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Physiological response to complex environments in annual *Polygonum* species of contrasting ecological breadth

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Abstract Individual physiological response to complex environments is a major factor in the ecological breadth of species. This study compared individual patterns of both long-term and short-term response to controlled, multifactorial environments in four annual *Polygonum* species that differ in field distribution (*P. cespitosum*, *P. hydropiper*, *P. lapathifolium*, and *P. persicaria*). To test long-term response, instantaneous net photosynthetic rate and stomatal conductance were measured in situ on one full-sib replicate from five inbred lineages from each of five field populations per species, raised in all possible combinations of low or high light; dry, moist, or flooded soil; and poor or rich nutrient status. Short-term plastic adjustment to changes in light level was examined by switching individual plants of the four species from one of six multifactorial growth environments to the contrasting light environment, and measuring assimilation rates 1 h after transfer. The *Polygonum* species differed significantly in their patterns of long-term photosynthetic response to particular resources and resource combinations. The species known to have relatively broad ecological distributions (*P. persicaria* and *P. lapathifolium*) maintained high photosynthetic performance in a variety of moisture and nutrient environments when grown in high light, while the more narrowly distributed P. *hydropiper* maintained such functional levels only if given both high light and ample macronutrients. *P. cespitosum*, a species limited to shaded habitats, maintained low photosynthetic rates across the environmental range. Complex differences among the species in instantaneous water use efficiency (WUE) reflected their highly specific and to some extent independent patterns of photosynthetic and stomatal response to the multifactorial environments. The species also differed significantly in short-term physiological adjustment to changes in light level. Plants of *P. persicaria* and *P. cespitosum* reached 78% and 98%, respectively, of their maximum photosynthetic rates 1 h after transfer from low to high light, but *P. hydropiper* and *P. lapathifolium* plants reached only *c*. 60% of their maximum rates. When switched from high to low light, *P. persicaria* and *P. cespitosum* plants maintained 64–76% of their maximum rates, while *P. hydropiper* and *P. lapathifolium* plants decreased photosynthetic rates sharply to less than 50% of their maximum rates. These results indicate that the latter two species will be less able to maintain effective functional levels in variable light environments, a result consistent with their distributions in the field.

Key words Photosynthetic response · Light acclimation · Phenotypic plasticity · Multiple stresses · Ecological breadth

Introduction

Differences in the ecological distribution of plant species reflect the differing capacities of individuals of those species to maintain function and hence reproductive fitness under diverse environmental conditions. One implication of this fundamental principle is that patterns of individual physiological response to environment are a major element in the realized ecological breadth of species (Bazzaz 1979; Clough et al. 1979; Björkman 1980; Gross 1984; Wulff 1987; Chow et al. 1988; Field 1988; Sultan 1992, 1995; Spencer and Teeri 1994; Mooney et al. 1995; Chazdon et al. 1996; Strauss-Debenedetti and Bazzaz 1996). Many careful studies of physiological response have focused on response to a single limiting resource (Chapin 1991). However, plants in mesic environments encounter combinations of environmental stresses arising from variability in several key resources (Chapin 1991; Bazzaz 1996; and references therein). Because a plant's physiological performance depends jointly on its adjustment to available light, macronutrients, and moisture, the effects of these resources on

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function may be interactive rather than additive (Berry and Downton 1982; Chapin et al. 1987; Bazzaz and Morse 1991; Bazzaz 1996). Studies of physiological response to complex multifactorial environments are thus a critical step toward understanding ecologically meaningful differences among species (Bazzaz 1996).

Photosynthetic rate in particular is a critical aspect of functional performance. Although a plant's lifetime carbon and water balance (and hence fitness) will also be influenced by myriad interacting traits such as allocation to plant organs, morphology and spatial deployment of leaves and roots, and leaf initiation and senescence patterns (Evans and Hughes 1961; Mooney and Chiariello 1984; Pearcy et al. 1987; Field 1988; Givnish 1988; Sims and Pearcy 1991; Ackerly and Bazzaz 1995; Dong 1995), rates of assimilation in a given environment are of clear importance to individual growth and fitness in that environment, and therefore to species distribution (Mooney 1972; Field 1988; Dudley 1996a; and references therein). For traits such as photosynthetic rate that contribute positively to growth, a pattern of high, stable response despite resource variability will maximize fitness across a set of environments (Waddington 1957; Lewontin 1957). Hence, equable (constant or "homeostatic") response patterns for such traits may be associated with broad ecological amplitude (Baker 1965; Bradshaw 1965; discussed in Sultan and Bazzaz 1993c). For example, individuals that maintain high levels of photosynthetic performance in a broad range of favorable and unfavorable environments will be more likely to successfully occupy diverse sites in the field (Spencer and Teeri 1994).

Note that a constant response per se has no necessary relation to ecological breadth, since species that are narrowly restricted to resource-poor environments are often characterized by stable *low* levels of function (Chapin 1991 and references therein). Although measures of response equability alone have been used to infer ecological amplitude (e.g., Levins' 7; Levins 1968), response patterns must be evaluated qualitatively as well as quantitatively: an ecologically meaningful assessment of physiological response must consider both effective utilization of resources when they are available (i.e., high photosynthetic rates in favorable conditions), and the maintenance of function close to this high level despite resource limits (Wulff 1987; Sultan and Bazzaz 1993a). For instance, a species that is unable to metabolically exploit favorable nutrient levels, or alternatively, that has high assimilation rates when ample nutrients are available but severely reduced rates in poorer soils, will be unlikely to maintain competitively viable growth rates and hence establish populations in both nutrient-rich and nutrient-poor conditions. Thus, high levels of function in favorable conditions as well as performance equability are relevant to ecological breadth.

Clearly, the range of habitats a species may potentially colonize is limited by the physiological breadth of its individuals (realized species distribution will depend as well on dispersability and biotic interactions such as competition; Colwell and Futuyma 1971). A species' habitat range is also determined by individual physiological response to the environmental variability that occurs *within* sites, since a species may be excluded from a habitat if variation in that habitat exceeds the range in which individuals of the species function well. Because resource levels vary at small spatial scales (Bazzaz and Sultan 1987; Bazzaz and Wayne 1994), individuals in a population must be able to function successfully across the range of microsites they may encounter through dispersal (Levins 1968; Sultan 1987). As with among-habitat environmental variation, tolerance of spatial variability within habitats depends on *long-term* aspects of response, i.e., the production in a given, constant microsite environment of a functionally effective phenotype.

