth limits because of reduced nutrient acquisition and compensatory plastic adjustments (Chapin 1980; Clarkson 1985). Inadequate nitrogen and phosphorus strongly limit plant growth by reducing both cell number and cell size; inadequate potassium inhibits cell expansion as well (Marschner 1986). Lower total biomass and reproductive output result from reduced photosynthetic area (because of fewer, smaller branches and leaves) and from constraints on assimilation rate arising from limits on nitrogen-based components of photosynthesis (Mooney and Chiariello 1984; Field and Mooney 1986; Chapin et al. 1987). In both *Polygonum* populations, total plant and fruit biomass decreased by about three-fourths in the very low nutrient treatment ($x/6$) compared with plants given ample nutrients ($5x$; figs. 2A, 5A). The overall biomass reduction largely reflects the production of fewer as well as smaller leaves (figs. 2; 5E,F) and less stem tissue.

Given the limits to growth imposed under low nutrient conditions, several functionally important characters were surprisingly constant across the nutrient gradient. Note that reductions in vegetative growth may in effect prevent tissue nutrient deficiency and thus permit normal plant function on a reduced scale (Gerloff 1976; Etherington 1982). First, plants grown at different nutrient levels maintained the same photosynthetic surface area relative to total biomass (leaf area ratio, table 1; figs. 2H, 5H), a critical determinant of plant growth (Potter and Jones 1977). More surprising, given the 96% decrease

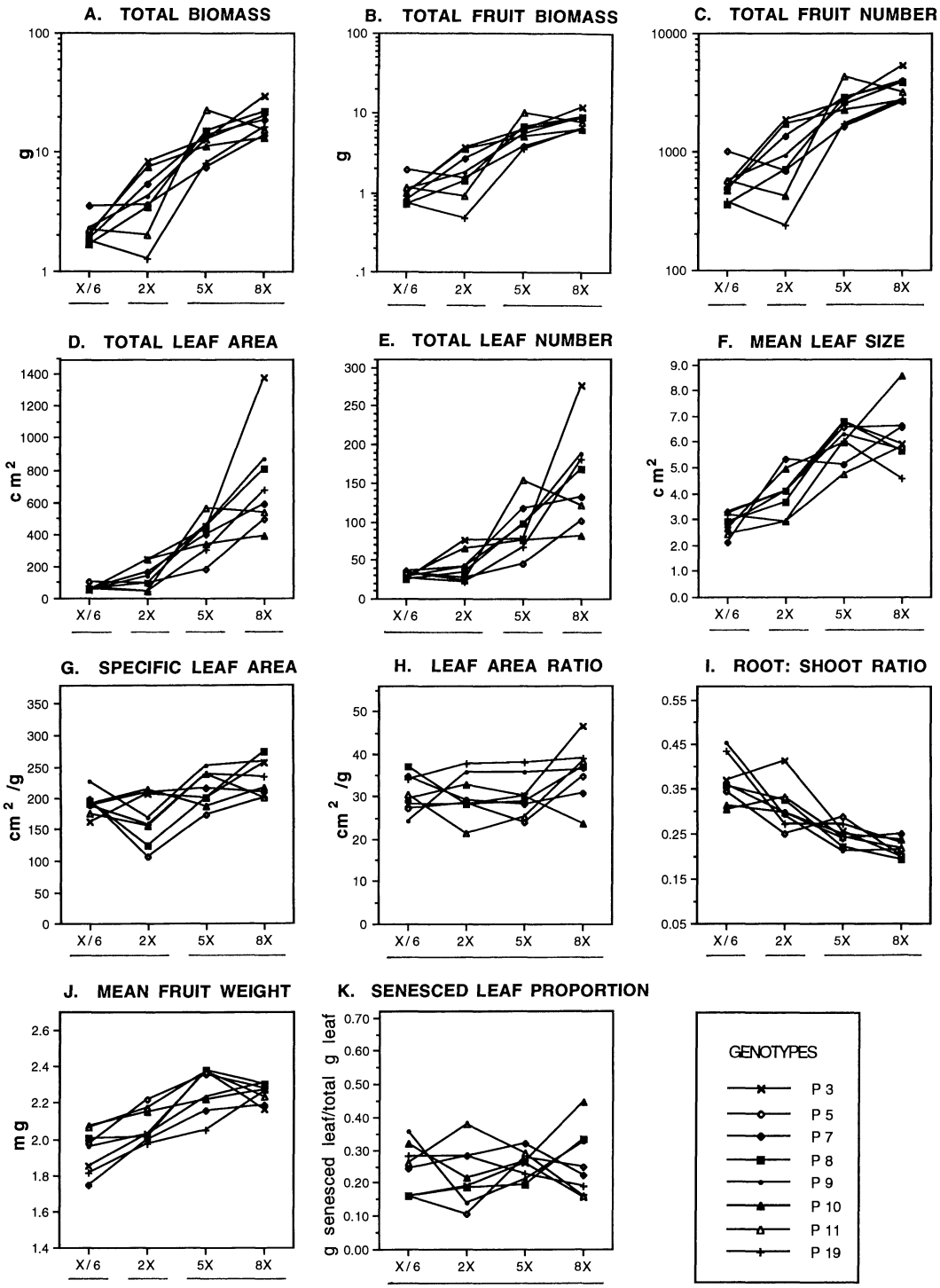

FIG. 5. Norm of reaction for eight Pond genotypes at four soil nutrient levels (means of four replicates). A, Total plant biomass; B, total fruit biomass; C, total fruit number; D, total plant leaf area; E, total leaf number; F, mean leaf size; G, specific leaf area; H, leaf area ratio; I, root-to-shoot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

