Phenotypic Plasticity in Polygonum persicaria. I. Diversity and Uniformity in Genotypic Norms of Reaction to Light
Author(s): S. E. Sultan and F. A. Bazzaz
Source: *Evolution*, Vol. 47, No. 4 (Aug., 1993), pp. 1009-1031
Published by: Society for the Study of Evolution
Stable URL: http://www.jstor.org/stable/2409972
Accessed: 19-04-2016 18:16 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
http://about.jstor.org/terms

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Wiley, Society for the Study of Evolution are collaborating with JSTOR to digitize, preserve and extend access to *Evolution*

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

Evolution, 47(4), 1993, pp. 1009–1031

PHENOTYPIC PLASTICITY IN *POLYGONUM PERSICARIA*. I. DIVERSITY AND UNIFORMITY IN GENOTYPIC NORMS OF REACTION TO LIGHT

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

Abstract.—Several aspects of genotype-environment interaction may act to modulate natural selection in populations that encounter variable environments. In this study the norms of reaction (phenotypic responses) of 20 cloned genotypes from two natural populations of the annual plant *Polygonum persicaria* were determined over a broad range of controlled light environments (8%–100% full sun). These data reveal both the extent of functionally adaptive phenotypic plasticity expressed by individual genotypes, and the patterns of diversity among genotypes for characters relevant to fitness, in response to an environmental factor that is both highly variable within populations and critical to growth and reproduction.

Each *Polygonum* genotype expressed a set of physiologically, allocationally, and morphologically diverse phenotypes in response to contrasting light conditions. These phenotypic adjustments were consistent with ecophysiological expectations for maximizing light interception under low light intensities, and resulted in the maintenance of relative photosynthetic efficiency as well as successful reproduction even under severe light limitation. Within light levels, the different genotypes exhibited uniform responses in several characters related to light capture. Genotypes differed significantly in other traits, but the differences were offset by negatively correlated differences in functionally related characters. As a result of the functional similarity of genotypes conferred by both phenotypic plasticity and interaction among characters, morphologically diverse genotypes within each population shared equivalent reproductive fitnesses across the full range of light environments. Enormous fitness differentials did result from light treatment itself, however. Such environmentally evoked fitness differences would act to promote the maintenance of genetic diversity within *Polygonum* populations.

Key words.—Annuals, character correlations, fitness, light response, norms of reaction, phenotypic plasticity, photosynthesis, *Polygonum persicaria*.

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

Phenotypic plasticity has long been considered a major means of individual adaptation to environmental heterogeneity (Johannsen 1911; Schmalhausen 1949; Lewontin 1957; Levins 1963, 1968; Jain 1979; Grime et al. 1986; Schlichting 1986; Bradshaw and Hardwick 1989). Its evolutionary significance arises from the ways in which plasticity may modulate the effects of natural selection (Wright 1931; Sultan 1987). First, plasticity may obviate genetic differentiation under local environmental pressures by conferring adaptive (functionally appropriate) phenotypic diversity on individual genotypes. In addition, by permitting diverse genotypes to converge on adaptive phenotypic responses, plasticity may allow the maintenance of genetic diversity in the face of uniform selection pressures. Adaptive phenotypic plasticity is thus a specific type of genotype-by-environment interaction that reduces precise matching of genotypes to environments.

Furthermore, even when genotypes differ in their phenotypic responses to environment, these differences may be shielded from selection. The set of phenotypes produced by a genotype in response to diverse environments is termed its "norm of reaction" (Schmalhausen 1949). The availability of genetic variation to selection will depend on both the patterns of diversity among genotypic norms of reaction and the distribution of environmental variation. In his classic paper on "nature and nurture," Haldane (1946) assessed patterns of genotype-environment interaction and their generality in natural systems. He pointed out that the "eugenicist's" model, in which genotypes are consistently superior and inferior in all environments, was a very small subset of possible distribution patterns. This pattern of diversity, in which norms of reaction for fitness-related traits are roughly parallel across a range of environments, would obviously reveal

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

©1993 The Society for the Study of Evolution. All rights reserved.
This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

clear-cut phenotypic differences among genotypes on which selection might act. However, if norms of reaction cross between environmental states that vary in nature, or if they differ only within certain environmental states and converge in others, selection for particular genotypes will be either partly or completely blocked (Via and Lande 1985; Via 1987). Moreover, patterns of interaction among phenotypic characters also affect the availability of genetic variation to selection. Response norms for functionally related characters may be negatively correlated within individuals, so that genotypes may differ with respect to particular traits but share similar overall fitnesses (Antonovics 1976).

This paper examines the norms of reaction of *Polygonum persicaria* genotypes to a broad range of light levels, in order to consider how phenotypic plasticity and genetic diversity for response to light affect fitness differentials and therefore selection in plant populations. Light is perhaps the primary resource in the plant environment, and is furthermore an element of the environment that varies both temporally and spatially within as well as between plant individuals (Bazzaz 1979; Gross 1986; Bazzaz and Morse 1991). In the case of environmental variation that is both critical to fitness and fine-grained in distribution, phenotypic plasticity rather than genotypic specialization is to be expected (Bradshaw 1965; Levins 1968). The functional consequences of variation in plant morphology, physiology, and allocation in different light environments have been extensively studied by plant ecophysiologists and are well understood (reviewed in Björkman 1980; Fitter and Hay 1981; Mooney and Chiariello 1984). However, little is known about genotypic variation for response to light (Zangerl and Bazzaz 1983). Although attempts have been made to identify light and shade ecotypes (e.g., Gauhl 1976), the existence of such genetically specialized ecotypes remains in doubt (Gross 1984).

Biologists have come to recognize that in order to understand the relation of phenotype to fitness, and therefore the nature of selection, it is essential to study ecologically relevant aspects of the phenotype—that is, to better integrate population genetics and ecology (Arnold 1983; Endler 1986; Travis and Mueller 1989; Jain 1990; Wade and Kalisz 1990). This is particularly true for studies of phenotypic plasticity, the evolutionary implications of which depend on whether phenotypes expressed in certain environments are indeed functionally advantageous in those environments (Falconer 1990). For instance, the predicted adaptive response of plants to low light is to increase relative biomass allocation to leaf tissue (Evans 1972) and to produce "shade leaves," which differ in area, structure, and photosynthetic capacity from "sun leaves" (Clements 1905; Hanson 1917; Björkman 1980), in order to maximize light capture. If individual genotypes do indeed possess adaptive phenotypic plasticity in response to light, their growth at low light should show these alterations compared with their growth at high light. In this paper, *Polygonum* norms of reaction are analyzed in ecophysiological terms in order to document the range of adaptive phenotypic response to light within individual genotypes. Patterns of diversity among genotypes are then examined in terms of specific growth characters to consider how the complex interaction of genotypes with light environment affects relative fitness and therefore natural selection in this system.

Few studies of either plants (Bradshaw and Hardwick 1989) or animals (Gupta and Lewontin 1982; Falconer 1990) document the phenotypic responses of naturally occurring genotypes to environmental variation. (Most experimental studies use artificially selected varieties or laboratory strains; compare families, populations or species rather than genotypes; or compare as genotypes field-collected perennial tissues in which environmental conditioning and genotype are confounded.) The species used in this study, *Polygonum persicaria,* offers two essential experimental attributes. First, clonal material of natural genotypes can be generated from plants grown under uniform environmental conditions. Second, *P. persicaria* is an annual plant that does not reproduce vegetatively in nature; consequently, total fruit biomass provides a straightforward estimate of fitness. Because norm-of-reaction research requires that experimental environments be controlled (Trexler et al. 1990) and be equal in breadth to those encountered by natural populations (Gillespie and Turelli 1989), plants were grown in an extremely broad range of carefully controlled light environments. We studied genotypes from two *Polygonum* populations that encounter different levels of light variability in order to compare the breadth of phenotypic plasticity and environmental tolerance of populations from more and less variable habitats and to examine genetic diversity in two populations rather than one.

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

Materials and Methods

Study System.—*Polygonum persicaria* L. (Polygonaceae) is a weedy annual species originally from Europe and now distributed virtually worldwide in a variety of habitats (Simmonds 1945; Mitchell and Dean 1978). Like many such species (Baker 1974), it has a mixed breeding system (and no evident inbreeding depression; Sultan 1990) as well as considerable propagule longevity. Fruit dispersal is by both gravity and animals. These attributes, along with typical population sizes of fewer than 100 individuals (Sultan 1990), suggest that populations of this species experience inbreeding (caused by self-fertilization) and genetic drift, counteracted by low levels of both outcrossing and long-range dispersal.

The 20 genotypes used in this study were collected from two populations (150 km apart) in contrasting habitats. These populations have probably occupied these sites for 100–250 generations and are known to be differentiated genetically (on the basis of significant population and/or population-by-environment sources of variance in photosynthetic rate, size and number of leaves and propagules, and other characters of greenhouse-grown progeny; S. Sultan unpubl. data). The Circle population (Carlisle, Mass.) occupies an open hilltop, formerly used as an agricultural field and now supporting a diverse herbaceous flora. The light environment at this site is extremely heterogeneous: available photosynthetically active radiation (PAR, sampled instantaneously at soil, mid-canopy, and canopy levels in 15 random microsites) varied from 100% to less than 10% of full sun within 15-min midday time intervals at each canopy level throughout two growth seasons (1986 and 1987, fig. 1A). The Pond population (East Brewster, Mass.) occupies the sparsely vegetated, south-facing sand beach of a freshwater pond on eastern Cape Cod. Light availability is high as well as spatially and temporally uniform: on five of six sampling dates, mean available PAR was over 90% of full ambient light at soil, mid-plant, and canopy levels (fig. 1B). Indeed, *P. persicaria* individuals growing in this site orient their leaves vertically rather than horizontally, presumably to lessen the high energy load. Mean PAR at the Pond site fell to about 75% on one sampling date, when plants were confined to a narrow strip of beach along the forest edge because of an exceptionally high spring water level. [See Sultan (1990) for complete profiles of these sites.]

Experimental Plant Material.—Achenes (one-seeded nutlike fruits) were collected on a single day from each of 15 randomly chosen individuals 1 m or more apart in each site. These fruits were germinated, grown to maturity, allowed to self-fertilize, and the progeny grown to the cutting stage, all under uniform glasshouse conditions, to minimize the effects of the original maternal environments. Single-node vegetative cuttings were taken from ten randomly selected individuals from each population, using only the third, fourth, and fifth nodes of secondary branches to promote uniformity (Sultan unpubl. data). After nine days, 18 rooted cuttings of approximately uniform size were selected from each genotype, and each was randomly assigned a replicate number, block, light level, and plot position.

Experimental Treatments.—Three hundred and sixty rooted cuttings (2 populations × 10 genotypes × 3 treatments × 6 replicates) were planted singly into 5-inch clay pots, each containing 1 liter of fertilized soil medium (details in Sultan 1990). Pots were placed in plastic saucers to prevent leaching and set in preassigned positions in a randomized complete block design. Each of six glasshouse benches was divided into three 140 × 160 cm plots, and each plot randomly assigned to one of three light levels: 100%, 37%, and 8% of available sunlight. Wooden frames covered with 37% or 8% neutral-density shade cloth were affixed to pulleys and suspended over the appropriate plots to form extendible shade tents. These experimental treatments encompassed the full range of natural light levels, from full summer sun to the minimum necessary for plant survival. Mean midday PAR ± standard deviations and ranges were as follows (based on 20 measurements per plot made with a LICOR 6200 PAR sensor between 10:00 A.M. and 2:00 P.M. July 23–29, for a total of 120 measurements per treatment): 100% treatment = 1019 ± 390 $\mu E/m^2$ s (250–1750); 37% treatment = 311 ± 142 $\mu E/m^2$ s (100–600); 8% treatment = 64 ± 35 $\mu E/m^2$ s (20–150). Note that light saturation occurs in this species at about 750 $\mu E/m^2$ s (S. Sultan unpubl. data). The experiment was designed to minimize the confounding effects of differential light quality, resource use, competition, and saturation deficit often associated with light treatments. Red/ far-red ratios (measured with a Skye SKR-1000 light sensor)

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

did not differ among the three treatments. Pots were subirrigated to insure consistent field capacity soil moisture in all treatments; nutrients were amply available throughout the experiment. The separate soil systems and large amount of aboveground space minimized interference among individuals. Relative humidity varied from 40% to 70%, and did not differ among treatments (as measured with a Licor 1600 steady-state porometer). Plants were grown for 9 wk (June 26–August 27 1987) at 27°/22°C day/night temperature with a 14-h daylength.