Individual plants in many terrestrial habitats also encounter dramatic temporal variability in resource levels, often on a scale of hours or minutes (Levins 1968; Benner and Bazzaz 1988; Wayne and Bazzaz 1993). Such short-term variation in light is particularly ubiquitous, due to transient, shifting patterns of illumination and shadow (Gross 1986; Pearcy 1988; Field 1988; Anderson et al. 1988; Bell and Lechowicz 1991). Although less well studied than response to constant conditions (Osmond and Chow 1988; Bazzaz 1996), *short-term* physiological responses of individual plants to rapid changes in light environment are also of key importance to ecological distribution (Chazdon and Pearcy 1991; Strauss-Debenedetti and Bazzaz 1991; Pearcy 1988; Chazdon et al. 1996; Bazzaz 1996). A species' ability to occupy temporally variable habitats will be influenced by two aspects of short-term photosynthetic response ("acclimation" *sensu* Strauss-Debenedetti and Bazzaz 1991; Chazdon et al. 1996). Species may differ in the extent to which previously shaded plants can rapidly increase photosynthetic activity so as to utilize intense light at close to maximal rates (Fitter and Hay 1987); prior nutrient and moisture status may also differently affect species' abilities to respond effectively to increased light (Bazzaz 1996). Species may also differ in their abilities to maintain effective photosynthetic rates during periods of decreased light intensity (see Chazdon et al. 1996). Long- and short-term physiological response thus correspond respectively to spatial and temporal aspects of environmental variability (Anderson et al. 1988). Both types of individual response are important factors in the ability of species to occupy diverse and variable field environments.

Comparative studies of physiological response to both long and short-term variation in multifactorial resource levels are a key means to illuminate the basis of ecologically broad versus narrow species distributions. However, such studies are quite laborious and hence rare. Furthermore, comparative studies of ecological breadth are often hindered by inadequate information regarding field distributions for key resources, and by confounding factors such as annual versus perennial life-history, or phylogenetic constraints (Schlichting and Levin 1986; Bazzaz 1987; Strauss-Debenedetti and Bazzaz 1991; but see Field 1988; Chazdon 1992; Mulkey et al. 1993 for comparative studies of tropical woody taxa that avoid these problems). This study focuses on instantaneous photosynthetic response to multifactorial environments to examine the relation between patterns of physiological response and ecological breadth in a model system. We compare the photosynthetic responses of four *Polygonum* species of contrasting ecological breadth to factorial combinations of low and high levels of light, moisture, and soil macronutrients.

The species constitute a well-studied comparative system that avoids the above-mentioned problems. *Polygonum persicaria*, *P. lapathifolium*, *P. hydropiper*, and *P. cespitosum* are closely related taxa within the monophyletic section *Persicaria* (Mitchell and Dean 1978; Weber and Wittman 1992). The four species share an identical life-history as obligately annual herbs of disturbed habitats, but differ markedly in ecological distribution with respect to light, moisture, and soil nutrient content (details in Sultan et al. 1998). The field distribution of *P. persicaria* covers the broadest environmental range: from full sun to moderate shade with occasional dark microsites, from flooded to extremely dry conditions, and from highly organic, nutrient-rich to extremely nutrient-poor soils. *P. lapathifolium* also occurs in a broad range of moisture and nutrient conditions, but is found only in high light habitats. *P. hydropiper* is narrowly restricted to high-light sites that also have highly organic, nitrogen-rich, and consistently moist or flooded soils. In contrast to these species, *P. cespitosum* is restricted to low-light habitats with consistently moist soils that do not flood (e.g., shaded roadsides and forest trails).

We address the following specific questions:

1. Do individuals of the four *Polygonum* species differ in patterns of photosynthetic response to high and low light, moisture, and nutrient levels?
2. Are the species differences in response to these resources additive or interactive (complex)?
3. Do the species differ in their abilities to maintain high levels of physiological performance in different constant and short-term environments?
4. Are these differences in response patterns consistent with the species' known differences in field distribution?

We evaluated individual physiological performance by comparing the ability of inbred replicates from a broad sample of lineages of each species to maintain high photosynthetic rates across the range of favorable and unfavorable resource levels. We examined photosynthetic response to both spatial and temporal environmental variation by testing long-term, in situ responses of plants raised in a given multifactorial "microsite" (experiment 1), as well as short-term plasticity of plants switched briefly from their growth environment to a contrasting light level (experiment 2). We also measured stomatal conductance, a key indicator of plant water status (Davies and Zhang 1991) and calculated water use efficiency, to more fully characterize species differences in patterns of physiological response.

Materials and methods

Experimental sample

Achenes were collected (September 1994) from five well-established populations of each species representing its range of habitats in northeastern North America (see Sultan et al. 1998 for characterization of field sites). Achenes collected from eight field parents per population were raised to maturity under uniform glasshouse conditions and inbred to provide selfed full-sib replicate achenes, using the following protocol. Achenes were stratified for 3 weeks in distilled water at 4°C, germinated in petri dishes in a dilute fungicide solution (20 November 1994), and planted singly into clay pots filled with a 5:2 mixture of sterile Promix and coarse sand. Two seedlings from each field family were grown to maturity in a random array in the glasshouse (temperature 21–24°C day/18–21°C night): plants were kept moist, fertilized once with Peters 20:20:20 NPK solution, and given supplementary high-intensity discharge (HID) lighting between 0700 and 1800 hours when external photosynthetically active radiation (PAR) fell below 700 μE.

Experiment 1

Environmental treatments

Twenty mature replicate achenes were collected from one glasshouse-grown offspring of each field parent (see above), stratified for 6 weeks at 4°C, and germinated in flats of moist vermiculite (5 April 1995). Five of these inbred seedling families (each descended from a different field grandparent) were randomly chosen from each population (in the case of *P. hydropiper*, certain families with slow germination were excluded), for a total sample of 5 families × 5 populations × 4 species ($n = 100$ families). One inbred replicate seedling of each family was randomly assigned to each of 12 environmental treatments (total $n = 1200$ plants, one plant per family in each treatment). Treatments consisted of all possible combinations of high or low light; dry, moist, or wet (flooded) soil; and rich or poor nutrients, for a total of 12 combinatorial treatments (see Table 1 for factor levels). Each seedling was transplanted into a pre-filled 10-cm clay pot and set in an assigned random position on one of five two-bench glasshouse blocks, in a randomized complete block design (28 April 1995).