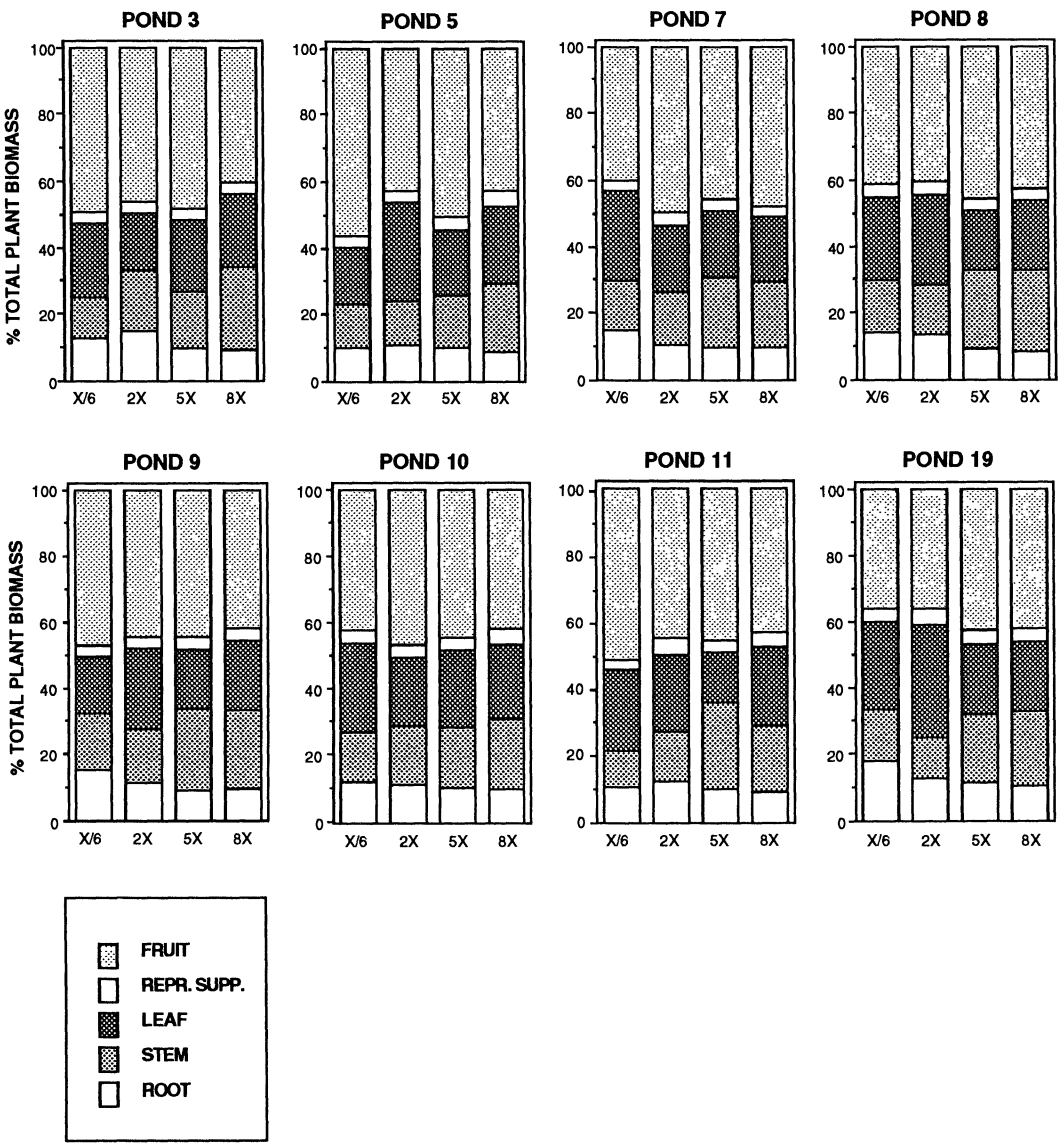

FIG. 6. Proportional biomass allocation for eight Pond genotypes at four nutrient levels. Root, stem, leaf, reproductive support, and fruit biomass presented as proportions of total plant biomass; means of four replicates.

in soil nitrogen content between the ample ($5x$) and very low ($x/6$) nutrient treatments, was the constancy of leaf nitrogen concentration across this range (fig. 4A). Because approximately three-fourths of leaf nitrogen goes into constituents of photosynthesis, photosynthetic capacity correlates strongly with leaf nitrogen concentration (Field and Mooney 1986; Field 1988; Evans 1989). Leaf nitrogen content and/or assimilation rate were likewise constant under low-nutrient conditions in *Triticum* (Evans 1983) and *Ambrosia* (Hunt and Bazzaz 1980). The maintenance of adequate leaf nitrogen concentration may be particularly important in annual species such as these, which have high metabolic rates (Chapin 1980; Mooney et al. 1981). In addition, annual species typically respond to nutrient deficiency by senescence of most leaves and translocation of the leaf carbohydrates and minerals to reproductive structures. The proportion of dead leaves thus generally increases under conditions in which available nutrients are depleted (Bazzaz

TABLE 4. Pond population: genotypic differences within nutrient treatments. Genotypes shown ranked by character value within each nutrient 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; boldface vertical line indicates that the genotype term is not significant ($P \geq 0.05$). Details in the *Methods* section.

TOTAL BIOMASS

X/6	2X	5X	8X
5	3	11	3
9	10	8	8
11	7	7	9
3	9	9	7
10	8	3	19
19	5	10	5
8	11	19	10
7	19	5	11
F 0.67	5.25	1.38	0.79
P .694	.001	.269	.606

TOTAL FRUIT BIOMASS

X/6	2X	5X	8X
5	3	11	3
9	10	8	7
11	7	7	8
3	9	9	9
10	5	3	19
8	8	10	5
7	11	5	11
19	19	19	10
1.07	5.86	1.32	0.62
.415	.001	.294	.734

TOTAL FRUIT NUMBER

X/6	2X	5X	8X
5	3	11	3
9	10	8	7
3	7	7	8
11	9	9	9
10	8	3	19
8	5	10	5
7	11	5	10
19	19	19	11
1.08	7.14	1.18	0.75
.407	.000	.357	.637

TOTAL LEAF AREA

X/6	2X	5X	8X
5	3	11	3
11	10	9	8
8	7	8	9
3	9	7	19
19	8	3	7
9	5	19	11
7	19	10	5
10	11	5	10
0.43	4.98	1.17	1.21
.871	.002	.360	.342

TOTAL LEAF NUMBER

X/6	2X	5X	8X
11	3	11	3
5	10	7	8
7	7	9	9
10	9	8	19
9	8	3	7
3	5	19	5
19	11	10	11
8	19	5	10
0.28	3.97	1.54	1.01
.957	.006	.211	.453

MEAN LEAF SIZE

X/6	2X	5X	8X
5	7	8	10
9	10	3	5
19	9	5	7
8	3	9	3
3	5	19	11
10	8	10	9
11	11	7	8
7	19	11	19
0.63	4.90	0.96	1.82
.726	.002	.483	.139

SPECIFIC LEAF AREA

X/6	2X	5X	8X
9	10	9	8
5	7	19	9
8	3	11	3
10	9	7	19
7	19	3	10
19	11	8	7
11	8	10	11
3	5	5	5
0.30	4.84	1.55	1.31
.946	.002	.209	.298

LEAF AREA RATIO

X/6	2X	5X	8X
8	19	19	3
7	9	9	19
19	10	10	11
11	7	3	8
10	5	8	9
3	3	7	5
5	8	11	7
9	11	5	10
1.22	1.69	3.07	1.11
.332	.164	.023	.397

ROOT: SHOOT RATIO

X/6	2X	5X	8X
9	3	5	7
19	11	19	10
3	8	3	19
7	10	10	11
8	7	11	9
5	9	7	5
10	19	8	3
11	5	9	8
0.99	2.34	1.26	0.55
.461	.060	.319	.785