Characters Measured.—Three to five successive measurements of photosynthetic rate were made in situ on one newly expanded leaf per plant using a LICOR 6200 portable photosynthesis system with 1/4-liter chamber (July 23–29, 1 block per day). Plant means were calculated from those measurements made at 40%–60% initial relative humidity with a change of 1% or less and with PAR of 21–150 $\mu E/m^2$ s for plants grown at 8% light, 200–550 $\mu E/m^2$ s for 37% plants, and ≥ 600 $\mu E/m^2$ s for 100% plants. (Light variation among these data was randomly dispersed among genotypes.) Genotype means in each treatment were based on the means of four to six replicate plants.

At harvest, aboveground plant material of all experimental plants was separated into live leaves, senescent leaves, stems, and infructescences. The numbers of live and senescent leaves were recorded (live + senescent = total leaf number), and the total area of live leaves (= total leaf area) determined on a Licor 3100 area meter. Root systems were washed. Infructescences were air-dried and sieved to separate fruits from reproductive support tissues (peduncles and bracts). Fruits were air-dried and other tissues oven-dried to a constant weight before weighing. Total biomass (dry weight) was calculated for each plant as the summed dry weights of all plant parts. Proportional biomass components were calculated for root, stem, total leaf, fruit, and reproductive support biomass. The following ratios were calculated: root-to-leaf ratio = [(root biomass)/(total leaf biomass)]; leaf-area ratio (LAR) = [(total leaf area)/(total plant biomass)]; specific leaf area (SLA) = [(total leaf area)/(live-leaf biomass)]; and mean leaf size = [(total leaf area)/(number of live leaves)]. The characters described above are viewed as growth characters, aspects of plant development and function that contribute to fitness (survival and reproduction). The following reproductive characters were considered as components of fitness: total fruit biomass (the air-dried weight of all mature and developing achenes); mean fruit weight [the mean individual weight of fully mature fruits, based on all (8% plants) or 100 randomly sampled mature fruits from each plant]; and total fruit number [(total fruit biomass)/(mean fruit weight)].

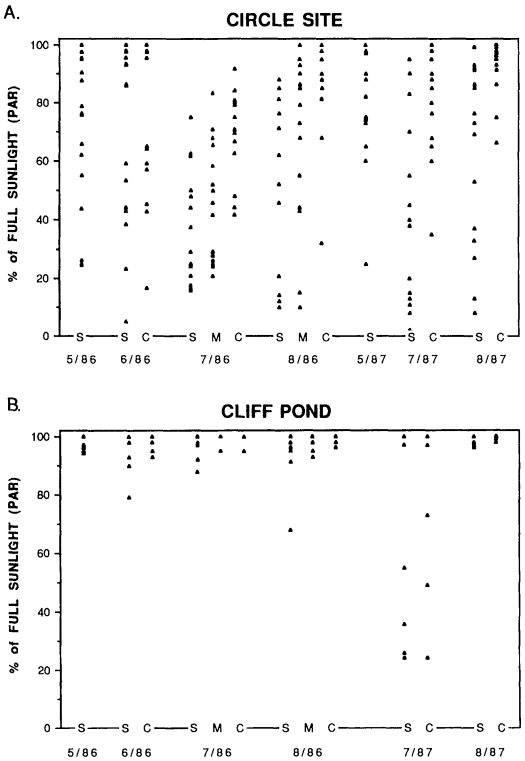

FIG. 1. Percentage of full light (PAR) at soil level (S), mid-plant (M), and *Polygonum* canopy (C), 1986–1987. A, Light measurements, Circle site (each point is 1 measurement; overlapping points appear single); means of all 15 measurements for each sampling date = 37%–80%, soil level; 45%–68%, mid-plant level; 69%–93%, canopy level. B, Light measurements, Pond site (see above); means at all levels for each sampling date $\geq 94\%$ of full light, except means for July 1987 = 73%–77%.

Data Analysis.—The analytical approach in this study is based on the principle that an individual genotype's response to environment is most precisely conveyed by means of a norm-of-reaction diagram showing the phenotypic state at each point along an environmental gradient (Sultan 1987). Since the clonal material was taken from plants grown under identical conditions, genetic and environmental sources of variation were not confounded. This allowed the use of analysis of variance (ANOVA) to assess the distribution of

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

phenotypic variation among environmental treatments and genotypes with respect to variation among replicates and blocks (Lewontin 1974; Mitchell-Olds and Rutledge 1986). This approach was chosen over other analytical methods available to study genotype-by-environment interaction (e.g., Finlay and Wilkinson 1963; Garbutt and Zangerl 1983; Schlichting and Levin 1984) because it is particularly straightforward to interpret and makes fewer assumptions about the structure of the data (see statistical critiques in Witcombe and Whittington 1971; Freeman 1973; Byth et al. 1976; Westcott 1986; Crespi 1990; Gomulkiewicz and Kirkpatrick 1992).

The populations were separately tabulated and analyzed in order to examine and compare the responses of genotypes within each population. Genotype treatment means and their standard errors were computed by the Statistics module of SYSTAT (3.0; Wilkinson and Bjerknes 1987). Characters were transformed as necessary to meet the assumptions of ANOVA (details in Sultan 1990). Mixed two-way plus block ANOVA was performed on each character using the Multivariate General Linear Hypothesis (MGLH) module of SYSTAT. (Because genotypes were randomly dispersed across the entire area of each light plot rather than placed in spatial subplots, the design was analyzed as a randomized complete block rather than a split plot; Little and Hills 1978; Snedecor and Cochran 1989). The genotype effect was treated as random and the light level as fixed; the light effect was tested over the interaction term and the genotype, interaction, and block terms, over the error (Scheffé 1959; Ayres and Thomas 1990; Fry 1992).

Because our purpose was to look very closely at a group of individual genotypes, we tested the genotypic responses in detail rather than use genetic correlations (Via 1987) to summarize the data. To assess variation among genotypes within light levels, separate one-way Model II ANOVAs were performed within each treatment using the model: variable = constant + genotype + block. When genotype terms were significant ($P < 0.05$), Student-Newman-Keuls (SNK) tests were performed on transformed genotype means, after removing block effects from the mean-square error term (Statistics module, SYSTAT 3.0). SNK is a stepwise multiple-range test that permits decisions as to which means differ among a set of means (Steele and Torrie 1960); the probability of Type I error was controlled at the 5% level because group (genotype) variances were homogeneous (according to Bartlett's tests), sample sizes virtually equal, and group means did not fall into several widely spaced sets (Day and Quinn 1989). In the few cases in which cells were missing, genotype means were adjusted for the (unbalanced) block effect. Post hoc linear contrasts were performed within particular treatments when one or several genotypes appeared to be responding distinctively. To maintain the specified error rate for these unplanned comparisons, the contrast F statistics were tested against a critical value determined by Scheffé's S (Steele and Torrie 1980; F tables in Rohlf and Sokal 1981).

Since the proportional components of biomass are interdependent, data for these five characters were analyzed by two-way MANOVA (MGLH module, SYSTAT 3.0). The main effects of light level, genotype, and block, and the genotype-by-light interaction, were then tested separately for overall effect on biomass proportions (multivariate F-statistic based on Wilks's lambda likelihood-ratio criterion) and, when multivariate tests were significant, for effects on each component of biomass (univariate F-tests). Separate ANOVAs (see above) were also performed on each of these characters in order to validate the use of nontransformed data by examining residuals. Relationships between organ size and number within genotypes were examined by estimating Pearson correlation coefficients for genotype means. Although the magnitude of these effects is of interest, their significance was not tested; with only ten data points, such tests would be extremely weak and the underlying distribution assumptions unverifiable.

Because plants from the two populations had different degrees of meristem limitation (see Geber 1990) and therefore responded differently to the cloning process, their growth responses were not directly compared.

Results

Circle Population.—Light level had a highly significant effect ($P \leq 0.001$) on all of the phenotypic characters considered, including all five proportional biomass components (tables 1, 2). In many cases, as described below, the general patterns of phenotypic response to light were common to all ten genotypes (fig. 2A–K). The following characters decreased monotonically with decreasing light: photosynthetic rate; total plant biomass; total fruit biomass; mean fruit weight; and leaf number. Root-to-leaf ratio de-

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

TABLE 1. Two-way plus block mixed ANOVA for growth and reproductive characters. Details in the *Methods* section. Tests for block effect in Sultan 1990.

	Genotype (df = 9)		Light level (df = 2)		Genotype-by-light (df = 18)		Error	
	MS	*F*	MS	*F*	MS	*F*	df	MS
Circle Population (N = 172)								
Photosynthetic rate	5.8	0.70 NS	5073.2	721.2***	7.0	0.86 NS	101	8.2
Total plant biomass	0.15	2.90**	128.92	1483.8***	0.09	1.68*	136	0.05
Total leaf area	27.6	2.22*	8373.8	244.8***	34.2	2.76***	136	12.4
Total leaf number	0.19	2.89**	93.29	262.7***	0.36	5.55***	137	0.06
Mean leaf size	33.75	24.05***	167.35	20.2***	8.29	5.91***	136	1.40
Specific leaf area	9568	3.11**	1,974,014	252.3***	7822	2.54**	136	3080
Leaf-area ratio	3.60	2.24*	1397.14	165.8***	8.43	5.24***	136	1.61
Root-to-leaf ratio	0.025	1.64 NS	2.670	76.1***	0.035	2.29**	136	0.015
Total fruit biomass	0.08	1.40 NS	69.96	1457.8***	0.05	0.87 NS	136	0.06
Total fruit number	0.42	1.51 NS	380.88	1685.8***	0.23	0.80 NS	136	0.28
Mean fruit weight	0.041	4.12***	5.397	386.0***	0.014	1.40 NS	136	0.010
Pond Population (N = 178)								
Photosynthetic rate	14.2	1.95 NS	4366.3	518.6***	8.4	1.16 NS	113	7.3
Total plant biomass	0.07	1.40 NS	152.72	1803.1***	0.09	1.61 NS	143	0.05
Total leaf area	28.1	1.73 NS	15,654.4	409.7***	38.2	2.35**	142	16.2
Total leaf number	0.26	2.72**	95.02	437.9***	0.22	2.25**	143	0.10
Mean leaf size	4.23	6.92***	76.63	48.6***	1.58	2.58**	142	0.61
Specific leaf area	4237	1.54 NS	1,937,678	722.4***	2682	0.97 NS	142	2758
Leaf-area ratio	1.36	1.14 NS	1546.97	1585.8***	0.98	0.82 NS	142	1.19
Root-to-leaf ratio	0.002	0.41 NS	1.582	266.4***	0.006	1.38 NS	143	0.004
Total fruit biomass	0.04	0.78 NS	66.89	957.4***	0.07	1.28 NS	141	0.06
Total fruit number	0.77	2.14*	481.44	831.4***	0.58	1.60 NS	134	0.36
Mean fruit weight	0.032	3.85***	1.726	275.5***	0.006	0.76 NS	134	0.008

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

TABLE 2. MANOVA for proportional components of biomass. Multivariate *F*-statistics based on Wilks's lambda shown with significance levels; details in the *Methods* section.