Each experimental block included an open plot (high light; H) and a shaded plot (low light; L). Each shaded plot consisted of a bench over which was suspended an adjustable aluminum tubing frame, the top and sides of which were covered with black plastic neutral-density shade cloth (80% grade, Dewitt Co., Florist Products, Schaumburg, Ill., USA). Moisture treatments were maintained by an automatic system that delivered reverse-osmosis-filtered water to 1 (dry; D), 2 (moist; M), or 4 (wet; W) Chapin watering tubes per pot via central feeder pipes on each bench plumbed to solenoid valves. The system was programmed to release 10 ml of water per tube daily at 0700 and 1100 hours, and on H benches additionally at 1400 hours, for daily per-pot totals of 30 ml (HD treatment), 60 ml (HM), 120 ml (HW), 20 ml (LD), 40 ml (LM), and 80 ml (LW). Watering volume on the H benches was increased on day 30 to 40 ml (HD), 80 ml (HM) and 160 ml (HW). Plants in the W treatment were submerged in 1-gallon white plastic tubs filled with water to within 2 cm of soil level; water levels in these tubs were manually maintained. Plants in the L treatment experienced equal or lower soil moisture than those in high light, so low light and higher moisture were not confounded as they are in many field situations. All plants were kept evenly moist for the first 5 days of the experiment to ensure establishment; on overcast days the watering system was run only as required to maintain consistent soil moisture treatments. Nutrient treatments consisted of 800 ml per pot of a 1:1:1 mixture of sterilized sandy loam: coarse sand: Turface fritted clay, with either no added nutrients (poor; P) or an addition of 2.5 g per pot of granular 15:8:12 NPK fertilizer (Agway Co.) (rich; R). Plants in all treatments were

Table 1 Experimental treatment levels

Light ($\mu E\ m^{-2}\ s^{-1}$)	Moisture (% H_2O by weight)	Nutrients (ppm)
Low (L) 185 ± 40	Dry (D) 13.2 ± 5.8%	Poor (P) NH_4 = 2, P = 5, K = 118
High (H) 1239 ± 108	Moist (M) 26.6 ± 4.1%	Rich (R) NH_4 = 46, P = 17, K = 310
	Wet (W) 48.1 ± 2.3%	

Light treatment means ± SDs are based on a random sample of 60 measurements per light treatment (12 per block) made with a Licor quantum sensor on 7 July 1995 between 1300 and 1330 hours (n = 120 measurements): low-light plots average 14.5% of PAR available in high-light (full-sun) plots. Moisture treatment means ± SDs are based on soil samples collected at 5 cm depth from 1 pot per species per factorial treatment combination, for a sample of 16 pots per moisture treatment (n = 48 samples). Within-bench variation was tested by measuring the volume of water emitted from 20 tubes on each bench to verify that the standard deviation among tubes was less than 5%. Nutrient treatment levels are based on Morgan-extraction soil analyses of a mixed sample collected prior to planting from 3 pots per nutrient treatment (University of Massachusetts Soil Testing Laboratory Amherst, Mass., USA). Macronutrient levels in the poor treatment corresponded to moderate potassium, low phosphorus, and very low ammonium levels for natural soils in this region; the rich treatment corresponded to a high phosphorous level, and in both potassium and ammonium was roughly double the level considered high for such soils (Fellows 1981)

kept at 22°C day/ 19°C night (ranges 21–24°C and 18–21°C); daily 24-h mean relative humidity ranged from 52% to 82% and did not differ significantly among blocks (J. Tufts, unpublished work).

Data collection

Physiological measurements were made on mature plants between 1000 and 1500 hours on 18 sunny days between 17 June and 20 July 1995, one experimental block at a time. Instantaneous net photosynthetic rate and stomatal conductance were measured in situ on the newest fully-expanded leaf of each plant, using a Licor 6200 portable photosynthesis system with 0.25-L chamber (Li-COR Inc., Lincoln, Neb., USA). Each measurement consisted of a mean of three successive measurements taken on the same leaf while enclosed in the chamber; total change in chamber relative humidity was $<1\%$ during the measurement. Only measurements collected under the following conditions were considered in the final data set: incident radiation 90–270 $\mu E\ m^{-2}\ s^{-1}$ (L treatment) or $>$ 900 $\mu E\ m^{-2}\ s^{-1}$ (H treatment; light saturation in these species occurs at *c.* 800 $\mu E\ m^{-2}\ s^{-1}$, S. Sultan unpublished work); initial ambient CO_2 330–380 ppm; and chamber relative humidity between 40% and 67% and within 3% of ambient glasshouse humidity. Data from wilted or senescent leaves were discarded; conductance data were discarded for one day (21 June) due to a programming error in one channel of the system. Leaf areas were determined by tracing the portion of each leaf enclosed in the chamber and measuring these tracings with a Licor LI-3100 moving-belt leaf area meter (Licor, Inc.). Instantaneous water use efficiency (WUE) was calculated for each plant as the ratio of photosynthetic rate to stomatal conductance (Dudley 1996a). It was not possible to remove photosynthetic rate from this analysis as a covariate to test rate-independence of WUE using ANCOVA, because photosynthetic rate itself varied significantly among environmental treatments (Winer 1971, pp. 753–755). Instantaneous WUE was therefore analyzed as a distinct ratio trait using ANOVA, after square-root transforming the data to meet the requisite assumptions.