MEAN FRUIT WEIGHT

X/6	2X	5X	8X
10	5	8	9
11	11	11	8
8	10	3	5
5	3	5	10
9	9	9	19
3	8	10	11
19	7	7	7
7	19	19	3
4.21	2.25	4.09	0.68
.004	.069	.006	.688

SENESCED LEAF PROPORTION

X/6	2X	5X	8X
9	11	7	10
10	19	11	8
19	7	5	9
11	10	10	5
7	3	3	7
8	8	19	19
3	9	9	11
5	5	8	3
1.22	1.74	0.64	1.00
.332	.150	.716	.462

and Harper 1977). Contrary to expectations, the proportion of total leaf biomass occurring in senesced leaves did not increase at low nutrient levels in the *Polygonum* plants (table 1; figs. 2K, 5K). This result suggests that the supply of nutrients obtained through changes in total growth, allocation, and morphology was adequate to maintain normal patterns of leaf turnover as well as leaf nitrogen concentration in these plants.

The major phenotypic adjustment made uni-

versally by *Polygonum* plants to low nutrient conditions was to increase substantially the ratio of root-to-shoot biomass in comparison with plants given ample nutrients (figs. 2I, 5I). Numerous studies of herbaceous species have reported similar increases in root-to-shoot ratio under low-nutrient conditions, because of both increased root allocation and decreased allocation to shoot tissues (e.g., Aung 1974; Hunt and Bazzaz 1980; Peace and Grubb 1982; Heywood and Levin 1986; Boutin and Morisset 1988; Stafford 1989). This developmental shift is thought to result from the inhibition of shoot growth due to accumulation of abscisic acid in nutrient-deficient tissues, such that roots become relatively stronger carbohydrate sinks (Clarkson 1985). In functional terms, this increase in relative root biomass reflects a greater absorptive surface per unit of weight of shoot tissue. This allows the root system to explore a relatively greater soil volume and thus increases the amount of nutrients available for uptake (Russell 1969), particularly slowly diffusing ions such as potassium and phosphorus (Hirose 1984; Clarkson 1985). Although a great deal of interest has focused on mineral uptake kinetics, in fact, nutrient acquisition in natural systems is determined largely by root-system extent and morphology (as well as exudate chemistry and soil characteristics affecting diffusion; Gerloff 1976; Nye and Tinker 1977; Chapin 1980; Clarkson 1985). Because of the physiological interdependence of shoot and root, increased energy allocation to roots in a nutrient-limited environment maintains a balance of light and nutrients favorable to plant growth (Aung 1974; Chapin et al. 1987).

Root systems of plants grown in low nutrient conditions typically exhibit several additional aspects of morphological and physiological plasticity that enhance nutrient acquisition; these may well be of importance in *P. persicaria* although they were not examined directly in this study. Roots that develop in poor soils may be smaller in diameter (Fitter and Hay 1981); such changes can markedly increase ion uptake rates by increasing the surface to volume ratio of roots (Gerloff 1976). Roots of nutrient-poor soils are also characterized by more frequent and longer root hairs, which effectively tap a greater volume of soil but require very little additional biomass (Robinson and Rorison 1983; Marschner 1986). In addition, the branching pattern of the root system as a whole varies in response to nutrient distribution: because lateral root growth is stimulated by high nutrient concentration, roots proliferate in nutrient rich soil zones (Epstein 1972; Chapin 1980; Fitter et al. 1988 and references). Such plasticity in root deployment has been shown to effectively compensate for both temporal and spatial variability in nutrient supply (Crick and Grime 1987; Jackson and Caldwell 1989).

Although total fruit biomass and number were much reduced at moderate and low compared with ample nutrient levels (table 1; figs. 2 B,C; 5B,C), proportional biomass allocation to fruit was either the same (Pond) or greater (Circle) (figs. 3, 6). This contrasts with the marked decrease in allocation to fruit that occurred in *Polygonum* plants grown under strongly limiting light conditions (Sultan and Bazzaz 1993a). Several other annual species maintain constant biomass allocation to propagules at low nutrient levels despite changes in other aspects of allocation (e.g., Harper and Ogden 1970; Hickman 1979; Parrish and Bazzaz 1982; Fenner 1986; Benner and Bazzaz 1988; Boutin and Morisset 1988).

Propagule quality depends on both weight and tissue nutrient concentration. Nitrogen content in particular is a key aspect of seed provisioning. Interestingly, the effects of low nutrient supply on these two aspects of fruit quality differed in the two populations examined. This result exemplifies the fact that genetically different entities possess different combinations of flexible and constrained responses in components of fitness (Marshall et al. 1986) that may result in similar outcomes (Sultan and Bazzaz 1993a). Circle plants produced fruits of the same mean weight at low nutrient levels, but with a slightly lower nitrogen concentration (figs. 2J, 4B). In the Pond population, fruits produced at reduced nutrient levels were smaller (fig. 5J) but had similar or slightly *higher* nitrogen concentrations (fig. 4B). In plants of both populations, the actual nitrogen content of fruits thus remained virtually identical at moderately low and ample nutrient conditions, and decreased by only about 20% at the extremely low nutrient treatment (fig. 4C). Such constancy in propagule quality despite differences in plant nutrient status results from increased allocation of mineral nutrients to reproduction at low nutrient conditions (Fenner 1986). Nitrogen in particular is preferentially allocated to developing seeds (Benner and Bazzaz 1988). Enhanced mineral allocation to fruits probably explains the production by severely nutrient-limited *Polygonum* plants of propagules that have

nitrogen content similar to that of plants raised at high nutrient levels.

The constancy of leaf area ratio, leaf nitrogen concentration, and fruit nitrogen content—which depends on alterations in biomass allocation, shoot and possibly root morphology, and nutrient distribution—may comprise aspects of functional homeostasis that act to maintain plant growth despite drastic reductions in nutrient supply. In this context, "homeostasis" is defined as an "adaptive constancy" in characters that contribute to fitness, made possible be means of variability in other characters (Lewontin 1957). Such homeostasis in functional characters may permit fitness to be maximized (although not held completely constant) under unfavorable environmental circumstances (Waddington 1957). Note that the approximately 75% decrease in reproductive output of plants grown in extremely low nutrient conditions compared with those given ample nutrients represents a considerable modulation of the 96% reduction in total available macronutrients these treatments impose.