	Genotype df = 9	Light level df = 2	Genotype-by-light df = 18
Circle Population (N = 172)			
Multivariate *F*	1.868**	94.152**	2.351**
Univariate *F*			
Root proportion	2.263*	31.397***	1.577 NS
Stem proportion	3.132**	138.736***	3.187***
Leaf proportion	0.932 NS	685.868***	4.483***
Reproductive support	1.628 NS	46.803***	2.349**
Fruit proportion	2.870**	216.012***	5.472***
Pond Population (N = 178)			
Multivariate *F*	2.108**	113.870**	1.517**
Univariate *F*			
Root proportion	1.016 NS	0.501 NS	1.910*
Stem proportion	2.602**	161.405***	2.083**
Leaf proportion	1.356 NS	1337.069***	1.181 NS
Reproductive support	2.284*	131.850***	1.505 NS
Fruit proportion	3.452**	616.856***	0.991 NS

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

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

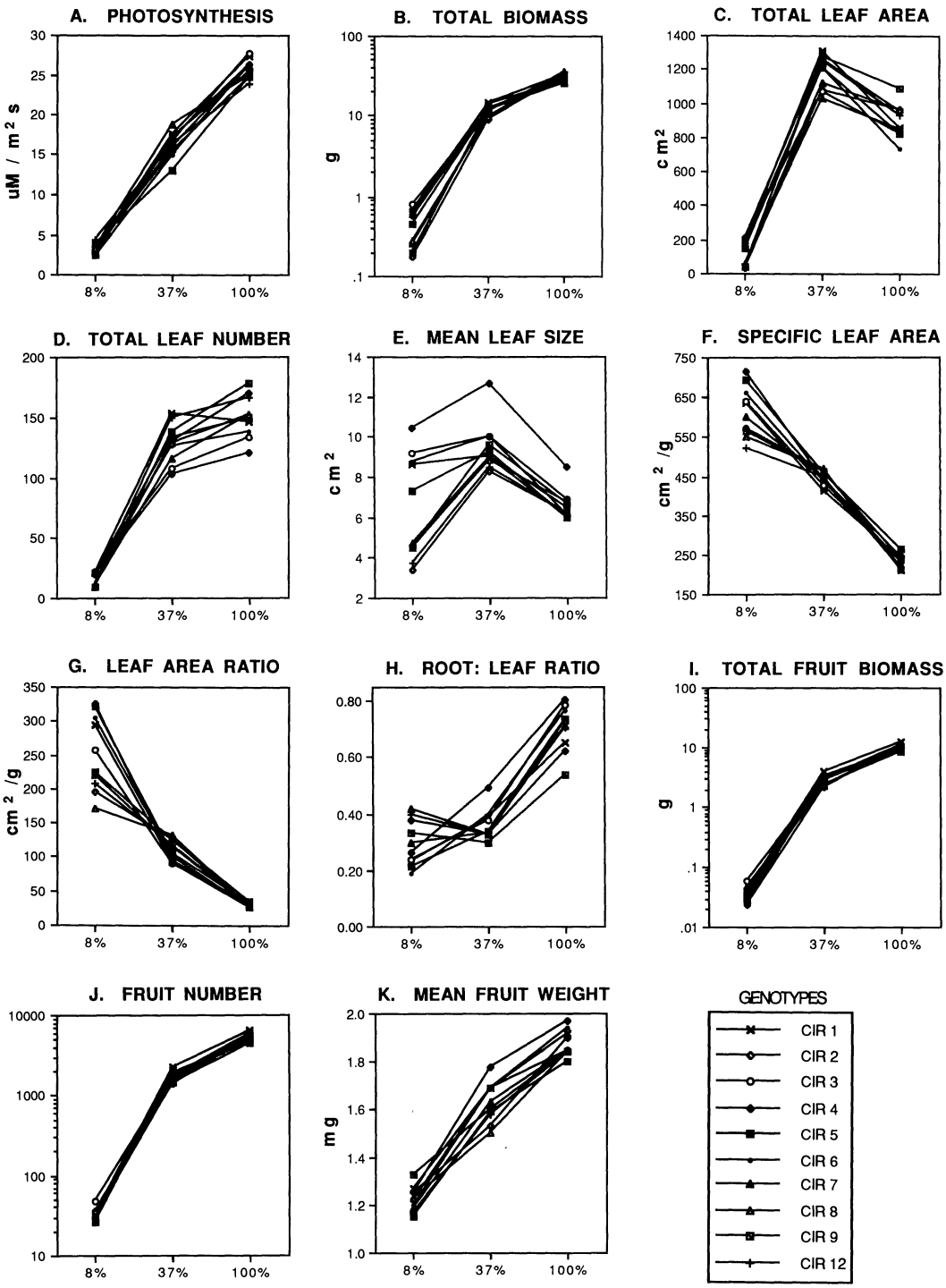

FIG. 2. Norms of reaction for ten Circle genotypes at three light levels (means of 6 replicates). A, Photosynthetic rate; B, total plant biomass; C, total plant leaf area; D, total leaf number; E, mean leaf size; F, specific leaf area; G, leaf area ratio; H, root-to-leaf ratio; I, total fruit biomass; J, total fruit number; K, mean fruit weight. (Each fruit is one seed unit.) With the exception of total leaf number, characters analyzed as log-transformed are shown on a log scale.

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

creased from high to moderate and low light. The steepness of this reduction varied depending on the trait: for example, fruit number was reduced by over 99% in very low light, but mean fruit weight by only 35%. Total leaf area varied between treatments in the order 37% > 100% ≫ 8%. Specific leaf area (SLA) and leaf area ratio (LAR) increased sharply and monotonically with decreasing light. Biomass allocation to leaf tissue nearly doubled from 100% to 37% light, and tripled from 100% to 8% light, as allocation to both stem and fruit biomass decreased (fig. 4). Root and reproductive support proportions also decreased slightly at very low light (fig. 4).

Genotypes can be said to have shown uniform responses over the light range when there is neither a significant genotype main effect nor a significant genotype-by-light level interaction. Circle genotypes exhibited such norms of reaction for only one growth character, photosynthetic rate, and for both fruit number and total fruit biomass (table 1). For all other characters, response norms of Circle genotypes differed: ANOVAs for most growth characters showed significant genotype effects as well as significant genotype-by-light interactions. However, with a single exception (next paragraph), these significant genotype effects did *not* reflect consistent between-genotype differences at all three light environments. The genotype effects for total biomass, leaf characters (leaf number, total area, LAR, and SLA), and root, stem, and fruit biomass proportions resulted largely from pronounced differences within the 8% treatment, between five genotypes that maintained higher growth levels (Circle 1, 3, 4, 5, 6) and five that produced extremely small plants with few, oddly shaped leaves (Circle 2, 7, 8, 9, 12; see fig. 2B–E). Furthermore, the significant main effect of genotype on these characters must be interpreted in terms of the highly significant genotype-by-light interactions. These interactions arose from the fact that the five genotypes that produced plants with lower total biomass, leaf number and area, leaf-biomass proportion, SLA, and LAR at very low (8%) light produced plants with slightly *higher* leaf proportion, LAR and SLA at moderate (37%) light, and higher leaf-biomass proportion, leaf number, and total biomass as well as lower SLA, at high (100%) light, compared with the remaining genotypes (all contrasts significant at $P < 0.01$ according to Scheffé's test except biomass at 100% light differs at $P < 0.05$; cf. table 3).

All genotypes produced larger leaves at moderate than at high light, but at very low light, five genotypes produced large leaves, whereas the others produced very small, misshapen leaves (fig. 2E). The highly significant genotype effect for mean leaf size reflects not only this response bifurcation at 8% light, but also the fact that one genotype (Circle 4) produced significantly larger leaves at all three treatments (table 3). This was the sole case in which any genotype revealed a distinctive norm of reaction, parallel to others across the entire light gradient (fig. 2E). The remaining nine genotypes were indistinguishable within both the 37% and the 100% light treatments (table 3). Norms of reaction for mean fruit weight were also roughly parallel across part of the light gradient: although all genotypes produced fruits of similar weight at very low light, certain genotypes produced consistently heavier or less heavy achenes at moderate and high light (fig. 2K; table 3).

Pond Population.—The effect of light level was highly significant ($P < 0.001$) for all phenotypic characters measured, with the single exception of biomass allocation to root tissue (tables 1, 2). Patterns of phenotypic response common to the Pond genotypes were identical with those expressed by the Circle genotypes: all Pond genotypes responded to reduced light availability by monotonic reductions in photosynthetic rate, total plant biomass, total fruit biomass, fruit number, mean fruit weight, leaf number, root-to-leaf biomass ratio, and biomass allocation to stem, fruit, and reproductive support tissue, and by sharp increases in biomass allocation to leaves, SLA, and LAR (cf. figs. 3A–K, 5). Although all plants produced much smaller fruits at 8% than at 100% light, the reduction from 100% to 37% was slight (fig. 3K).

Unlike the Circle plants, Pond genotypes responded equivalently within all three light levels with respect to most growth characters (figs. 3, 5): neither the genotype main effect nor the genotype-by-light interaction was significant for photosynthetic rate, total plant biomass, root-to-leaf ratio, LAR, SLA, or leaf-biomass proportion (tables 1, 2). However, genotypes differed significantly with respect to leaf size and number. All genotypes varied the mean size of individual leaves in the order 37% > 8% ≥ 100%, but certain genotypes produced relatively small or large leaves within all treatments, and the degree of variation differed among genotypes (fig. 3E). In contrast, differences among Pond genotypes in

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

TABLE 3. Circle population: genotypic differences within light treatments. Genotypes shown ranked by character value within each light 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 genotype term is not significant ($P \geq 0.05$). Genotypes identified by boldface numerals differ significantly in linear contrasts with remaining genotypes ($P < 0.05$). Details in the *Methods* section.