Experiment 2

Environmental treatments

Mature, inbred achenes were collected from one glasshouse-grown offspring of a single field parent randomly chosen from each of four populations per species, stratified in vials of distilled H_20 for 6 weeks at 4°C, and sown into flats of moist vermiculite. Flats were randomized on two benches in a glasshouse maintained at 24°C day/20°C night (18 March 1996), for a total of 16 experimental families (1 family per population × 4 populations per species × 4 species). *P. hydropiper* achenes were scarified prior to sowing to promote synchronous germination. One inbred full-sib seedling replicate from each experimental family was randomly assigned to each of six environmental treatments, transplanted into a pre-filled 10-cm clay pot, and set in an assigned random position on one of four glasshouse blocks (11 April 1996), for a total sample of n = 96 plants (1 plant per family per treatment). Plants were kept uniformly moist for the initial 4 days of the experiment, and then grown to maturity in the following six combinatorial treatments: moist/rich, dry/rich, and moist/poor soil in both low and high light (treatment design and levels were as described for experiment 1, except that mean soil moisture in the dry, moist, and wet treatments were 8.0 ± 3.2%, 32.3 ± 3.7%, and 49.2% ± 2.6% respectively).

Data collection

Physiological measurements were made on mature plants between 0930 and 1530 hours during 8 sunny days between 1 June and 15 June 1996, one experimental block at a time. First, instantaneous net photosynthetic rate was measured in situ on the newest fully expanded leaf of each plant, as described above. Plants were then transferred to the contrasting light treatment, allowed to equilibrate for 1 h, and then measured under the "switched" light conditions. Thus, plants grown at high light, moist soil, and rich nutrients were measured both at high light and after transfer to low light; plants grown at low light, moist soil, and rich nutrients were measured both in low light and after transfer to high light, and the same for plants grown in dry/rich and moist/poor soil at the two light levels. Leaves of plants in the high/moist/poor treatment were beginning to senesce; as this was equally true in all four species it did not affect species rank order. Only measurements collected under the following conditions were considered in the final data set: incident radiation of 200–320 $\mu E\ m^{-2}\ s^{-1}$ (L) or >1100 $\mu E\ m^{-2}\ s^{-1}$ (H); initial ambient CO_2 320–380 ppm; and chamber relative humidity between 40% and 70% and within 3% of ambient glasshouse humidity.

Results

Experiment 1: functional performance in long-term factorial environments

Species differences in photosynthetic response

Leaf-level net photosynthetic rate on an area basis was strongly affected by light, nutrient, and moisture level, and by the interactive effects of all three environmental factors (Table 2). The species differed overall, due largely to the consistently low photosynthetic rates of *P. cespitosum* plants (Fig. 1). In addition, the specific patterns of response to contrasting levels of each resource differed among the species (significant two-way interactions of species by environmental factor; Table 2). The species differed markedly in response to light level: *P. cespitosum* plants increased photosynthetic rate by only one-third in high (100%) compared with low (15%) light, while assimilation rates doubled in all three of the remaining species (Fig. 1).

Significant complex interactions indicate that the *Polygonum* species differed in their photosynthetic responses to particular combinations of resource states; i.e., the species differences in response to light depended on both nutrient and moisture availability (species × light × nutrient effect and species × light × moisture effect, Table 2). Plants of *P. persicaria* and *P. lapathifolium* increased photosynthetic rates at high light even in nutrient-poor soil (Fig. 2a, b). In contrast, unless they were also given high nutrients, *P. hydropiper* plants increased photosynthetic rates in high light only very slightly, and *P. cespitosum* plants not at all (Fig. 2c, d).

The *Polygonum* species also responded differently to specific combinations of light and moisture. In all four species, the effect of moisture treatment on photosynthetic rate was not significant in low light, where assimilation rates were strongly reduced regardless of soil moisture ($0.096 \leq P \leq 0.489$ in separate ANOVA for each species; see Tukey's tests for moisture effect within the L treatment, Fig. 3a-d). In high light, plants of *P. persicaria*, *P. lapathifolium*, and *P. hydropiper* grown in dry soil increased photosynthetic rates most steeply (Fig. 3a–c). In *P. cespitosum*, both dry- and moist-grown plants increased assimilation rate only marginally in high light compared with plants in the wet treatment. Note that the non-significant Tukey's tests for moisture effect within the H treatment for *P. hydropiper* and *P. cespitosum* reflect the enormous variance due to nutrient treatment (cf. Fig. 2c, d).

Differences among the species in photosynthetic response patterns were highly specific to multi-factor conditions (see nearly significant four-way interaction of species × light × moisture × nutrients; Table 2). For example, although all four species decreased photosynthetic rates slightly in the high/moist/poor treatment compared with high/wet/poor conditions, *P. lapathifolium* and especially *P. persicaria* sharply increased assimilation in the high/dry/poor treatment, while in contrast *P. hydropiper* and *P. cespitosum* plants decreased photosynthesis slightly in this treament (Fig. 4).

Table 2 Effects of species and environmental factors on photosynthetic rate. (n = 677; squared multiple r of ANOVA model = 0.768)

Source	*df*	MS	*F* ratio	*P*
Species	3	498.54	94.33	**0.000**
Light	1	3731.12	705.99	**0.000**
Moisture	2	121.10	22.91	**0.000**
Nutrients	1	1865.16	352.92	**0.000**
Block	3	4.391	0.83	0.477
Light × moisture	2	156.42	29.60	**0.000**
Light × nutrients	1	737.41	139.53	**0.000**
Moisture × nutrients	2	22.11	4.18	**0.016**
Light × moist × nutrients	2	19.05	3.61	**0.028**
Species × light	3	330.32	65.50	**0.000**
Species × moisture	6	46.49	8.80	**0.000**
Species × nutrients	3	30.17	5.71	**0.001**
Sp × light × moisture	6	34.55	6.54	**0.000**
Sp × light × nutrients	3	59.39	11.24	**0.000**
Sp × moisture × nutrients	6	8.18	1.55	0.160
Sp × light × moist × nutrients	6	10.27	1.94	0.072
Population (within sp)	16	7.10	1.34	0.165