Opportunistic Response to Excessive Nutrient Conditions

The 8x nutrient treatment represents a highly concentrated soil solution, containing 45 times as much nitrogen, phosphorus, and potassium as the lowest experimental treatment, and 1.6 times as much as the favorable 5x treatment (see the Methods). Plants grown at excessively high mineral concentrations often accumulate toxic quantities of nutrients and therefore experience reduced growth and vigor (Marschner 1986). *Polygonum* plants grown at the 8x treatment, however, had total biomass, leaf area, and reproductive output as high as those of plants grown at the favorable 5x treatment, and produced fruits of equal mean weight (figs. 2A–D, J; 5A–D, J) and similar nitrogen concentration (fig. 4B,C). The ability to use extremely high amounts of nutrients is typical not only of crop varieties that have been selected for precisely this response (Rorison 1969), but also of successful colonizing species (Christie and Moorby 1975; Bazzaz 1979; Benner and Bazzaz 1988). The very high leaf nitrogen concentrations of *Polygonum* plants grown at the 8x treatment (fig. 4A) apparently represent excess mineral reserves ("luxury consumption"). Concentrations of nitrogen as well as phosphorus, potassium, calcium, and magnesium increased with extremely high nutrient supply in six annual species studied by Parrish and Bazzaz (1982), suggesting that such "opportunism" in accumulating and storing excess nutrients may be common among early-successional annuals such as *P. persicaria.*

Ecological Breadth and the Evolution of Specialization for Nutrient Environment

All genotypes of both populations survived and reproduced successfully in nutrient conditions ranging from extremely deficient to excessively high. Each genotype produced an average of at least 350 viable fruits in the low-nutrient (x/6) treatment (figs. 2C, 5C; Sultan unpubl. data), and maintained equally high reproductive output at the excessive (8x) nutrient treatment as at the favorable (5x) treatment (figs. 2B, 5B). These individuals were thus universally able both to maintain adequate nutrition in extremely poor soil and to use large amounts of macronutrients when available.

This degree of within-genotype ecological breadth suggests that expectations regarding evolutionary specialization for soil types be reexamined. Because many edaphic factors differ at a relatively large spatial scale, and because nutrient availability strongly influences plant success, it is often assumed that selection necessarily produces ecotypes specially adapted to particular soil types (Bradshaw 1969; Snaydon 1970). Indeed, the most powerful examples of adaptive selection in plants are ecotypes of metalliferous and serpentine soils (Antonovics et al. 1971 and references) which, like mine-contaminated soils, are high in heavy-metal ions (Etherington 1982). Such ecotypes evolve in cases in which plants differ genetically in the ability to tolerate specific heavy-metal toxins, and in which such tolerance entails a fitness disadvantage in nontoxic soils (Antonovics 1971; Epstein 1972). Note that even in the case of heavy-metal tolerance, the existence of such costs depends on the system involved. In some species, genotypes universally possess inherent tolerance to metal ions so that population differentiation is precluded (e.g., Gibson and Risser 1982; Higgins and Mack 1987). Population differentiation also is known to occur in response to extremely acidic versus calcareous soils (Snaydon 1970), possibly because of the existence of a specific physiological trade-off between iron uptake and aluminum tolerance (Etherington 1982). In these cases, then, tolerance for a particular soil environment entails either a physiological or a fitness cost in other environments.

However, tolerance for high and low macronutrient levels may be quite different, in that the mechanisms on which such tolerance depends (i.e., flexibility in allocation, root morphology and deployment, nutrient uptake, and translocation) may not entail this sort of cost. This question has important implications: in the absence of costs, genomes that confer ecological breadth for nutrient conditions will be evolutionarily favored over specialists (Lewontin 1957; Moran 1992). As noted above, individuals inhabiting the Circle site each encounter a wide range of nutrient conditions, whereas Cliff Pond plants experience a consistently very low-nutrient environment (fig. 1). Despite these quite different patterns of variability, and the fact that these populations are genetically well differentiated (Sultan and Bazzaz 1993a), plants of both populations showed similarly broad ecological tolerance for both sub- and supraoptimal nutrient levels. Because the nature of the Pond site substrate precludes even occasional high nutrient levels, it seems very unlikely that the capacity for response to such conditions could be maintained selectively in the population if such a capacity carried any significant cost. These results thus indirectly suggest that phenotypic plasticity in response to nutrient level may not impose significant physiological or fitness costs.

Similarly, genotypes from the Circle population, which are not subject to soil flooding and only rarely encounter severe moisture deficits, revealed similar plasticity and tolerance to an extreme range of moisture conditions as did those from the highly heterogeneous Pond site (Sultan and Bazzaz 1993b). As in *P. persicaria,* genotypes from *Carex flacca* populations that do not experience soil flooding were able to root adventitiously when subjected to flood treatments just as well as those from flooded sites, and did not differ in total biomass at any moisture treatment from such genotypes (Heathcote et al. 1987). Thus, the developmental and physiological adjustments that enable plants to survive and reproduce in diverse soil moisture environments may not be associated with metabolic costs or fitness trade-offs. The absence of such costs would explain why broad-niched moisture "generalists" did not suffer in competition with narrower "specialists" in a comparison of fundamental niche breadth among six annual species (Pickett and Bazzaz 1978), as would be predicted on the basis of the conventional "Jack of all trades is Master of none" assumption that underlies mathematical models for the evolution of plasticity (Gomulkiewicz and Kirkpatrick 1992). Finally, the plastic responses of Pond population genotypes to light limitation were as pronounced as those of Circle genotypes, despite the absence of shade conditions at the Pond site (Sultan and Bazzaz 1993a). Indeed, the physiological and developmental plasticity relevant to light use bears no known physiological or structural cost (Gross 1984). Having evolved in variable environments, phenotypically plastic genotypes are maintained even in the absence of environmental variation, unless such plasticity entails metabolic costs or other deleterious effects on fitness (Schmalhausen 1949). These results suggest that phenotypic plasticity for major environmental factors cannot be presumed to impose such costs (see Sultan 1992 and references).

Plastic norms of reaction to nutrient conditions might evolve owing to a fitness advantage conferred by the ability to use the occasional pulses of nutrients that occur in seasonal and disturbed environments (Benner and Bazzaz 1988). This type of "opportunistic" response to soil nutrient supply has been observed in a number of annual species, in contrast to many perennial species that fail to use added mineral nutrients (Parrish and Bazzaz 1982; Benner and Bazzaz 1985). The mechanisms that permit Pond plants to exploit the occasional slight nutrient pulses that occur in their native habitat may also enable them to take advantage of much higher nutrient levels. Indeed, it is extremely unlikely that plants of either population evolved in a selective regime encompassing excessive nutrient levels such as those imposed in the $8x$ treatment. Their favorable growth responses to this extreme environment must reflect not a specifically adapted norm of reaction but rather a general capacity to respond appropriately to enhanced soil nutrient availability. Similarly, the ability to respond appropriately to deficient macronutrient supplies would be advantageous to all plants, since nutrient availability depends on soil moisture and therefore fluctuates to some extent in nearly all habitats.