	PHOTOSYNTHESIS			TOTAL BIOMASS			TOTAL LEAF AREA			TOTAL LEAF NUMBER		
	8%	37%	100%	8%	37%	100%	8%	37%	100%	8%	37%	100%
	12	8	3	3	1	**8**	4	1	9	3	1	**9**
	7	1	1	4	4	**12**	3	9	2	5	12	**2**
	9	5	6	1	6	**2**	1	4	8	4	9	**12**
	2	2	7	6	3	**1**	6	12	4	1	5	**7**
	1	3	2	5	5	**3**	5	6	12	6	2	5
	4	12	5	**9**	**9**	**9**	**9**	5	7	**12**	8	**8**
	3	7	8	**8**	**12**	**4**	**8**	8	1	**9**	6	1
	5	4	9	**12**	**7**	**7**	**12**	2	5	**2**	7	6
	6	6	4	**2**	**8**	6	**7**	3	3	**7**	3	3
	8	9	12	**7**	**2**	5	**2**	7	6	**8**	4	4
F	0.80	1.95	0.63	6.80	2.49	1.27	12.6	1.39	0.83	7.45	2.40	1.98
P	.616	.082	.766	.000	.021	.277	.000	.223	.591	.000	.026	.064

	MEAN LEAF SIZE			SPECIFIC LEAF AREA			LEAF AREA RATIO			ROOT: LEAF RATIO		
	8%	37%	100%	8%	37%	100%	8%	37%	100%	8%	37%	100%
	4	4	4	4	**8**	5	4	**8**	9	8	4	4
	3	6	3	5	**2**	4	5	**2**	5	12	6	3
	6	3	8	6	**9**	1	6	**9**	4	2	1	6
	1	9	9	3	5	**9**	1	**12**	2	7	3	5
	5	5	1	1	**12**	6	3	**7**	12	9	5	8
	9	1	12	**7**	**7**	3	**9**	5	7	4	7	7
	8	7	2	**2**	4	**2**	**12**	6	8	3	2	12
	7	8	6	**9**	6	**12**	**7**	4	6	1	8	1
	12	12	5	**8**	3	**7**	**2**	1	1	5	12	2
	2	2	7	**12**	1	**8**	**8**	3	3	6	9	9
F	19.1	8.13	6.31	3.05	1.92	2.39	7.27	2.78	1.43	2.77	1.93	2.15
P	.000	.000	.000	.008	.074	.026	.000	.011	.202	.014	.072	.044

	FRUIT BIOMASS			FRUIT NUMBER			MEAN FRUIT WEIGHT		
	8%	37%	100%	8%	37%	100%	8%	37%	100%
	3	1	1	3	1	1	9	4	4
	2	4	3	6	5	3	1	6	6
	6	3	2	1	3	8	7	3	1
	1	5	8	2	4	2	2	1	2
	8	6	6	8	6	9	4	7	7
	4	9	9	7	12	12	8	9	3
	9	12	12	5	9	5	3	5	12
	5	7	4	4	7	6	6	12	8
	7	2	5	12	2	4	12	2	9
	12	8	7	9	8	7	5	8	5
F	1.59	1.45	1.88	0.93	1.17	1.87	0.68	3.72	3.57
P	.156	.196	.079	.510	.337	.082	.719	.001	.002

the total number of leaves produced varied from treatment to treatment: several genotypes produced relatively high or low leaf numbers at one or two treatments, but none was consistently high or low at all three light levels (fig. 3D). As a result, norms of reaction for total leaf area (the joint outcome of leaf number and size) crossed between the low, moderate, and high light treatments (fig. 3C). For example, the two genotypes with the highest leaf areas at 100% light (P5 and P7) had among the lowest leaf areas at both moderate and low light levels. This crossing pattern resulted in a highly significant genotype-by-light interaction in the absence of a significant genotype effect (table 1).

Like the Circle plants, Pond genotypes shared uniform norms of reaction with respect to total fruit biomass: all genotypes produced equivalent fruit biomass within each of the three light treatments (table 4). The overall genotype effect for total fruit number was, however, marginally significant because of the very high number of fruit produced by genotype P19 at 8% light (table 4). Because this plant also produced relatively small

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

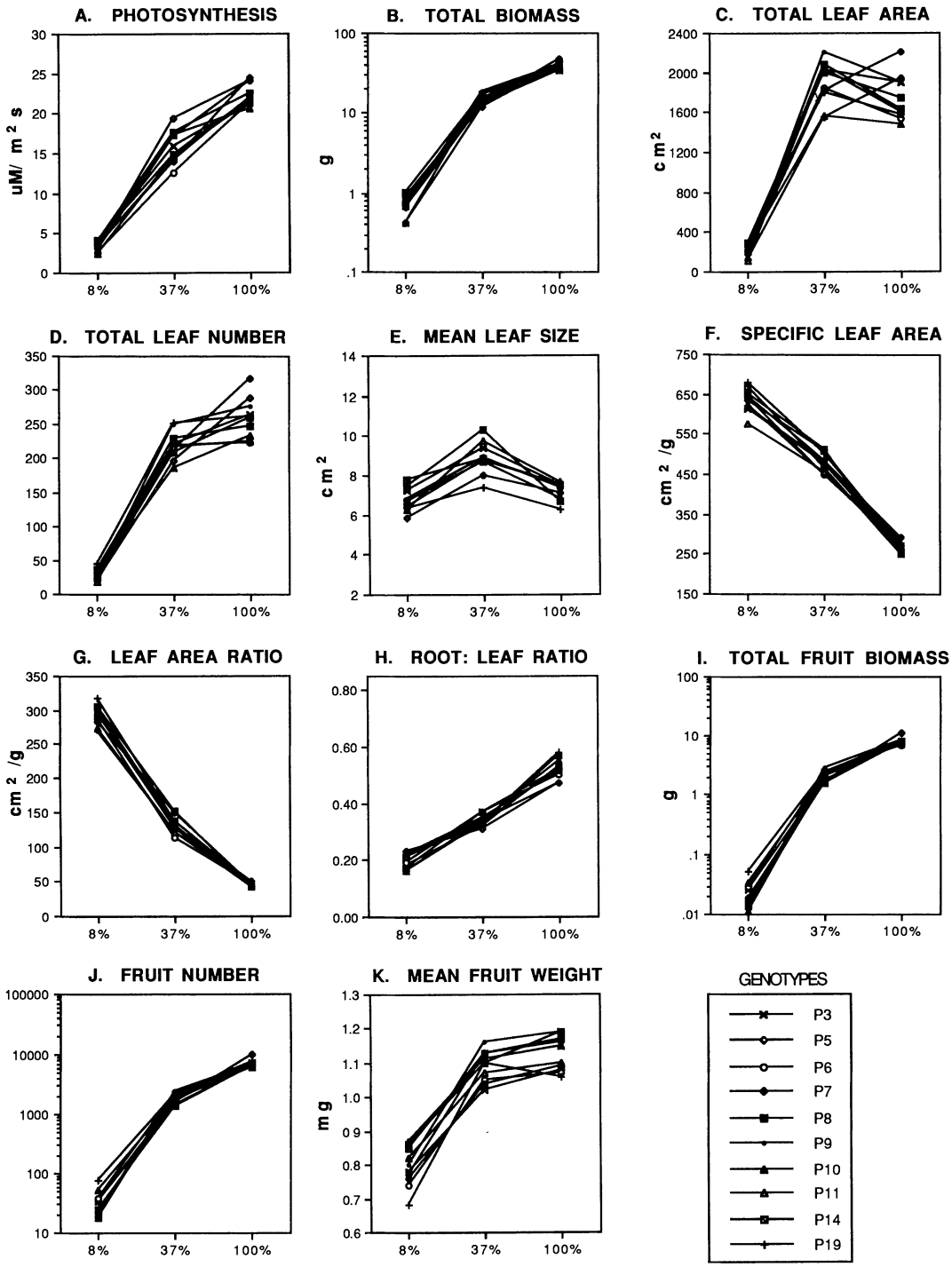

FIG. 3. Norms of reaction for ten Pond genotypes at three light levels (means of 6 replicates). A, Photosynthetic rate; B, total plant biomass; C, total plant leaf area; D, total leaf number; E, mean leaf size; F, specific leaf area; G, leaf area ratio; H, root-to-leaf ratio; I, total fruit biomass; J, total fruit number; K, mean fruit weight. Details as for figure 2.

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

fruits at the 8% treatment (contrast of P19 with all other genotypes significant at $P \leq 0.01$ according to Scheffé's test), the total biomass of fruit it produced at this treatment did not differ significantly from that of other genotypes (table 4). In general, fruit number and mean weight were negatively correlated within genotypes ($r = -0.355$ across environments). Although, as with the Circle plants, reaction norms for mean individual fruit weight were roughly parallel across the light range, Pond genotypes differed significantly in mean fruit weight only at the high light treatment (fig. 3K).

Discussion

This study demonstrates several ways in which the flexibility and complexity of individual development may interact with environmental variability to minimize genotypic fitness differentials and thus allow genetic diversity to be maintained. The discussion addresses two major questions: (1) Do the norms of reaction expressed by *Polygonum* genotypes represent adaptive responses to variation in light intensity, and therefore permit individual genotypes to tolerate a range of light environments? (2) What are the patterns of genetic diversity for growth characters across a range of light environments, and how do these patterns of diversity relate to differences in individual fitness?

Phenotypic Plasticity in Response to Light

All of the phenotypic variation expressed by individual genotypes in different environments cannot be assumed to represent adaptive plasticity (Schmalhausen 1949; Stearns 1982; Taylor and Aarssen 1988), here defined as phenotypic response to an environment that enhances plant function and therefore fitness in that environment (Sultan 1987). Phenotypic responses to suboptimal environmental circumstances simultaneously reflect both growth limits, which are due to low resource levels, and developmental flexibility that enhances resource availability. The interpretation of phenotypic response to light intensity must take into account this interplay between growth limits and adaptive plasticity. Because photosynthesis and therefore plant growth depend directly on available light energy, they decrease sharply in all *Polygonum* genotypes grown at reduced light intensities (figs. 2A,B,D,I,J; 3A,B,D,I,J). However, all genotypes from both populations in the study also expressed a number of developmental modifications at low light levels which maximized light interception. These responses are discussed in detail below in order to establish that individual *Polygonum* genotypes possess a range of adaptive phenotypic responses to different light environments. Note that despite the rarity of low light conditions at the Pond site, genotypes from this population exhibited equally pronounced functional adjustments to low light as those from the very heterogeneous Circle site (fig. 1A,B).

Because low light severely limits photosynthetic rate per unit of leaf area, plant growth can be sustained only by compensatory increases in the amount of photosynthetically active surface area per unit of plant biomass, that is, by enhanced light interception (Fitter and Hay 1981). Such increases occurred in *Polygonum* genotypes grown at low light as a result of several allocational and morphogenetic changes. First, proportional biomass allocation to leaves ("leaf weight ratio," sensu Evans 1972) increased nearly twofold from 100% to 37% light and threefold from 100% to 8% light in all genotypes (figs. 4, 5). Such sustained production of particular tissues under resource limitation may result from different sensitivities to growth substances under diverse environmental conditions (Trewavas 1986). This higher leaf proportion at low light was associated with reduced allocation to both fruit and stem tissue (figs. 4, 5). Shade-evoked decreases in stem and reproductive proportions also accompany increased leaf allocation in several other herbaceous species (Clough et al. 1979b; Ashmun et al. 1985; Grime et al. 1986). In such cases, reduced fruit allocation may follow from the commitment of a limited number of meristems as vegetative rather than reproductive shoots (Watson and Casper 1984). Root proportion remained consistently about 10% in all light treatments (figs. 4, 5), suggesting that uptake and mechanical support requirements may vary in constant proportion to total plant biomass when water and nutrients are in ample supply. However, the ratio of root to leaf biomass decreased sharply in plants grown at moderate and low light (figs. 2H, 3H), which accords with decreased transpirational demands (Björkman et al. 1972; see also Boutin and Morisset 1988).

The ratio of photosynthetic surface area to plant biomass depends on leaf structure as well as on allocation of biomass to leaves. Specific leaf area (SLA) describes the within-leaf distribution of tissue: increased SLA at low light implies not

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

TABLE 4. Pond population: genotypic differences within light treatments. Genotypes shown ranked by character value within each light 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.