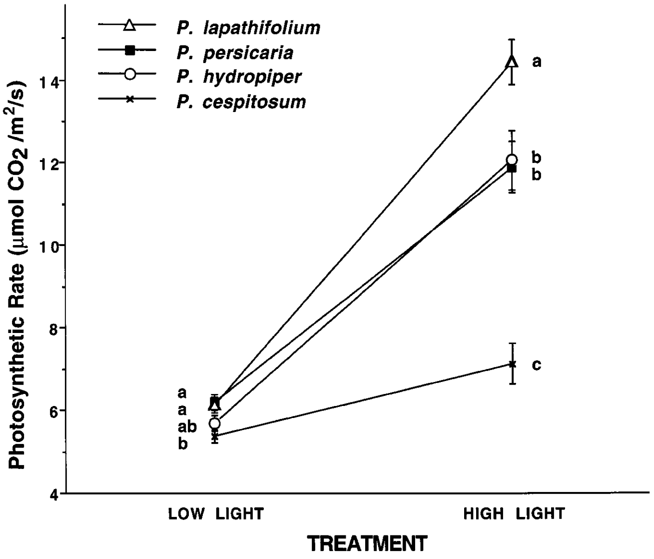


Fig. 1 Photosynthetic rates of *Polygonum* species in contrasting light environments. Means and standard errors of each species in low and high light (means in low light include plants in LDP, LDR, LMP, LMR, LWP, and LWR treatments; same for high light (*L* low light, *H* high light, *D* dry soil, *M* moist soil, *W* wet soil, *P* poor nutrient status, *R* rich nutrient status)). Results are shown of Tukey's pairwise multiple comparison test for species differences within each light level; species marked with the same *letter* do not differ at a probability of $P \leq 0.05$

Species' photosynthetic performance across the environmental range

To assess the ability of each species to maintain photosynthetic performance across the range of experimental environments, its mean photosynthetic rate in each treatment was adjusted as a percentage of that species' highest treatment mean (i.e., the mean rate at the HDR treatment for *P. persicaria*, *P. hydropiper*, and *P. lapathifolium*, and the mean for the HWR treatment in *P. cespitosum*). According to this performance index, plants of *P. persicaria* and *P. lapathifolium* photosynthesized at > 50% of their respective maximum rates in five of the six high-light treatments, but *P. hydropiper* and *P. cespitosum* exceeded 50% of their maximum rates in only three of the six H treatments. The equability of photosynthetic performance across the 12 environments can be described by summing the 12 adjusted treatment means ("Adler's *F*"; F. Adler, personal communication; this index is similar to Levins' β for niche breadth but does not differently weight treatment responses by

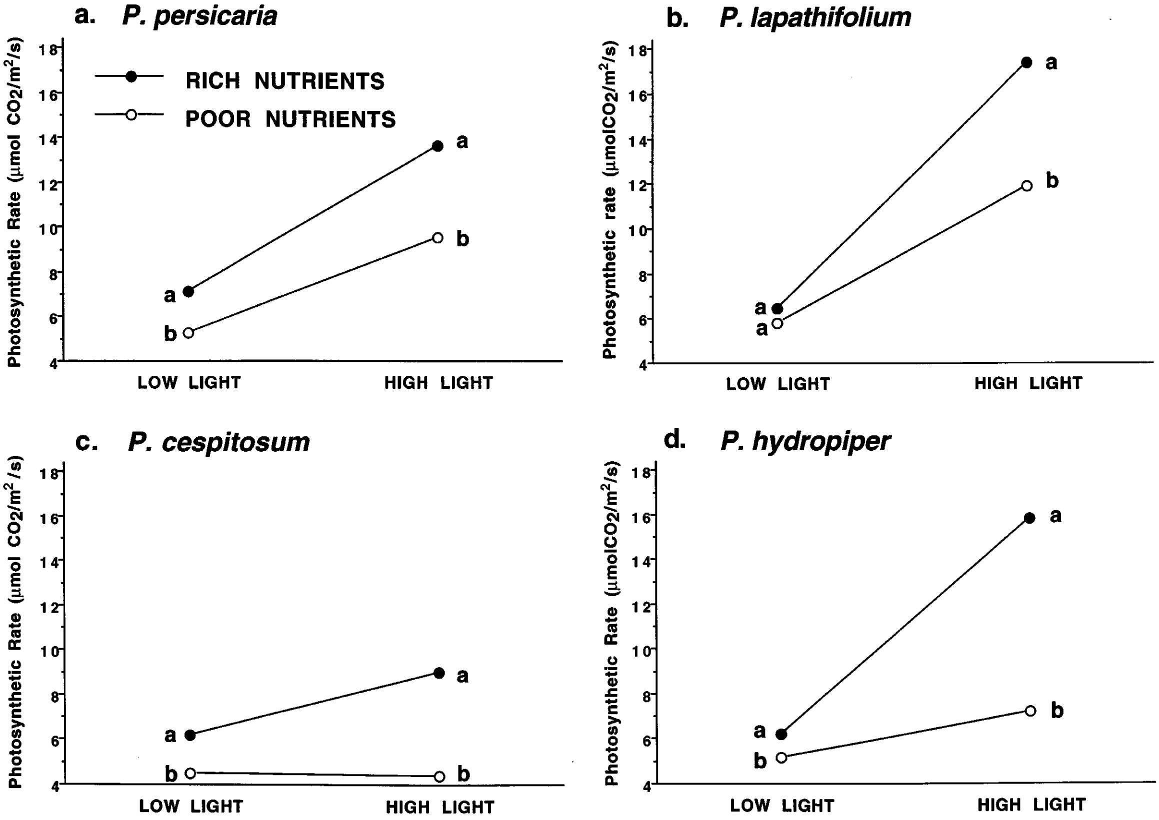


Fig. 2 Effect of nutrient treatment on photosynthetic response to high and low light. Mean photosynthetic rate of each species in factorial combinations of rich NPK, poor NPK, high light, and low light (means include plants in dry, moist, and wet treatments for each light and nutrient combination). Results are shown of Tukey's pairwise multiple comparison test for nutrient effect within each light level; species marked with the same *letter* do not differ at a probability of $P \leq 0.05$

squaring the adjusted means). According to this index, *P. cespitosum* shows the most even photosynthetic performance across the environmental range (i.e., a flat, low response pattern; Adler's $F = 667$). Of the species that show high photosynthetic rates in favorable conditions, the rank order for performance equability is :