The evolution of specialists for macronutrient supply requires that genotypes differ in fitness within low and high nutrient levels and that different genotypes have higher fitness in each environment. Overall, genotypes of each *Polygonum* population responded very similarly to the experimental nutrient gradient. There was no significant genotype-by-nutrient interaction for any

aspect of proportional biomass allocation (table 3), nor in 20 of 22 other cases (11 characters in two populations; table 1). Moreover, in neither population did genotypes differ in any phenotypic trait when grown under severe nutrient limitation ($x/6$ treatment). If all genotypes converge on a low-nutrient phenotype with a certain reproductive fitness, particular genotypes will not be distinguished by selection as the basis of a low-nutrient ecotype. The greater similarity of plants in extremely low-nutrient conditions supports the notion that convergence in function-related characters may be a particularly important aspect of phenotypic plasticity in response to strong environmental stress (Sultan and Bazzaz 1993a).

Little is known about genetic diversity for plant nutrient uptake and use in natural systems. In general, the evidence for genetic diversity in nutrient response is thought to have been overstated (Gerloff 1976; Marschner 1986). Indeed, a recent study of barley showed strains selected under high-nitrogen conditions and wild genotypes native to nutrient-poor soils to be equally effective in absorbing nitrogen from solutions of widely varying nitrogen concentration (Bloom 1985). The two *Polygonum* populations studied do not reveal patterns of genetic variation that might lead to selective divergence for high versus low nutrient environments. Rather, they consist of genotypes that universally exhibit plasticity in response to nutrient level. The evolution of such plasticity reflects the high variable nutrient environment plants experience, because of fluctuations not only in soil minerals but in complex interacting factors.

General Conclusions: Phenotypic Plasticity in *Polygonum persicaria*

Individual response plasticity has long been recognized as a ubiquitous aspect of adaptation to the "inescapably heterogeneous" nature of real environments (Waddington 1968). Yet this issue has received remarkably little direct attention from students of evolutionary processes (Sultan 1992). Only very recently has within-genotype phenotypic flexibility been widely recognized as a valid "alternative picture" to the conventional neo-Darwinian view of genetically based adaptation to determinate selection pressures (Bradshaw and Hardwick 1989). No new discovery or technical breakthrough has precipitated this change in perspective; rather it reflects a shift in focus from simple to complex interactions between organisms and their environments.

The study presented in this series of papers reveals a remarkable range of adaptive phenotypic plasticity in naturally occurring genotypes of the widespread annual species *Polygonum persicaria* in response to major environmental factors. In general, *Polygonum* individuals adjusted appropriately to poor light, moisture, and nutrient conditions by allocating biomass preferentially to those organs that acquire the most strongly limiting resource (Chapin et al. 1987), and by specific morphological and structural alterations understood in ecophysiological terms to be advantageous under given conditions. Such responses evidently promote functional stability despite the growth limits imposed by low resource availability and potentially phytotoxic excesses ("homeostasis" sensu Waddington 1957 quoted in Lewontin 1957). By effectively modulating unfavorable conditions, phenotypic responses to environment may maximize fitness under diverse environmental circumstances (Lewontin 1957; Bradshaw 1965).

The results further demonstrate the specificity of phenotypic responses to environment. Characters are not "plastic" or "fixed" in general; a particular character may vary markedly from one environmental state to another but remain constant elsewhere on the same or another resource gradient. Moreover, the specific response in a given trait depends on both the environmental factor involved and its precise level. For example, the weight of individual propagules decreased in low light, increased in dry soil, and remained constant across a range of nutrient conditions. Nor do these differences in achene mass reflect like changes; rather they reflect changes in pericarp thickness in certain cases and in seed mass in others (Sultan unpubl. MS). The plastic responses of *Polygonum* genotypes thus conform to the descriptions by Schmalhausen (1949) and Bradshaw (1965) of broad genotypic repertoires from which particular phenotypes are elicited in precise response to environmental circumstances. Although this specificity has been invoked to suggest that every aspect of plastic response has been shaped by natural selection (e.g., Bradshaw and Hardwick 1989), it can be seen rather to demonstrate the codependence of phenotypic expression on a historically shaped genotype and its environmental circumstances. (The precise mechanism by which selection acts on plasticity is the subject of ongoing debate; Scheiner and

Lyman 1991; Via 1993; Schlichting and Pigliucci 1993.)

The remarkable breadth of phenotypic expression inherent in *Polygonum* genotypes is associated with their ability to survive and reproduce amply at an extraordinary range of controlled environmental conditions. It should be noted that this full range of within-genotype tolerance for extremes of light availability, soil moisture, and nutrient supply would be unlikely to hold in nature. Because these experiments were performed using established vegetative cuttings, they do not reveal the possible effects of environmental extremes on germination and seedling survival. Furthermore, individuals under natural conditions experience compound rather than single environmental stresses (Bazzaz and Morse 1991). Tolerance for extremes of a particular factor may narrow in the presence of other biotic and abiotic stresses (Bazzaz 1987). Nonetheless, the results of these experiments demonstrate an extraordinary breadth of ecological tolerance within single genotypes. These *Polygonum* individuals thus exemplify the "general purpose genotypes" described by Baker (1965) as the basis of ecological amplitude in many colonizing species.

It cannot be argued from these results that the great plasticity and ecological tolerance inherent to these genotypes is characteristic of all plants. *Polygonum persicaria* is no more or less "typical" of natural taxa than any other single species. In particular, annual species such as *P. persicaria* may be expected to have evolved plasticity to maximize reproduction at different resource levels, whereas perennials have a more complex set of alternative responses to transient environmental stresses. However, these data do lead to an important general conclusion. Since the response capacity of single genotypes can successfully accommodate widely divergent light, moisture, and nutrient levels, the kinds of adjustment these factors demand evidently need not require specialized genetically based mechanisms. Furthermore, different environments elicit from these genotypes the kind of morphological diversity generally thought to characterize differently adapted species, as for example the production of a superficial adventitious root system in response to soil flooding. The existence of such phenotypic breadth within individual genotypes requires that individual plasticity be recognized as a major aspect of plant diversity. Although plant biologists have sought to identify particular adaptive features of species in relation to their habitats in order to infer species evolution by natural selection, it may be that many aspects of functional adaptation to environment occur within individuals, and that to the extent that species differences reflect selection they pertain to canalized aspects of morphology such as floral characters. (See Conner and Via [1993] for a comparison of relative plasticity in floral and growth characters.) Adaptive divergence of populations and ultimately species thus may generally pertain to environmental pressures that are not only more constant, but are accommodated by genetically determined rather than facultative phenotypic states (Sultan 1987).