PHOTOSYNTHESIS			TOTAL BIOMASS			TOTAL LEAF AREA			TOTAL LEAF NUMBER		
8%	37%	100%	8%	37%	100%	8%	37%	100%	8%	37%	100%
8	5	7	14	9	7	14	9	7	19	19	7
3	14	5	19	11	3	19	8	5	14	9	5
14	11	9	10	6	14	10	11	9	6	14	9
11	9	14	6	14	9	6	3	3	3	6	3
7	3	19	3	3	5	3	14	14	10	3	19
19	8	8	8	8	8	8	6	11	8	11	8
5	10	10	9	19	11	7	19	8	7	7	14
9	19	3	7	7	19	9	7	19	9	8	10
6	7	6	11	10	10	5	10	6	5	5	11
10	6	11	5	5	6	11	5	10	11	10	6
F 1.32	2.12	0.83	1.54	2.68	1.21	2.21	2.54	2.04	2.54	2.41	1.87
P .257	.058	.596	.164	.014	.315	.040	.019	.057	.019	.025	.081

MEAN LEAF SIZE			SPECIFIC LEAF AREA			LEAF AREA RATIO			ROOT: LEAF RATIO		
8%	37%	100%	8%	37%	100%	8%	37%	100%	8%	37%	100%
14	8	11	19	8	5	19	8	5	5	6	19
8	11	3	14	7	9	8	7	9	9	14	8
3	3	14	8	19	19	5	3	7	11	9	10
9	6	7	5	5	10	10	19	6	8	7	3
6	9	6	6	10	7	3	10	3	7	10	14
10	14	9	7	3	6	14	5	19	6	19	11
7	7	5	9	14	3	6	14	10	3	11	9
19	10	10	10	11	11	7	9	14	14	8	6
11	5	8	3	9	8	11	11	11	19	3	5
5	19	19	11	6	14	9	6	8	10	5	7
F 2.74	8.85	2.71	1.02	3.12	1.67	0.83	2.09	1.57	2.66	0.49	1.66
P .013	.000	.013	.441	.005	.123	.593	.050	.154	.015	.876	.127

FRUIT BIOMASS			FRUIT NUMBER			MEAN FRUIT WEIGHT		
8%	37%	100%	8%	37%	100%	8%	37%	100%
19	9	7	19	9	7	10	9	8
10	19	9	6	19	19	8	5	9
6	6	14	8	6	3	14	14	14
3	14	19	5	14	9	11	10	5
5	11	5	11	11	11	9	8	10
8	10	8	10	3	14	3	19	11
7	3	3	9	10	5	5	11	7
14	5	11	3	5	8	7	6	3
9	7	10	14	7	6	6	7	6
11	8	6	7	8	10	19	3	19
F 1.63	1.10	1.45	3.88	1.14	1.54	1.67	1.86	3.22
P .138	.380	.198	.002	.357	.163	.132	.085	.004

only a relative increase in leaf surface area, but also a number of underlying anatomical and biochemical changes that enhance the light-harvesting efficiency of leaf tissue under conditions of low photon-flux density (Hiesey et al. 1971; Björkman et al. 1972; Osmond et al. 1980). All genotypes of both *Polygonum* populations increased SLA nearly twofold at 37%, and two and one-half- to threefold at 8% light relative to that at 100% light (figs. 2F, 3F). Striking SLA increases under reduced light have been reported for numerous species; this has long been recognized as a very flexible aspect of the plant phenotype (references in Evans 1972; Fitter and Hay 1981; Sultan 1990).

The joint outcome of leaf biomass proportion and SLA is the leaf-area ratio (LAR), leaf area per unit of plant biomass. This relative capacity for light interception has been shown in numerous cases to be of primary importance to plant growth under low light (Potter and Jones 1977; Gross 1989). In most species, the increase in LAR at low light is roughly similar to the change in SLA, since leaf proportion changes are slight or even negative; indeed allocation to leaves is assumed to be relatively inflexible (Björkman

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

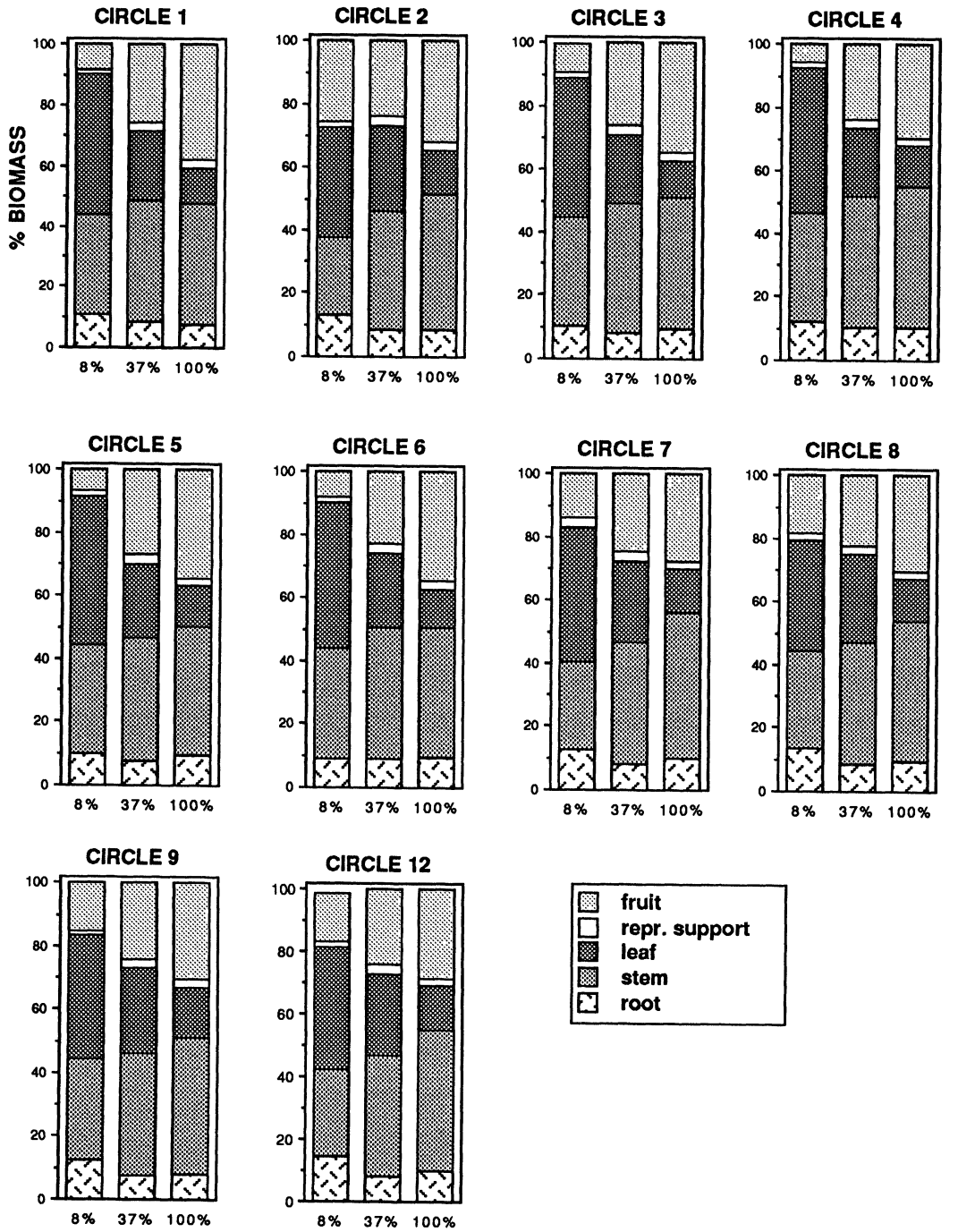

FIG. 4. Proportional biomass allocation for ten Circle genotypes at three light levels. Root, stem, leaf, reproductive support, and fruit biomass presented as proportions of total plant biomass; means of six replicates.

1980; Fitter and Hay 1981; Hunt 1982). Since *Polygonum* genotypes steeply increase both SLA *and* leaf proportion in diminished light, LAR increases dramatically: three- to fourfold at 37% light, and seven- to ninefold at 8% light, compared with LAR at full sunlight (figs. 2G, 3G). Allocational and morphogenetic flexibility thus combine to afford these genotypes remarkable

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

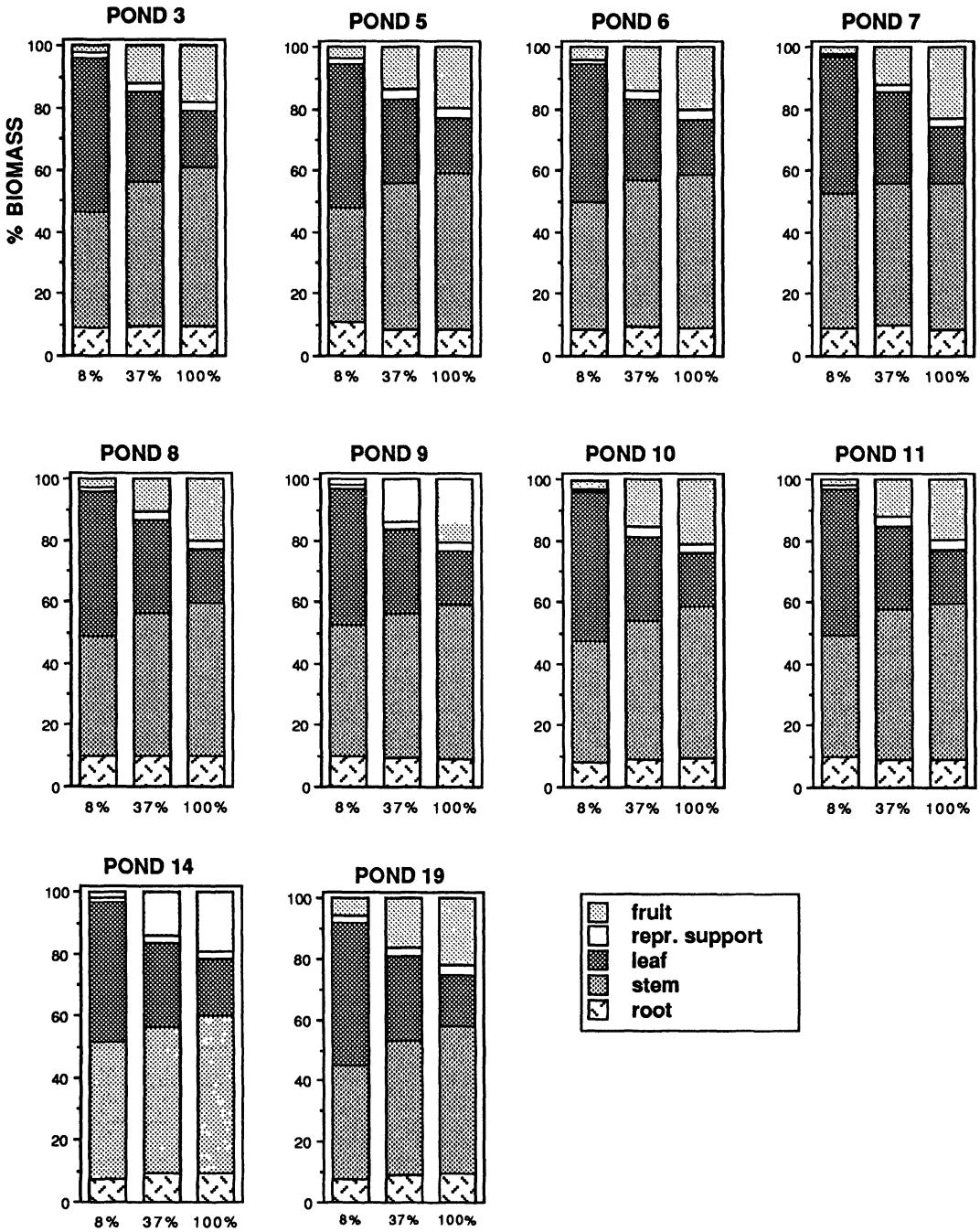

FIG. 5. Proportional biomass allocation for ten Pond genotypes at three light levels. Root, stem, leaf, reproductive support, and fruit biomass presented as proportions of total plant biomass.

plasticity in the relative amount of light-capturing surface displayed under different light intensities.