P. persicaria ($F = 625$) > *P. lapathifolium* ($F = 551$) ≥ *P. hydropiper* ($F = 544$).

Species differences in stomatal conductance and WUE

Significant differences in stomatal conductance among the *Polygonum* species mirrored the rank order differences in photosynthetic rate shown in Fig. 1: averaged across environments, conductance in *P. lapathifolium* > *P. persicaria* = *P. hydropiper* > *P. cespitosum* (all pairwise comparisons significant at $P \leq 0.000$ according to Tukey's tests except *P. hydropiper* vs. *P. persicaria* $P \leq 0.25$). In addition, conductance was strongly affected by environmental treatments and their interactive effects, as well as by block (due to variation in relative humidity among measurement days; Table 3). Note that these treatment-dependent changes in conductance were not always correlated with changes in photosynthetic rate. For instance, all species decreased stomatal conductance in the dry treatment relative to plants in moist and wet soil (Fig. 5; see increased photosynthetic rates in dry treatment; Fig. 3a, b, d). Furthermore, the species differed in patterns of stomatal response to the environmental treatments (cf. significant two- and three-way interactions of species × environmental factor; Table 3). For example, *P. persicaria* plants showed the greatest increase in conductance in wet compared with moist soil (Fig. 5; see significant species × moisture effect, Table 3), and the least change between high and low light (cf. significant species × light effect, Table 3).

WUE also varied significantly among the environmental treatments in species-specific patterns (Table 4). This reflects the above-noted fact that differences among environments in photosynthetic rate were not always accompanied by like changes in conductance (shown graphically in Fig. 6; note that treatment means for photosynthesis plotted against conductance do not fall on the single, rate-dependent line predicted by the species mean). All four species maintained similar WUE in moist compared with wet soil, and increased WUE sharply in the dry treatment (Fig. 7).

Experiment 2: short-term photosynthetic response to contrasting light conditions

Plants of the four species grown in a subset of the factorial treatments showed the same rank order for in situ

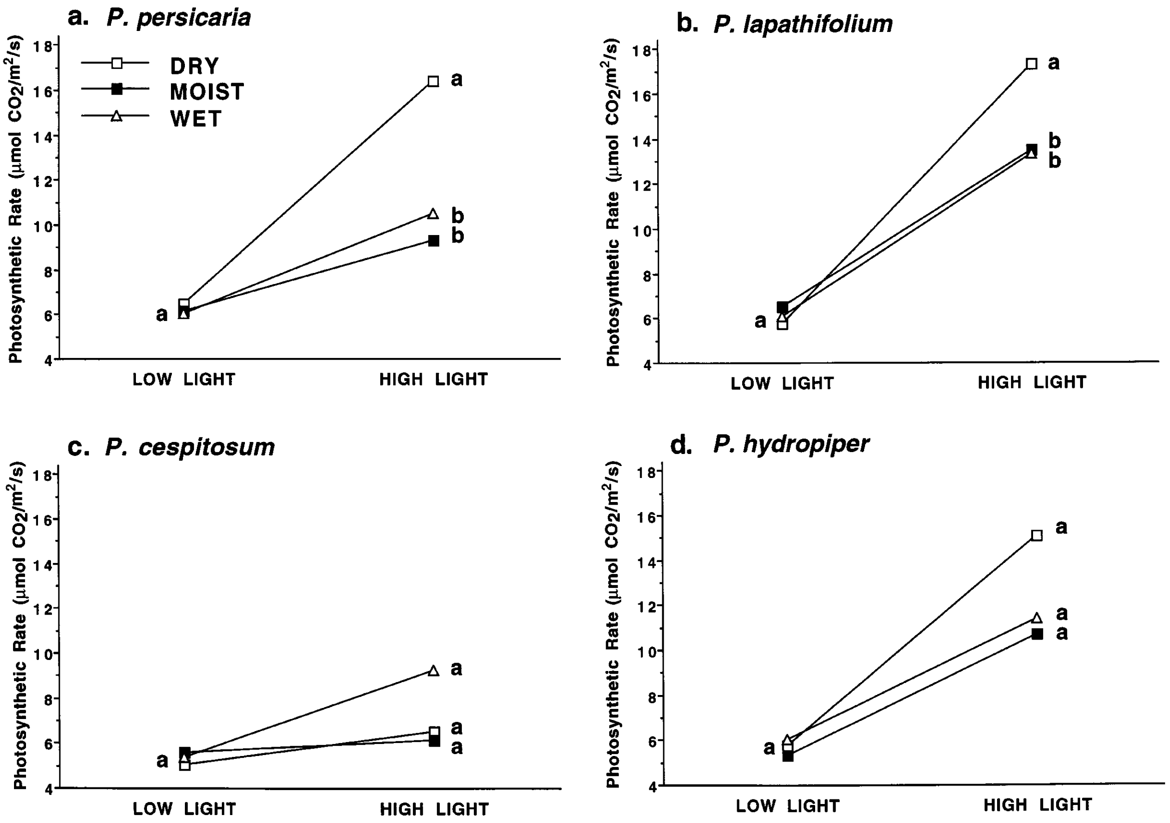


Fig. 3 Effect of moisture treatment on photosynthetic response to high and low light. Mean photosynthetic rate of each species in factorial combinations of dry soil, moist soil, wet soil, high light, and low light (means include plants in poor NPK and rich NPK treatments for each light and moisture combination). Results are shown of Tukey's pairwise multiple comparison test for moisture effect within each light level; species marked with the same *letter* do not differ at a probability of $P \leq 0.05$

photosynthetic response to those treatments as in Experiment I (compare Figs. 8a and 1; effects of species, treatment, and species × treatment on photosynthetic rate in situ were significant at $P \leq 0.001$ according to 2-way fixed ANOVA, $n = 171$). The species differed significantly in their short-term photosynthetic response to transfers from low to high light and from high to low light (effect of species on photosynthetic rate of switched plants significant at $P \leq 0.001$, $n = 83$). Specifically, *P. hydropiper* plants showed strongly reduced photosynthetic rates following transfer to contrasting light conditions, such that transferred plants of this species did not differ significantly in photosynthetic rate from those of *P. cespitosum* (linear contrast of *P. cespitosum* vs. *P. hydropiper* switched plants NS at $P \leq 0.600$; Fig. 8b).