A surprising outcome of this study was that genotypes from relatively constant and enormously variable light, moisture, and nutrient environments exhibited similar repertoires of plastic and homeostatic responses, and were equally tolerant of diverse resource levels, including extreme conditions beyond the recent selective experience of the population. This result is particularly striking because the two populations are clearly genetically differentiated. How does it happen that both populations consist of these broadly tolerant genotypes, and what can be inferred from their persistence? The ability to maintain growth and reproduction under heavy shade or in flooded soil may have been strongly favored during rare, stringent selective events in the species' history, or in the history of the separate populations. Similarly, the capacity to tolerate and exploit excessive nutrient concentrations may have been selectively favored in rare situations when plants germinated in contact with feral animal droppings or manure heaps. Although norms of reaction are often expected to closely mirror a population's present range of environmental circumstances (Bradshaw and Hardwick 1989), like other products of evolution they may be largely shaped by exceptional selective events (Travis and Mueller 1989). The maintenance of these broad norms of reaction in the absence of ongoing selective pressure suggests that the maintenance of these facultative response systems may not bear significant physiological or fitness costs. Indeed there is at present no empirical evidence of such a cost (Sultan 1992).

Moreover, those response systems that confer selective advantages under rare, extreme conditions may also permit adaptive adjustment to small-scale variability of the type that is frequently encountered, and vice versa. This raises

an important point regarding environmental heterogeneity: when attempts are made to sample environmental variability rather than means (Levins and Lewontin 1985), and when interacting abiotic and biotic aspects of the environment are taken into account (Bazzaz 1987), it becomes clear that no organism encounters a homogeneous environment. Although habitats may differ in the range of variation that occurs, plants in all habitats will encounter a certain amount of variability in all three of the environmental factors here addressed. Thus, facultative adjustment rather than genetic specialization should be the expected evolutionary response (in the absence of specific genetic or developmental limits).

In addition to characterizing phenotypic plasticity in naturally occurring plant genotypes, these norms-of-reaction data form a case study of the nature of diversity among such genotypes. They make clear the dependence of genetic variance among a given set of genotypes upon both the particular characters and the precise range of environments studied (Gupta and Lewontin 1982). A striking result was the extreme rarity of parallel (consistently higher or lower) norms of reaction: of 68 arrays of 7 to 10 genotypic norms (11–12 growth and reproductive characters examined in each of two populations across three environmental gradients), in only a single case was any genotype significantly different than any other across an entire gradient, and this case involved a morphological rather than a reproductive trait. Although larger sample sizes might well resolve such differences statistically in some cases, it seems patently unlikely that natural selection would discern differences that do not appear among sets of clonal replicates grown under highly controlled conditions. Moreover, on the basis of rank order alone (apart from statistical significance), no genotype was the highest or lowest in reproductive output at every point on any of the three environmental gradients in either population. As a result, in no case was there a significant genotype effect on reproductive output in the absence of a significant genotype-by-environment interaction. Parallel norms of reaction were termed by Haldane (1946) a "eugenic" model: in such a case certain genotypes can be distinguished as consistently superior and inferior, regardless of environmental circumstances. Clearly, genetic diversity of this type would provide ready material for directional change by natural selection in variable as well as constant environments. The absence of genotypes with higher relative fitness in all environments may contribute significantly to the maintainence of genetic variation in natural populations (Gillespie and Turelli 1989). Although parallel norms may be common among artificially selected, inbred laboratory animals (Gupta and Lewontin 1982) and plant varieties (Bradshaw and Hardwick 1989), they may be quite rare among naturally occurring genotypes (Haldane 1946).

For most characters in which genotypes within populations differed significantly, *Polygonum* norms of reaction were not parallel, but either became more similar or reversed relative order from one environmental state to another. In such cases, whether or not average differences exist among genotypes, the ability of selection to discern genotypic differences depends on the distribution of environments. If environmental conditions vary at a fine scale, as in the *Polygonum* habitats, fitness differentials that occur within particular environmental states will be obscured. Both variation in the magnitude of genotypic differences and crossover interaction hinder selective elimination in heterogeneous environments, and thereby maintain genetic diversity (Mitchell-Olds and Rutledge 1986; Via 1987; Turelli 1988). A third, convergent, pattern of genotypic diversity characterized *Polygonum* norms of reaction for characters relating directly to function under particular limiting resources. The ability of diverse genotypes to share similar appropriate responses to environmental demands is a major way in which phenotypic plasticity acts to minimize fitness differentials within as well as across environmental states (Sultan 1987; Levin 1988). Indeed, genotypic differences in reproductive output within environments were very often not significant, since in general genotypic variance was quite low. It is interesting to note that the greatest differences among *Polygonum* genotypes in reproductive fitness (though not in morphology) occurred not at extreme, limiting conditions but at moderate or favorable treatments. Genotypes may thus differ in their ability to exploit plentiful resources more than in their ability to tolerate limiting conditions.

The picture that emerges from these data is a complex one. *Polygonum* genotypes are not consistently "superior" and "inferior": genotypic differences in characters relating to fitness varied in magnitude and often in sign depending on environmental circumstances. Furthermore, re-

productive fitness differences among genotypes within particular environmental states were minimized by plastic convergence and by compensatory interactions among underlying growth characters. Such character interaction may permit morphologically diverse genotypes to converge on equivalent reproductive fitnesses (see also Antonovics et al. 1988). In contrast to these subtle and shifting differences among genotypes, environmental effects on growth and reproduction were profound. These results support Haldane's argument (1946) that it is very rare for a genotype to be "better" in all environments, but there are environments which are relatively unfavorable to all genotypes. Environmentally elicited fitness differences were generally far greater in magnitude than those between genotypes, a situation considered by Dobzhansky (1941) to be generally true for natural systems (see also Barton and Turelli 1989; Stratton 1992). These constitute an overwhelming genotype-random influence on relative fitnesses which varies in direction as well as intensity (Travis and Mueller 1989), and which is further complicated by the fact that such influences on plants are not additive but interactive (Bazzaz 1987). In this shifting mosaic of favorable and unfavorable influences on genotypes that vary in relative fitness, selective differentials among individuals are necessarily both obscure and transitory.

Acknowledgments

This manuscript was improved by the comments of R. Chazdon and one anonymous reviewer. We also acknowledge with thanks R. C. Lewontin for valuable discussion of these ideas, and R. C. Crabtree, M. Jasienski, A. H. Knoll, and R. M. Tryon for comments on an earlier version of the manuscript. We also thank E. G. Reekie, D. C. Tremmel, and J. S. Coleman for practical advice, and C. A. Lindell for able technical 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.

Literature Cited

Antonovics, J. 1971. The effects of a heterogeneous environment on the genetics of natural populations. American Scientist 59:592–599.