Absolute changes in total leaf area are more difficult to interpret, because the number of leaves diminishes sharply as light intensity, and therefore plant size, decreases. By separating total leaf area into leaf number and mean leaf size, it is

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

possible to assess the extent to which morphological flexibility in leaf development can mitigate the reduction in leaf number dictated by low light conditions. In all genotypes, the approximately 15% reduction in leaf number at moderate (37%) light was offset by a marked increase in leaf size (45% in Circle and 24% in Pond plants; cf. figs. 2D,E; 3D,E). Because of this morphological overcompensation, total leaf areas were actually *greater* at 37% than at 100% light, although plant biomass was reduced by two-thirds (figs. 2B,C; 3B,C). In contrast, no genotype produced larger leaves at 8% light than at 37%, so the reduction in leaf number at very low light did result in sharply reduced total leaf area (figs. 2C–E; 3C–E). This may reflect a biomechanical limit to the size of extremely thin leaves such as those produced at very low light (D. Ackerly pers. comm. 1990), or alternatively this extreme environment may impose metabolic limits on cell division and/or expansion. The diversity of response among Circle plants in mean leaf size suggests the possibility of such a threshold effect in this character.

All genotypes in both populations were able to maintain a positive carbon balance at very low light as well as to exploit high levels of light energy by means of sharp increases in photosynthetic rate (figs. 2A, 3A). Such physiological response breadth is typical of early successional plants, which generally encounter extremely variable light conditions (Bazzaz 1979; Bazzaz and Carlson 1982). As discussed above, plant growth in low light conditions can only be sustained by increases in leaf allocation and size that offset the inevitable, severe reduction in photosynthetic rate. The extent to which these opposing trends balance one another can be roughly estimated by calculating the relative photosynthetic efficiency (RPE) of each genotype as follows (respiration per gram of biomass is assumed constant across light levels; Evans and Hughes 1961; Wulff 1987):

$$\begin{aligned} \text{RPE} &= (\text{photosynthetic rate per unit area}) \\ &\quad \cdot(\text{specific leaf area}) \\ &\quad \cdot(\text{leaf proportion of biomass}) \\ &= (\text{mg } CO_2/\text{cm}^2\ \text{s})(\text{cm}^2\ \text{leaf/g leaf}) \\ &\quad \cdot(\text{g leaf/g total plant}) \\ &= \text{mg } CO_2/\text{g plant tissue s} \end{aligned}$$

In *Polygonum* genotypes, developmental plasticity effectively counteracted the reductions in photosynthetic rate that occurred at both moderate and very low light (fig. 6). The one-third decline in photosynthetic rate per unit of leaf area at 37% light was more than offset by a tripling in LAR: RPE actually *doubled* at 37% compared with the rate at full sun. At 8% light, increases in LAR balanced the 80%–90% drop in photosynthetic rate, so that RPE remained 94%–105% of that at full sun. Similar patterns of LAR overcompensation at moderate light were found in *Impatiens parviflora* (Evans and Hughes 1961), *Fragaria vesca* (Chabot 1978), *Geum urbanum* (cited in Hunt 1982), and *Abutilon theophrasti* (Rice and Bazzaz 1989b). The well-documented phenotypic flexibility of such annual species may thus reflect high degrees of adaptive plasticity to varying light conditions.

The environmental gradient created in this experiment encompassed virtually the full breadth of light conditions encountered in temperate habitats. Unlike most controlled studies of light response, the high light level in this experiment was well above light saturation for the species, and close to full natural sunlight. The lowest treatment was particularly limiting because there were no occasional flecks of high light as would occur in a naturally shaded microsite. It is striking, then, that every genotype of both *Polygonum* populations was able to accommodate the entire light range: all survived and produced viable progeny in every treatment, including the extremely low (8%) light level (8% and 37% progeny showed no reduction in the percentage of germination or seedling growth rate; S. Sultan in prep.).

It is not possible to empirically test the contribution of a particular character state toward the maintenance of reproductive fitness, because other aspects of the phenotype cannot be held constant. Neither can entire phenotypes elicited by different treatments be compared under uniform conditions, as transferred plants immediately begin phenotypic adjustment (Evans 1972; Rice and Bazzaz 1989a). Statistical attempts to identify the contribution of a particular response to fitness are swamped by the strong positive correlations of favorable light conditions with reproductive output (the "silver spoon" effect; Grafen 1988; see Geber 1990 and references). Thus, a causal relationship cannot be established between the specific phenotypic modifications that occurred in *Polygonum* genotypes grown at reduced light levels, and the maintenance of reproductive fitness. Nonetheless, these data clearly demonstrate that the high plasticity of *P. persicaria* genotypes in characters relating to light

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

capture and use is associated with the ability of those genotypes to tolerate an extremely broad range of light environments. To the extent that phenotypic plasticity permits individual adaptation to various environments, it constitutes an evolutionary alternative to genetically based environmental specialization (Bradshaw and Hardwick 1989; Sultan 1992).

Patterns of Genetic Diversity for Norms of Reaction to Light

In certain characters, all genotypes within each population shared a uniform norm of reaction. In other words, genotypes did not differ significantly in these traits at any point on the light gradient, so that their norms of reaction overlapped completely. Uniform environmental response by diverse genotypes has been termed "plastic convergence": the ability of different genotypes to express a similar, appropriate phenotype in response to a particular environmental stress (Sultan 1987; Levin 1988). Although they differed significantly in most other growth characters, *Polygonum* genotypes from both populations shared convergent norms of reaction for photosynthetic rate (tables 3, 4; figs. 2A, 3A). Uniform responses to different light levels in photosynthetic rate (as well as chlorophyll content and SLA) were also found in 29 of 30 *Solanum* genotypes studied by Clough et al. (1979a). Convergent norms of reaction for a genetically complex, environmentally dependent physiological character central to fitness, such as photosynthetic rate in plants, may evolve under selection for maximal performance under directly limiting conditions. Similarly, convergent patterns of stomatal response to moisture conditions have been found among both genotypes (Begg and Turner 1976) and populations from drastically contrasting habitats (Roy and Mooney 1982), and convergent norms of reaction for developmental rate were found for morphologically diverse genotypes of *Drosophila pseudoobscura* (Gupta and Lewontin 1982).

Pond genotypes also shared convergent response norms for specific leaf area, LAR and root-to-leaf ratio (fig. 3F–H). Genotypes in this population thus responded virtually identically to variation in light in the characters most directly related to functional adjustment to light level. When grown in a range of soil-moisture levels, genotypes within both populations converged completely in norms of reaction for root-biomass allocation and root-to-shoot ratio, although they

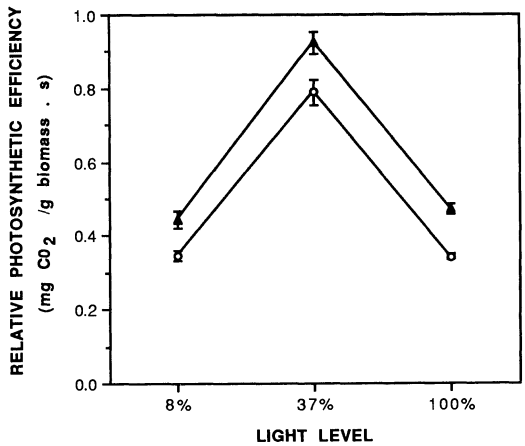

FIG. 6. Relative photosynthetic efficiency, population means ± 2 standard errors at three light levels. Open circles, Circle population; triangles, Pond population. Means based on per-plant means ($N = 60$) calculated as: (photosynthetic rate) × (specific leaf area) × (leaf biomass proportion).

differed significantly in all other traits measured (Sultan and Bazzaz 1993a). Both the light and moisture experiment results support the view that such plastic convergence may be particularly common in characters that contribute directly to functional adjustment to environment. Circle genotypes grown on a nutrient gradient converged in root-to-shoot ratio at low and moderate nutrient treatments but differed significantly at ample and excessive nutrient levels (Sultan and Bazzaz 1993b). Likewise, cultivated *Phaseolus* varieties (Gerloff 1976) and *Plantago* individuals from different macronutrient habitats (Lotz and Blom 1986) produced equal root-to-shoot ratios in low-nutrient conditions but diverged at high levels of nutrients. If root-to-shoot ratio is an important determinant of fitness under nutrient limitation but not when nutrients are abundant, this pattern of greater phenotypic convergence at low nutrient levels may be common in natural populations. Thus, the occurrence of plastic convergence may reflect the variable selective importance of different functional characters under various conditions.

Where *Polygonum* norms of reaction differed, they were not parallel (consistently higher or lower) but either crossed (i.e., reversed in relative rank from one light treatment to another) or differed significantly in certain environments but responded identically in others. Such changes in the direction and magnitude of genetic differ-

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

ences between environments are a critical aspect of genotype-environment interaction (see discussion in Sultan and Bazzaz 1993a). Genotypes of the Circle population illustrate the former pattern: those with the poorest vegetative growth at very low light produced more biomass at high light (table 3; Results section). Similarly, Pond genotypes with relatively high leaf number and total leaf area in certain treatments were relatively low in others (table 4; fig. 3C,D). In the latter type of pattern, the response of a particular genotype was distinct at one or two light levels but indistinguishable from others elsewhere on the light gradient. In such cases, genetic variation itself varied with environment. For example, one of the Pond genotypes (P 19) produced a significantly greater number of fruit than others at very low light, but all genotypes produced equal numbers of fruit at both moderate and high light (table 4). In general, genotypes of both populations were more phenotypically similar at 100% light than at the two reduced light levels (tables 3, 4).

It is well known (though often ignored) that the relative amount of genetic variance estimated in a population depends on the environments considered as well as the genotypic sample (Harberd 1957; Steel and Torrie 1960; Feldman and Lewontin 1976). These data amply demonstrate both this fact and the equally critical point that the relative magnitude of genetic differences also varies among phenotypic characters. Arguments about variation available to selection should be based on characters that contribute to fitness and not on other aspects of the phenotype that are assumed to mark genetic diversity. For this reason evolutionary biologists should determine with care which characters to study, rather than simply measure a convenient set of morphological traits.

Character Interaction and Individual Fitness

All aspects of the phenotype jointly determine the functional "fitness" of the individual to its environment (Mooney and Chiariello 1984) and, ultimately, its reproductive output, its fitness in the evolutionary sense. Growth characters such as photosynthetic rate or number and size of plant organs are the complex products of numerous underlying events and processes. Such characters likewise interact to produce higher-level aspects of the phenotype, such as total leaf area and whole-plant carbon assimilation. Genotypes possess differential fitnesses only to the extent that they differ phenotypically at levels which directly influence plant function, survival, and ultimately reproductive output (see Vrba and Gould 1986). As a result of phenotypic plasticity in functionally important traits, genotypes may express similar adaptations to environmental conditions, as discussed above. Furthermore, to the extent that genotypes differ in particular traits, those differences may be negatively correlated so as to preclude differences in higher-level traits. The results of this study demonstrate that diverse underlying character states may indeed balance to result in equivalent fitnesses. In this way character interaction can render genetic diversity for growth characteristics unavailable to selection. This argument is fully developed by Antonovics (1976) and Via and Lande (1985) in terms of "negative genetic correlations" among traits that contribute to fitness (see also Crespi 1990; Conner and Via 1993 and references). Antonovics suggests that the high genetic variability of plant populations for phenotypically expressed traits is largely due to the limits such character correlations impose on selection.

In both *Polygonum* populations, genotypes differed in many underlying characters (see significant genotype and/or genotype-by-light interaction terms, tables 1 and 2), but produced equivalent total fruit biomass at every light level (tables 3, 4). Thus, a particular level of reproductive fitness can be achieved by diverse genotypes, each with a unique set of developmental responses and constraints. For example, the absolute reproductive output of an individual plant depends jointly on its total biomass and the proportion of that biomass that is allocated to reproduction. At very low light, Circle genotypes 2, 7, 8, 9, and 12 had poor vegetative growth and produced less total biomass than the other five genotypes in the population (table 3; Results section). However, since they also had *higher* allocation to fruit tissue (contrast significant at $P < 0.01$ according to Scheffé's test), they produced the same total fruit biomass and number as the other genotypes (table 3).