Differences among the species in short-term photosynthetic plasticity are most clear when the photosynthetic rates of transferred plants of each species are expressed relative to that species' maximum rate; in this experiment, the mean rate of plants in constant High light (as shown in Fig. 8a; Fig. 9 shows the mean rates of transferred plants of each species as a percent of the relevant species' maximum). The species differed significantly in the percent of maximum rate achieved by transferred plants ($P \leq 0.001$). One hour after transfer, *P. persicaria* and *P. cespitosum* plants switched from low to high light reached 78% and 98% of their maximum photosynthetic rates, while low-light grown plants of *P. lapathifolium* and *P. hydropiper* functioned at only *c.* 60% of their maximum rates after transfer to high light (Fig. 9). *P. hydropiper* plants increased photosynthetic rate only marginally in response to increased light (Fig. 9). Note that the very steep change in *P. lapathifolium* reflects the species' extremely low relative photosynthetic rate in constant low light (Fig. 9). Similarly, the photosynthetic rates of plants switched from high to low light decreased more sharply in the latter species than in *P. persicaria* and *P. cespitosum*, which respectively maintained 64% and 76% of their maximum rates after transfer to low light (Fig. 9).

There was no significant effect of previous moisture environment (dry vs. moist) on the photosynthetic rate of plants switched from low to high light (effect of growth moisture treatment NS at $P \leq 0.48$; species × moisture interaction effect also NS at $P \leq 0.48$). This may partly reflect the low sample size for these tests ($n = 23$). In contrast, plants of all species given low nutrients showed reduced photosynthetic rates when switched from L to H (effect of poor vs. rich nutrient growth conditions significant at $P \leq 0.012$, $n = 30$). The magnitude of this effect was similar in all species (species × nutrient interaction NS at $P \leq 0.710$). As a result, the effect of prior nutrient treatment did not alter

Fig. 4 Species differences in photosynthetic response to moisture level of plants in high light, poor NPK environments. Mean photosynthetic rate with standard error of each species in high light, poor NPK, and either dry, moist, or wet soil (means based on *c.* 10 plants per species per combinatorial treatment)

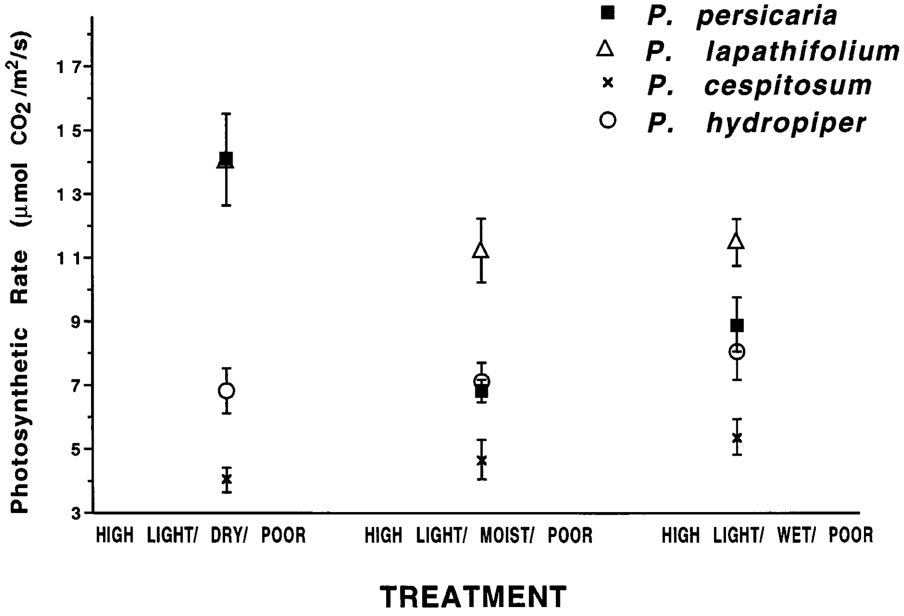


Table 3 Effects of species and environmental factors on stomatal conductance. Data were transformed according to the equation $x' = \sqrt{(x + 1)}$. Six outliers were deleted. (n = 559; squared multiple r of ANOVA model = 0.615)

Source	*df*	MS	*F* ratio	*P*
Species	3	498.54	94.33	**0.000**
Light	1	3731.12	705.99	**0.000**
Moisture	2	121.10	22.91	**0.000**
Nutrients	1	1865.16	352.92	**0.000**
Block	3	4.391	0.83	**0.000**
Light × moisture	2	156.42	29.60	**0.000**
Light × nutrients	1	737.41	139.53	0.075
Moisture × nutrients	2	22.11	4.18	**0.000**
Light × moist × nutrients	2	19.05	3.61	0.550
Species × light	3	330.32	65.50	**0.001**
Species × moisture	6	46.49	8.80	**0.001**
Species × nutrients	3	30.17	5.71	0.336
Sp × light × moisture	6	34.55	6.54	**0.006**
Sp × light × nutrients	3	59.39	11.24	**0.002**
Sp × moisture × nutrients	6	8.18	1.55	**0.017**
Sp × light × moist × nutrients	6	10.27	1.94	0.263
Population (within sp)	16	7.10	1.34	0.098

the rank order of switched plants described above: among LMP plants transferred to high light, *P. persicaria* and *P. cespitosum* photosynthesized at 70% and 82% of their respective maximum rates, while *P. hydropiper* and *P. lapathifolium* reached only 55% and 57%, respectively.

Discussion

An important result of the study was that differences among annual *Polygonum* species in patterns of physiological response to environment were extraordinarily complex (though statistically robust). The magnitudes and patterns of photosynthetic response to one environmental factor were contingent on other factors. Moreover, the species differed in how they altered photosynthesis, stomatal conductance, and hence WUE in response to highly specific combinations of light, moisture, and nutrients. In other words, the availability of each one of the resources affected the four species differently; furthermore the effects of all three resources on species function were interactive rather than additive (Tables 2–4). Thus, to the extent that photosynthetic performance influences growth and hence relative fitness, patterns of individual response to combinatorial states of these environmental factors are implicated in the realized distribution of the species. Although multifactorial data are seldom available, the field distribution of many plant species may well reflect complex physiological responses to several variable resources, rather than response to a single, apparently dominant resource such as light or moisture alone (Chapin et al. 1987; Bazzaz and Morse 1991). This complexity has important implications for studies of the competitive and coevolutionary species interactions that shape ecological communities (Bazzaz 1996).