Antonovics, J., A. D. Bradshaw, and R. G. Turner. 1971. Heavy metal tolerance in plants. Advances in Ecological Research 7:1–85.

Antonovics, J., N. C. Ellstrand, and R. N. Brandon. 1988. Genetic variation and environmental variation: expectations and experiments. Pp. 275–303 *in* L. D. Gottlieb and S. K. Jain, eds. Plant evolutionary biology. Chapman and Hall, London.

Aung, L. H. 1974. Root-shoot relationships. Pp. 29–62 *in* E. W. Carson, ed. The plant root and its environment. University Press of Virginia, Charlottesville.

Baker, H. G. 1965. Characteristics and modes of origin of weeds. Pp. 147–172 *in* H. G. Baker and G. L. Stebbins, eds. The genetics of colonizing species. Academic Press, New York.

Barton, N. H., and M. Turelli. 1989. Evolutionary quantitative genetics: How little do we know? Annual Review of Genetics 23:337–370.

Bazzaz, F. A. 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics 10:351–371.

———. 1987. Experimental studies on the evolution of niche in successional plant populations. Pp. 245–271 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, eds. Colonization, succession, and stability. Blackwell Scientific, London.

Bazzaz, F. A., and J. L. Harper. 1977. Demographic analysis of the growth of *Linum usitatissimum*. New Phytologist 78:193–208.

Bazzaz, F. A., and S. R. Morse. 1991. The response of annual plants to multiple stresses. Pp. 283–299 *in* W. Winner, E. Pell, and H. A. Mooney, eds. The response of plants to multiple stresses. Academic Press, New York.

Benner, B. L., and F. A. Bazzaz. 1985. Response of the annual *Abutilon theophrasti* Medic. (Malvaceae) to timing of nutrient availability. American Journal of Botany 72:320–323.

———. 1988. Carbon and mineral element accumulation and allocation in two annual plant species in response to timing of nutrient addition. Journal of Ecology 76:19–40.

Bloom, A. J. 1985. Wild and cultivated barleys show similar affinities for mineral nitrogen. Oecologia 65: 555–557.

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

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

———. 1969. An ecologist's viewpoint. British Ecological Society Symposium 9:415–427.

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

Chapin, F. S., III. 1980. The mineral nutrition of wild plants. Annual Review of Ecological Systematics 11:233–260.

———. 1989. The cost of tundra plant structures: evaluation of concepts and currencies. American Naturalist 133:1–19.

Chapin, F. S., III, and K. van Cleve. 1989. Approaches to studying nutrient uptake, use, and loss in plants. Pp. 185–207 *in* R. W. Pearcy, Jr., J. R. Ehleringer, H. A. Mooney, and P. W. Rundel, eds.

Plant physiological ecology. Chapman and Hall, London.

Chapin, F. S., III, A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant responses to multiple environmental factors. Bioscience 37:49–57.

Christie, E. K., and J. Moorby. 1975. Physiological responses of semiarid grasses. I. The influence of phosphorous supply on growth and phosphorous absorption. Australian Journal of Agricultural Research 26:423–436.

Clarkson, D. T. 1985. Factors affecting mineral nutrient acquisition by plants. Annual Review of Plant Physiology (Bethesda) 36:77–115.

Conner, J., and S. Via. 1993. Patterns of phenotypic and genetic correlation among morphological and life-history traits in wild radish, *Raphanus raphanistrum*. Evolution 42:704–711.

Crick, J. C., and J. P. Grime. 1987. Morphological plasticity and mineral nutrient capture in 2 herbaceous species of contrasted ecology. New Phytologist 107:403–414.

Crossley, G. K., and A D. Bradshaw. 1968. Differences in response to mineral nutrients of populations of ryegrass, *Lolium perenne* L., and orchardgrass, *Dactylis glomerata* L. Crop Science 8:383–387.

Davidson, R. L. 1969. Effects of soil nutrients and moisture on root : shoot ratios in *Lolium perenne* L. and *Trifolium repens* L. Annals of Botany (NS) 33:571–577.

Dobzhansky, Th. 1941. Genetics and the origin of species, 2d ed. Columbia University Press, New York.

Epstein, E. 1972. Mineral nutrition of plants: principles and perspectives. Wiley, New York.

Etherington, J. R. 1982. Environment and plant ecology, 2d ed. Wiley, New York.

Evans, J. R. 1983. Nitrogen and photosynthesis in the flag leaf of Wheat (*Triticum aestivum* L.). Plant Physiology (Bethesda) 72:297–302.

———. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78:9–19.

Fellows, G. W. 1981. Intepretation of soil test results. University of Massachusetts Soil and Plant Tissue Laboratory, Waltham, Mass.

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

Field, C. B. 1988. On the role of photosynthetic responses in constraining the habitat distribution of rainforest plants. Australian Journal of Plant Physiology 15:343–358.

Field, C. B., and H. A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. Pp. 25–55 *in* T. J. Givnish, ed. On the economy of plant form and function. Cambridge University Press, Cambridge.

Fitter, A. H., and R.K.M. Hay. 1981. Environmental physiology of plants. Academic Press, London.

Fitter, A. H., R. Nichols, and M. L. Harvey. 1988. Root system architecture in relation to life history and nutrient supply. Functional Ecology 2:345–351.

Gerloff, G. C. 1976. Plant efficiencies in the use of nitrogen, phosphorous, and potassium. Pp. 161–173 *in* M. J. Wright, ed. Plant adaptation to mineral stress in problem soils. Special Publication, Cornell University Agriculture Expt. Station, Ithaca, N.Y.

Gibson, D. J., and P. G. Risser. 1982. Evidence for the absence of ecotypic development in *Andropogon virginicus* (L.) on metalliferous mine wastes. New Phytologist 92:589–599.

Gillespie, J. H., and M. Turelli. 1989. Genotype-environment interactions and the maintenance of polygenic variation. Genetics 121:129–138.

Gomulkiewicz, R., and M. Kirkpatrick. 1992. Quantitative genetics and the evolution of reaction norms. Evolution 46:390–411.

Gross, L. J. 1984. On the phenotypic plasticity of leaf photosynthetic capacity. Pp. 2–14 *in* S. Levin and T. Hallam, eds. Mathematical ecology: proceedings, Trieste 1982. Springer, Berlin.

Gupta, A. P., and R. C. Lewontin. 1982. A study of reaction norms in natural populations of *Drosophila pseudoobscura*. Evolution 36:934–948.

Haldane, J.B.S. 1946. The interaction of nature and nurture. Annals of Eugenics 13:197–205.

Harper, J. L., and J. Ogden. 1970. The reproductive strategy of higher plants. 1. The concept of strategy with special reference to *Senecio vulgaris* L. Journal of Ecology 58:681–698.