Characters are not all equally flexible; furthermore, particular characters may be constrained in certain genotypes and flexible in others (see Lechowicz and Blais 1988). An important aspect of plasticity may be its role within the phenotype in balancing constrained responses through flexibility in functionally related characters. For instance, two Pond genotypes have relatively inflexible leaf size (fig. 3E). These genotypes are not however limited to "sun" or

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

"shade" leaves in the different light treatments, since their norms of reaction for SLA act to offset these size constraints: Pond 19 has small leaves in all treatments but relatively high SLA; Pond 14 has consistently large leaves but, at high light where thin leaves might be maladaptive, low SLA (table 4). Plasticity in leaf structure may thus compensate functionally in these genotypes for reduced plasticity in leaf size. A second example involves the interaction of photosynthetic rate and total leaf area, on both of which total plant carbon gain depends. The Pond genotype with the lowest total leaf area at 37% light had the highest photosynthetic rate at that treatment (table 4; although genotype means did not differ significantly, when treated as a planned comparison the contrast of this genotype with all others was significant at $P < 0.05$). A similar result was found in a comparison of *Phleum alpinum* ecotypes (Callaghan and Lewis 1971). When grown under uniform conditions, these ecotypes "achieved similar growth rates in different ways": the population with lower leaf-area ratio had a higher net photosynthetic rate per unit of area, and vice versa. Here, too, the same outcome with respect to fitness was achieved by different combinations of constrained and plastic characters in different genotypes.

In contrast to the crossing and convergent norm of reaction arrays for other growth characters across the light gradient, in general both Pond and Circle genotypes tended to produce relatively large or small leaves and fruits in all light treatments (cf. highly significant genotype terms, table 1). At the level at which these size characters might influence fitness, however, they appear to be balanced by negatively correlated differences in organ number. For example, genotype Circle 4 produced significantly larger leaves than most or all other Circle genotypes at every light level (table 3). Here, then, was a case (the only one found in this study) of a genotype expressing a consistently different phenotype—a higher, parallel, norm of reaction (fig. 2E)—which would presumably be available to selection. With respect to fitness in the functional sense, however, the salient character would be not the size of individual leaves, but the total leaf area of the plant. Although Circle 4 produced large leaves, it also produced relatively *few* leaves (table 3; fig. 2D), so that it did not differ from other genotypes in total leaf area (table 3). Differences in mean leaf size among genotypes of both populations tended to be offset by negatively correlated differences in leaf number [coefficients for genetic correlations of leaf number and mean size based on genotype means across treatments were -0.793 (Circle) and -0.463 (Pond)]. Leaf number and size also correlated negatively in Circle population genotypes grown on a moisture gradient ($r = -0.610$) and at excessive nutrient levels ($r = -0.820$); correlations were weaker when genotypes did not differ significantly in leaf size (Sultan and Bazzaz 1993a,b). Note however that for a given set of genotypes, such correlations vary with environment. For example, because five of the Circle genotypes produced fewer *and* smaller leaves at very low light, at this treatment the genetic correlation was highly positive ($r = +0.925$). Thus correlations among growth characters are not the inevitable consequences of either genotype or development. Such correlations are sensitive not only to changes in gene frequency (Mitchell-Olds and Rutledge 1986) but to the precise conditions in which phenotypes are expressed (Lechowicz and Blais 1988).

Although differences among genotypes in mean fruit weight were less pronounced than those in leaf size, most genotypes tended to consistently produce relatively large or small achenes (table 1). However, as a result of generally negative genetic correlations with fruit number (coefficients from -0.517 to $+0.222$ depending on population and treatment), total fruit biomass did not differ among genotypes in either population within any light treatment. For example, at very low light, genotype Pond 19 produced relatively small fruits, but also a greater number of fruits, so that its total fruit output was statistically indistinguishable from that of other Pond genotypes (table 4). Related genotypes grown on a moisture gradient differed more strongly in mean fruit weight, and showed even stronger negative correlations of fruit size and number ($r = -0.421$ for Circle genotypes and -0.815 for Pond genotypes; Sultan and Bazzaz 1993a).

Thus, *Polygonum* genotypes tended to produce either many, slightly lighter fruits, or fewer, somewhat heavier fruits. Propagule number and mean weight were also negatively correlated among genotypes of *Oenothera biennis* grown on a density gradient (Kromer and Gross 1987) and siblings of *Xanthium strumarium* grown at a range of moisture and nutrient levels (Lechowicz and Blais 1988; additional references in Venable 1992). Such differences have been described in comparisons of species that "absorb stress" in one or the other component of reproductive out-

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

put (Marshall et al. 1986). These alternatives do not necessarily constitute different levels of fitness. Although propagule mass has been positively correlated with adult fitness components in numerous cases (e.g., Stanton 1984a; Mazer 1987; Schmitt and Ehrhardt 1990), larger seeds are not advantageous under all conditions (Stanton 1984b; Venable and Brown 1988). Thus, variation in seed weight can operate by analogy to genetic polymorphism in affording plants diverse ways to reproduce successfully (Jain 1979; Cavers and Steel 1984). Moreover, the mean weight as well as number of propagules produced by *Polygonum* individuals was even more strongly affected by light treatment than by genotype (table 1). Such strong environmental effects on propagule size are known to occur in many species (reviewed in Schaal 1984; Roach and Wulff 1987). Finally, the nitrogen concentration as well as the weight of propagules may vary with environment, and different genotypes may "absorb" nitrogen limitation by reducing either trait to produce fruits of identical nitrogen content (Sultan and Bazzaz 1993b). Because nitrogen content is a key aspect of seed provisioning, such compensatory interactions may also reduce the importance of genetic and environmental effects on mean fruit weight for the actual quality of progeny.

Although *Polygonum* genotypes did not differ in reproductive output, enormous, consistent reproductive fitness differentials did occur between light levels (table 1). Mean total fruit biomass of plants grown at 8% light was as little as one-eighth of 1% of that of the same genotype grown at 100% light; the mean within-genotype reduction was 99.7% (see figs. 2I, 3I). Such profound environmental effects on plant fitness are very well documented, and have been shown in many cases to persist over several generations (reviewed in Bazzaz and Sultan 1987). In fact, differences between naturally occurring genotypes are inevitably confounded to some extent with past variation in maternal-plant environment (Stanton 1984b; Tonsor 1989). Narrow-sense heritabilities for fitness characters are consistently low or zero in both plant and animal species studied; environmental effects on plant growth and reproduction are typically far greater in magnitude than genotypic differences (Sultan 1987, 1990). For example, Stratton (1992) found that environmental components of variance for fitness-related traits in *Erigeron annuus* exceeded genetic variance components by at least an order of magnitude, even at very small spatial scales. In the present study, the magnitude of differences resulting from light treatment was greater than that resulting from genotype in all characters (mean squares from 5 to 860 times as large, table 1). Note that additive genetic variation for a character contributing to individual fitness can persist in populations if the expression of that character is simultaneously influenced by environmental factors (Price et al. 1988; Alatalo et al. 1990). Because of the highly heterogeneous and fluctuating nature of light availability in natural habitats, these effects of light environment are a particularly important source of fitness variation in plant populations.

Conclusions

Light is an element of the plant environment that critically affects growth and fitness, yet exhibits minimal spatial and temporal constancy (Bazzaz 1979; Gross 1986). Plant genotypes might therefore be expected to have evolved greater plasticity in response to diverse light conditions than to discretely distributed environmental variation (Sultan 1987). Individual *Polygonum* genotypes can indeed give rise to diverse adaptive phenotypes under different light levels. Such plasticity permits individual adaptation in two ways: by allowing one genotype to express different phenotypes as required in different environments, and by allowing different genotypes to converge on a single phenotype appropriate to a particular environment (Wright 1980). Both aspects of plasticity evidently contribute to the remarkable environmental tolerance shown by these genotypes, which were all able to survive and reproduce across an extreme range of light levels.

These norm of reaction data provide several insights into the nature of genetic diversity in these populations and its relation to fitness differences. In the case of certain complex physiological characters, genetically diverse individuals expressed similar, appropriate phenotypes. To the extent that *Polygonum* genotypes differed phenotypically, these differences were not consistent but rather varied in magnitude and direction among light levels. Moreover, differences among genotypes in characters such as organ number and size were negatively correlated so as to offset one another. Such character interactions may shield genetic differences for underlying phenotypic characters by producing convergence in characters that more directly

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

determine fitness. Indeed, reproductive fitness differences among genotypes were completely absent from both populations, either within any light treatment or averaged overall. This result is particularly interesting since it clearly does not derive from a lack of genetic variability in either population, but rather suggests variability maintained in a "state of poise" (Wright 1931). Selective arguments are often founded on differences among genotypes in easily measured constituent traits such as plant height or total biomass. Because of interactions among characters, however, such differences cannot be simply extrapolated to differences in survival or reproductive fitness. Even an environmentally constant difference among genotypes in a functionally important aspect of the phenotype may be unavailable to selection. The very complexity of morphogenesis may blunt selection on particular aspects of the phenotype that jointly contribute to fitness.

Although genotypes shared equivalent reproductive fitnesses within each light environment, the effect of light level on reproductive fitness was extremely dramatic. When the environmental variability that gives rise to fitness differentials is randomly distributed with respect to genotype, as is the case for available light, more subtle genotypic differences that may exist within a population will be unavailable to selection (Sultan 1987).

Acknowledgments

This manuscript was improved by the comments of T. Meagher and two anonymous reviewers. We also acknowledge with thanks valuable criticism of earlier versions of the paper by D. Ackerly, R. Dorit, R. Grosberg, A. Knoll, R. Lewontin, W. Morris, C. Schlichting, J. Schmitt, M. Stanton, and R. Tryon; statistical consultation with K. McConnaughay, P. Taylor, N. Willits, and L. Roseman; and practical advice from K. Garbutt and E. Reekie. Able laboratory assistance was provided by C. Johnston. We also thank the staff of Great Brook Farm State Park for their cooperation. 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, Harvard University, to S.E.S.

Literature Cited

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

Antonovics, J. 1976. The nature of limits to natural selection. Annals of the Missouri Botanical Garden 63:221–247.

Arnold, S. J. 1983. Morphology, performance, and fitness. American Zoologist 23:347–361.

Ashmun, J. W., R. L. Brown, and L. F. Pitelka. 1985. Biomass allocation in *Aster acuminatus*: Variation within and among populations over 5 years. Canadian Journal of Botany 63:2035–2043.

Ayres, M. P., and D. L. Thomas. 1990. Alternative formulations of the mixed-model anova applied to quantitative genetics. Evolution 44:221–226.

Baker, H. G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics 5:1–24.

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

Bazzaz, F. A., and R. W. Carlson. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. Oecologia 54:313–316.

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, San Diego, Calif.

Bazzaz, F. A., and S. E. Sultan. 1987. Ecological variation and the maintenance of plant diversity. Pp. 69–93 *in* K. M. Urbanska, ed. Differentiation patterns in higher plants. Academic Press, London.

Begg, J. E., and N. C. Turner. 1976. Crop water deficits. Advances in Agronomy 28:161–215.

Björkman, O. 1980. Responses to different quantum flux densities. Pp. 57–107 *in* A. Pirson and M. H. Zimmerman, eds. Encyclopedia of plant physiology, vol. 12A. Springer, Berlin.

Björkman, O., N. K. Boardman, J. M. Anderson, S. W. Thorne, D. J. Goodchild, and N. A. Pyliotis. 1972. Effect of light intensity during growth of *Atriplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. Carnegie Institution of Washington Yearbook 71: 115–135.