Heathcote, C. A., M. S. Davies, and J. R. Etherington. 1987. Phenotypic flexibility of *Carex flacca* Shreb.: tolerance of soil flooding by populations from contrasting habitats. New Phytologist 105:381–391.

Heywood, J. S., and D. A. Levin. 1986. Interactions between seed source, planting arrangement, and soil treatment in determining plant size and root allocation in *Phlox drummondii*. Oecologia 68:285–290.

Hickman, J. C. 1979. The basic biology of plant numbers. Pp. 232–263 *in* O. Solbrig et al., eds. Topics in plant population biology. Columbia Press, New York.

Higgins, S. S., and R. N. Mack. 1987. Comparative responses of *Achillea millefolium* ecotypes to competition and soil type. Oecologia 73:591–597.

Hirose, T. 1984. Nitrogen use efficiency in growth of *Polygonum cuspidatum* Sieb. et Zucc. Annals of Botany 54:695–704.

Hunt, R., and F. A. Bazzaz. 1980. The biology of *Ambrosia trifida* L. V. Response to fertilizer, with growth analysis at the organismal and sub-organismal levels. New Phytologist 84:113–121.

Jackson, R. B., and M. M. Caldwell. 1989. The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. Oecologia 81:149–153.

Levin, D. A. 1988. Plasticity, canalization and evolutionary stasis in plants. Pp. 35–45 *in* A. J. Davy, M. J. Hutchings, and A. R. Watkinson, eds. Plant population ecology. Blackwell Scientific, Oxford.

Levins, R. 1968. Evolution in a changing environment. Princeton University Press, Princeton, N.J.

Levins, R., and R. C. Lewontin. 1985. The dialectical biologist. Harvard University Press, Cambridge, Mass.

Lewontin, R. C. 1957. The adaptation of populations to varying environments. Cold Spring Harbor Symposia on Quantitative Biology 22:395–408.

Marschner, H. 1986. Mineral nutrition of higher plants. Academic Press, London.

Marshall, D. L., D. A. Levin, and N. L. Fowler. 1986. Plasticity of yield components in response to stress in *Sesbania macrocarpa* and *S. vesicaria* (Leguminosae). American Naturalist 127:508–521.

Mitchell-Olds, T., and J. J. Rutledge. 1986. Quantitative gentics in natural plant populations: a review of the theory. American Naturalist 127:379–402.

Mooney, H. A., and N. R. Chiariello. 1984. The study of plant function: the plant as a balanced system. Pp. 305–323 *in* R. Dirzo and J. Sarukhán, eds. Perspectives on plant population ecology. Sinauer, Sunderland, Mass.

Mooney, H. A., C. Field, S. L. Gulmon, and F. A. Bazzaz. 1981. Photosynthetic capacity in relation to leaf position in desert versus old-field annuals. Oecologia 50:109–112.

Moran, N. 1992. The evolutionary maintenance of alternative phenotypes. American Naturalist 139: 971–989.

Nye, P. H., and P. B. Tinker. 1977. Solute movement in the soil: roots system. Blackwell Scientific, Oxford.

Parrish, J.A.D., and F. A. Bazzaz. 1982. Responses of plants from three successional communities to a nutrient gradient. Journal of Ecology 233–248.

Peace, W.J.H., and P. J. Grubb. 1982. Interaction of light and mineral nutrient supply in the growth of *Impatiens parviflora.* New Phytologist 90:127–150.

Pickett, S.T.A., and F. A. Bazzaz. 1978. Divergence of two co-occurring successional annuals on a soil moisture gradient. Ecology 57:169–176.

Potter, J. R., and J. W. Jones. 1977. Leaf area partitioning as an important factor in growth. Plant Physiology 59:10–14.

Robinson, D., and I. H. Rorison. 1983. Relationships between root morphology and nitrogen availability in a recent theoretical model describing nitrogen uptake from soil. Plant, Cell and Environment 6:641–647.

Rorison, I. H. 1969. Ecological inferences from laboratory experiments on mineral nutrition. British Ecological Society Symposium 9:155–177.

Russell, E. W. 1969. A soil scientist's viewpoint. British Ecological Society Symposium 9:429–436.

Scheiner, S. M., and R. F. Lyman. 1991. The genetics of plasticity. II. Response to selection. Journal of Evolutionary Biology 4:23–50.

Schlichting, C. D., and M. Pigliucci. 1993. Control of phenotypic plasticity via regulatory genes. American Naturalist 142:367–371.

Schmalhausen, I. I. 1949. Factors of evolution. Blakiston Press, New York.

Snaydon, R. W. 1970. Rapid population differentiation in a mosaic environment. I. The response of *Anthoxanthum odoratum* populations to soils. Evolution 254:257–269.

Stafford, R. A. 1989. Allocation responses of *Abutilon theophrasti* to carbon and nutrient stress. American Midland Naturalist 121:225–231.

Stratton, D. A. 1992. Life-cycle components of selection in *Erigeron annuus.* II. Genetic variation. Evolution 46:107–120.

Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. Evolutionary Biology 21:127–176.

———. 1990. Evolutionary implications of phenotypic plasticity: genetic diversity for norms of reaction to resource gradients in *Polygonum persicaria* L. Ph.D. dissertation. Harvard University, Cambridge, Mass.

———. 1992. Phenotypic plasticity and the Neo-Darwinian legacy. Evolutionary Trends in Plants 6:61–71.

Sultan, S. E., and F. A. Bazzaz. 1993a. Phenotypic plasticity in *Polygonum persicaria.* I. Diversity and uniformity in genotypic norms of reaction to light. Evolution 47:1009–1031.

———. 1993b. Phenotypic plasticity in *Polygonum persicaria.* II. Norma of reaction to soil moisture and the maintenance of genetic diversity. Evolution 47:1032–1049.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.

Travis, J., and L. D. Mueller. 1989. Blending ecology and genetics: progress toward a unified population biology. Pp. 101–124 *in* J. Roughgarden, R. M. May, and S. A. Levin, eds. Perspectives in ecological theory. Princeton University Press, Princeton, N.J.

Turelli, M. 1988. Phenotypic evolution, constant covariances, and the maintenance of additive variance. Evolution 42:1342–1347.

Via, S. 1987. Genetic constraints on the evolution of phenotypic plasticity. Pp. 47–71 *in* V. Loeschke, ed. Genetic constraints on adaptive evolution. Springer, Berlin.

———. 1993. Adaptive phenotypic plasticity: target or by-product of selection in a variable environment? American Naturalist 142:352–365.

Waddington, C. H. 1968. The paradigm for the evolutionary process. Pp. 37–45 *in* R. C. Lewontin, ed. Population biology and evolution. Syracuse University Press, Syracuse, N.Y.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16:97–159.

Corresponding Editor: T. Meagher