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

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

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

Byth, D. E., R. L. Eisemann, and I. H. DeLacy. 1976. Two-way pattern analysis of a large data set to evaluate phenotypic adaptation. Heredity 37:215–230.

Callaghan, T. V., and M. C. Lewis. 1971. The growth of *Phleum alpinum* L. in contrasting habitats of a sub-antarctic station. New Phytologist 70:1143–1154.

Cavers, P. B., and M. G. Steel. 1984. Patterns of

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

change in seed weight over time on individual plants. American Naturalist 124:324–335.
Chabot, B. F. 1978. Environmental influences on photosynthesis and growth in *Fragaria vesca*. New Phytologist 80:87–98.
Clements, E. S. 1905. The relation of leaf structure to physical factors. Transactions of the American Microscopical Society 26:19–102.
Clough, J. M., J. A. Teeri, and R. S. Alberte. 1979a. Photosynthetic adaptation of *Solanum dulcamara* L. to sun and shade environments. I. A comparison of sun and shade populations. Oecologia 38:13–21.
Clough, J. M., R. S. Alberte, and J. A. Teeri. 1979b. Photosynthetic adaptation of *Solanum dulcamara* L. to sun and shade environments. II. Physiological characterization of phenotypic response to environment. Plant Physiology (Bethesda) 64:25–30.
Connor, J., and S. Via. 1993. Patterns of phenotypic and genetic correlation among morphological and life-history traits in wild radish, *Raphanus raphanistrum*. Evolution 47:704–711.
Crespi, B. J. 1990. Measuring the effect of natural selection on phenotypic interaction systems. American Naturalist 135:32–47.
Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59:433–463.
Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, N.J.
Evans, G. C. 1972. The quantitative analysis of plant growth. Studies in Ecology, vol. 1. Blackwell Scientific Publications, Oxford.
Evans, G. C., and A. P. Hughes. 1961. Plant growth and the aerial environment. I. Effect of artificial shading on *Impatiens parviflora*. New Phytologist 60:150–180.
Falconer, D. S. 1990. Selection in different environments: effects on environmental sensitivity (reaction norm) and on mean performance. Genetical Research 56:57–70.
Feldman, M. W., and R. C. Lewontin. 1976. The heritability hang-up. Science 190:1163–1168.
Finlay, K. W., and G. N. Wilkinson. 1963. The analysis of adaptation in a plant-breeding programme. Australian Journal of Agricultural Research 14:742–754.
Fitter, A. H., and R.K.M. Hay. 1981. Environmental physiology of plants. Academic Press, London.
Freeman, G. H. 1973. Statistical methods for the analysis of genotype-environment interactions. Heredity 31:339–354.
Fry, J. D. 1992. The mixed-model analysis of variance applied to quantitative genetics: biological meaning of the parameters. Evolution 46:540–550.
Garbutt, K., and A. R. Zangerl. 1983. Application of genotype-environment interaction analysis to niche quantification. Ecology 64:1292–1296.
Gauhl, E. 1976. Photosynthetic response to varying light intensity in ecotypes of *Solanum dulcamara* L. from shaded and exposed habitiats. Oecologia 22:275–286.
Geber, M. A. 1990. The cost of meristem limitation in *Polygonum arenastrum*: negative genetic correlations between fecundity and growth. Evolution 44:799–819.
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 Agricultural Experiment Station, Ithaca, N.Y.
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.
Grafen, A. 1988. On the uses of data on lifetime reproductive success. Pp. 454–471 *in* T. H. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.
Grime, J. P., J. C. Crick, and J. E. Rincon. 1986. The ecological significance of plasticity. Pp. 5–29 *in* D. H. Jennings and A. J. Trewavas, eds. Plasticity in plants. Symposia of the Society for Experimental Biology 40.
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.
———. 1986. Photosynthetic dynamics and plant adaptation to environmental variability. Lectures in Mathematics in the Life Sciences 18:135–169.
———. 1989. Plant physiological ecology: a theoretician's perspective. Pp. 11–24 *in* R. M. May, J. Roughgarden, and S. A. Levin, eds. Perspectives in ecological theory. Princeton University Press, Princeton, N.J.
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. Ann. Eugen. 13:197–205.
Hanson, H. C. 1917. Leaf structure as related to environment. American Journal of Botany 4:533–560.
Harberd, D. J. 1957. The within population variance in genealogical trials. New Phytologist 56:269–280.
Hiesey, W. M., M. A. Nobs, and O. Björkman. 1971. Experimental studies on the nature of species. V. Biosystematics, genetics, and physiological ecology of the *Erythranthe* section of *Mimulus*. Carnegie Institution of Washington Publ. 628.
Hunt, R. 1982. Plant growth curves. University Park Press, Baltimore, Md.
Jain, S. K. 1979. Adaptive strategies: polymorphism, plasticity, and homeostasis. Pp. 160–187 *in* O. Solbrig, S. K. Jain et al., eds. Topics in plant population biology. Columbia University Press, New York.
———. 1990. Variation and selection in plant populations. Pp. 199–230 *in* K. Wohrmann and S. K. Jain, eds. Population biology: ecological and evolutionary viewpoints. Springer, Berlin.
Johannsen, W. 1911. The genotype concept of heredity. American Naturalist 45:129–159.
Kromer, M., and K. L. Gross. 1987. Seed mass, genotype, and density effects on growth and yield of *Oenothera biennis* L. Oecologia 73:207–212.
Lechowicz, M. J., and P. A. Blais. 1988. Assessing the contributions of multiple interacting traits to plant reproductive success: environmental dependence. Journal of Evolutionary Biology 1:255–273.
Levin, D. A. 1988. Plasticity, canalization and evo-

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

lutionary 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. 1963. Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. American Naturalist 97:75–90.

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

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

———. 1974. The analysis of variance and the analysis of causes. American Journal of Human Genetics 26:400–411.

Little, T. M., and F. J. Hills. 1978. Agricultural Experimentation: design and analysis. Wiley, New York.

Lotz, L. A. P., and C.W.P.M. Blom. 1986. Plasticity in life-history traits of *Plantago major* L. ssp. *pleiosperma* Pilger. Oecologia 69:25–30.

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

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

Mitchell, R. S., and J. K. Dean. 1978. *Polygonaceae* of New York State. *In* Contributions to a flora of New York State I. New York State Museum, Bulletin 431. University of the State of New York, Albany.

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

Mooney, H. A., and N. 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.

Osmond, C. B., O. Björkman, and D. J. Anderson. 1980. Physiological processes in plant ecology: toward a synthesis with *Atriplex*. Ecological Studies 36. Springer, Berlin.

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

Price, T., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. Science 240:798–799.

Rice, S. A., and F. A. Bazzaz. 1989a. Quantification of plasticity of plant traits in response to light intensity: comparing phenotypes at a common weight. Oecologia 78:502–507.

———. 1989b. Growth consequences of plasticity of plant traits in response to light conditions. Oecologia 78:508–512.

Roach, D. A., and R. D. Wulff. 1987. Maternal effects in plants. Annual Review of Ecology and Systematics 18:209–235.

Rohlf, F. J., and R. R. Sokal. 1981. Statistical tables, 2d ed. W. H. Freeman, New York.

Roy, J., and H. A. Mooney. 1982. Physiological adaptation and plasticity to water stress of coastal and desert populations of *Heliotropium curassavicum* L. Oecologia 52:370–375.

Schaal, B. A. 1984. Life-history variation, natural selection, and maternal effects in plant populations. Pp. 188–206 *in* R. Dirzo and J. Sarukhán, eds. Perspectives on plant population ecology. Sinauer, Sunderland, Mass.

Scheffé, H. 1959. The analysis of variance. Wiley, New York.

Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. Annual Review of Ecology and Systematics 17:667–693.

Schlichting, C. D., and D. A. Levin. 1984. Phenotypic plasticity of annual *Phlox:* tests of some hypotheses. American Journal of Botany 7(2):252–260.

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

Schmitt, J., and D. W. Ehrhardt. 1990. Enhancement of inbreeding depression by dominance and suppression in *Impatiens capensis*. Evolution 44:269–278.

Simmonds, N. W. 1945. *Polygonum persicaria* L. Entry *in* Biological flora of the British Isles. Journal of Ecology 33:121–131.

Snedecor, G. W., and W. G. Cochran. 1989. Statistical methods, 8th ed. Iowa State University Press, Ames.

Stanton, M. L. 1984a. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. Ecology 65:1105–1112.

———. 1984b. Developmental and genetic sources of seed weight variation in *Raphanus raphanistrum* L. (Brassicaceae). American Journal of Botany 71: 1090–1098.

Stearns, S. C. 1982. The role of development in the evolution of life histories. Pp. 237–258 *in* J. T. Bonner, ed. Evolution and development. Springer, Berlin.

Steele, R.G.D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, New York.

———. 1980. Principles and procedures of statistics, 2d ed. McGraw-Hill, New York.

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*. II. Norms of reaction to soil moisture and the maintenance of genetic diversity. Evolution 47:1032–1049.

———. 1993b. Phenotypic plasticity in *Polygonum persicaria*. III. The evolution of ecological breadth for nutrient environment. Evolution 47:1050–1071.

Taylor, D. R., and L. W. Aarssen. 1988. An interpretation of phenotypic plasticity in *Agropyron re-*

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms

pens (Graminae). American Journal of Botany 75: 401–413.

Tonsor, S. J. 1989. Relatedness and intraspecific competition in *Plantago lanceolata.* American Naturalist 134:897–906.

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.

Trewavas, A. 1986. Resource allocation under poor growth conditions: a major role for growth substances in developmental plasticity. Pp. 31–76 *in* D. H. Jennings and A. J. Trewavas, eds. Plasticity in plants. Symposia of the Society for Experimental Biology 40.

Trexler, J. C., J. Travis, and M. Trexler. 1990. Phenotypic plasticity in the Sailfin Molly, *Poecilia latipinna.* II. Laboratory experiment. Evolution 44: 157–167.

Venable, D. L. 1992. Size-number trade-offs and the variation of seed size with plant resource status. American Naturalist 140:287–304.

Venable, D. L., and J. S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. American Naturalist 131:360–384.

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

Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution 39:505–522.

Vrba, E. S., and S. J. Gould. 1986. The hierarchical expansion of sorting and selection: Sorting and selection cannot be equated. Paleobiology 12:217–228.

Wade, M. J., and S. Kalisz. 1990. The causes of natural selection. Evolution 44:1947–1955.

Watson, M. A., and B. B. Casper. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. Annual Review of Ecology and Systematics 15:233–258.

Westcott, B. 1986. Some methods of analysing genotype-environment interaction. Heredity 56:243–253.

Wilkinson, L., and M. Bjerknes. 1987. Systat version 3.1 for Macintosh. SYSTAT, Evanston, Ill.

Witcombe, J. R., and W. J. Whittington. 1971. A study of the genotype by environment interaction shown by germinating seeds of *Brassica napus.* Heredity 26:397–411.

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

———. 1980. Genic and organismic selection. Evolution 34:825–841.

Wulff, R. D. 1987. Effects of irradience, temperature, and water status on growth and photosynthetic capacity in *Hyptis suaveolens.* Canadian Journal of Botany 65:2501–2506.

Zangerl, A. R., and F. A. Bazzaz. 1983. Plasticity and genotypic variation in photosynthetic behavior of an early and a late successional species of *Polygonum.* Oecologia 57:270–273.

Corresponding Editor: T. Meagher

This content downloaded from 129.133.90.199 on Tue, 19 Apr 2016 18:16:37 UTC
All use subject to http://about.jstor.org/terms