One such ecologically relevant complex response was the different effect of particular combinations of light and nutrient levels on photosynthetic rates in the four species (Fig. 2). Specifically, the ability to significantly increase assimilation rate in high light depended on ample macronutrient supply in *P. hydropiper and P. cespitosum*, while plants of *P. lapathifolium* and *P. persicaria* substantially increased photosynthetic rates even in nutrient-poor soil. The restriction of *P. hydropiper* in the field to sites that are both open and nutrient-rich (early-season mean canopy PAR 82–99%, mean soil cation exchange capacity ≥ 12.5, and nitrate content ≥ 8.3 ppm; Sultan et al. 1998) may reflect the fact that plants of this species effectively utilize high light only with ample nutrient supplies. In contrast, plants of

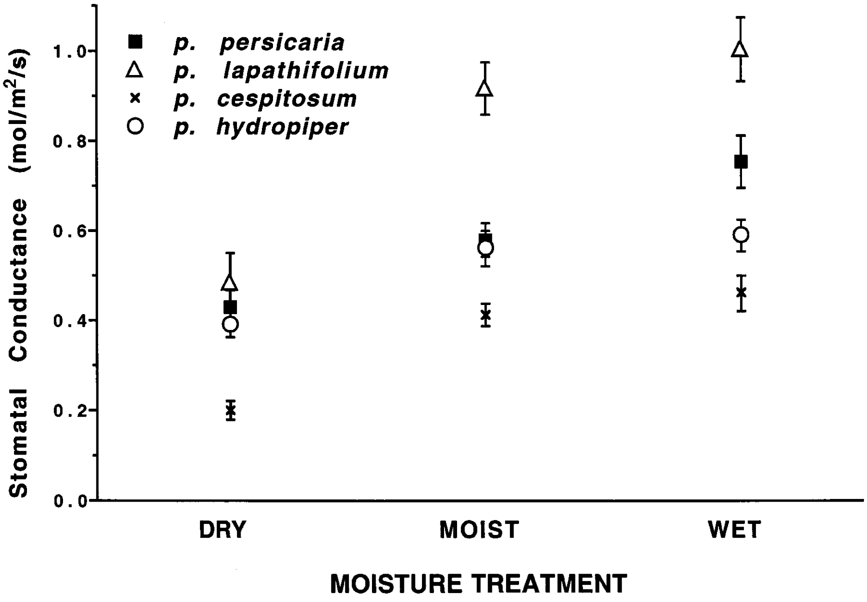


Fig. 5 Stomatal conductance rates of four *Polygonum* species in contrasting environments. Means and standard errors for stomatal conductance of each species in dry, moist, and wet treatments (means in each moisture treatment include plants in all combinations of high light, low light, rich NPK, and poor NPK)

Table 4 Effects of species and environmental factors on water use efficiency. Data were transformed according to the equation $x' = \surd(x + 1)$. Six outliers were deleted. (n = 559; squared multiple r of ANOVA model = 0.648)

Source	*df*	MS	*F* ratio	*P*
Species	3	498.54	94.33	**0.000**
Light	1	3731.12	705.99	**0.000**
Moisture	2	121.10	22.91	**0.000**
Nutrients	1	1865.16	352.92	**0.000**
Block	3	4.391	0.83	**0.000**
Light × moisture	2	156.42	29.60	**0.005**
Light × nutrients	1	737.41	139.53	**0.000**
Moisture × nutrients	2	22.11	4.18	**0.000**
Light × moist × nutrients	2	19.05	3.61	0.198
Species × light	3	330.32	65.50	**0.008**
Species × moisture	6	46.49	8.80	**0.001**
Species × nutrients	3	30.17	5.71	**0.001**
Sp × light × moisture	6	34.55	6.54	**0.033**
Sp × light × nutrients	3	59.39	11.24	0.815
Sp × moisture × nutrients	6	8.18	1.55	**0.000**
Sp × light × moist × nutrients	6	10.27	1.94	0.562
Population (within sp)	16	7.10	1.34	0.202

P. persicaria and *P. lapathifolium* occur in open sites that are nutrient-poor as well as those that are nutrient-rich (e.g., *P. persicaria* LP site, with early-season mean PAR of 99% and nitrate content 3.0 ppm; *P. lapathifolium* WP site with 97% canopy PAR and 3.7 ppm soil nitrate; Sultan et al. 1998). (The exclusion of *P. cespitosum* from open sites may be partly due to its inability to physiologically exploit high levels of PAR relative to neighbors even in the presence of ample nutrients).

It is well known that carbon assimilation depends on both light availability and mineral supply, and that nitrogen limitation in particular has a greater negative impact in high light (Mooney and Gulmon 1979; Osmond 1983; Field and Mooney 1986; Field 1988; but see Chapin 1991). However, the mechanisms by which closely related taxa may be more or less physiologically constrained by this interactive effect are still poorly understood (Mooney et al. 1995). Individuals of species such as *P. persicaria* and *P. lapathifolium* may be better able to maintain leaf nitrogen supplies, possibly by means of plastic adjustments to root systems (Sultan and Bazzaz 1993c; Hilbert et al. 1991), more effective translocation of minerals within the plant body (Aerts and Caluwe 1994), or greater plasticity for nitrogen allocation to different functions within the leaf (Chazdon et al. 1996).

Note that the maintenance of relatively constant, high photosynthetic performance across a range of resource levels is the result of functionally adaptive phenotypic alteration of underlying mechanistic traits. Instantaneous net photosynthetic rate in a given environment reflects the plant's allocational, anatomical, biochemical, ultrastructural, and stomatal adjustment to environmental factors such as macronutrient supply, water availability, and photon flux density (Berry and Downton 1982; Pearcy et al. 1987). Hence plants that maximize nitrogen acquisition and efficiency by plastic adjustments in root morphology and deployment, mineral translocation, and leaf biochemistry can maintain relatively high photosynthetic rates in low- as well as high-nitrogen soils (see Field and Mooney 1986; Chapin et al. 1987; Hilbert 1990). In general, photosynthetic *constancy* across environments is made possible by adaptive *plasticity* for these specific, underlying traits. A high, relatively stable level of function in diverse environments thus indicates the existence of adaptive phenotypic plasticity in traits that contribute to function, which may be extremely difficult to measure directly. Although it may seem paradoxical, promoting constancy in key fitness-related traits despite environmental variation is thus a major role of adaptive phenotypic

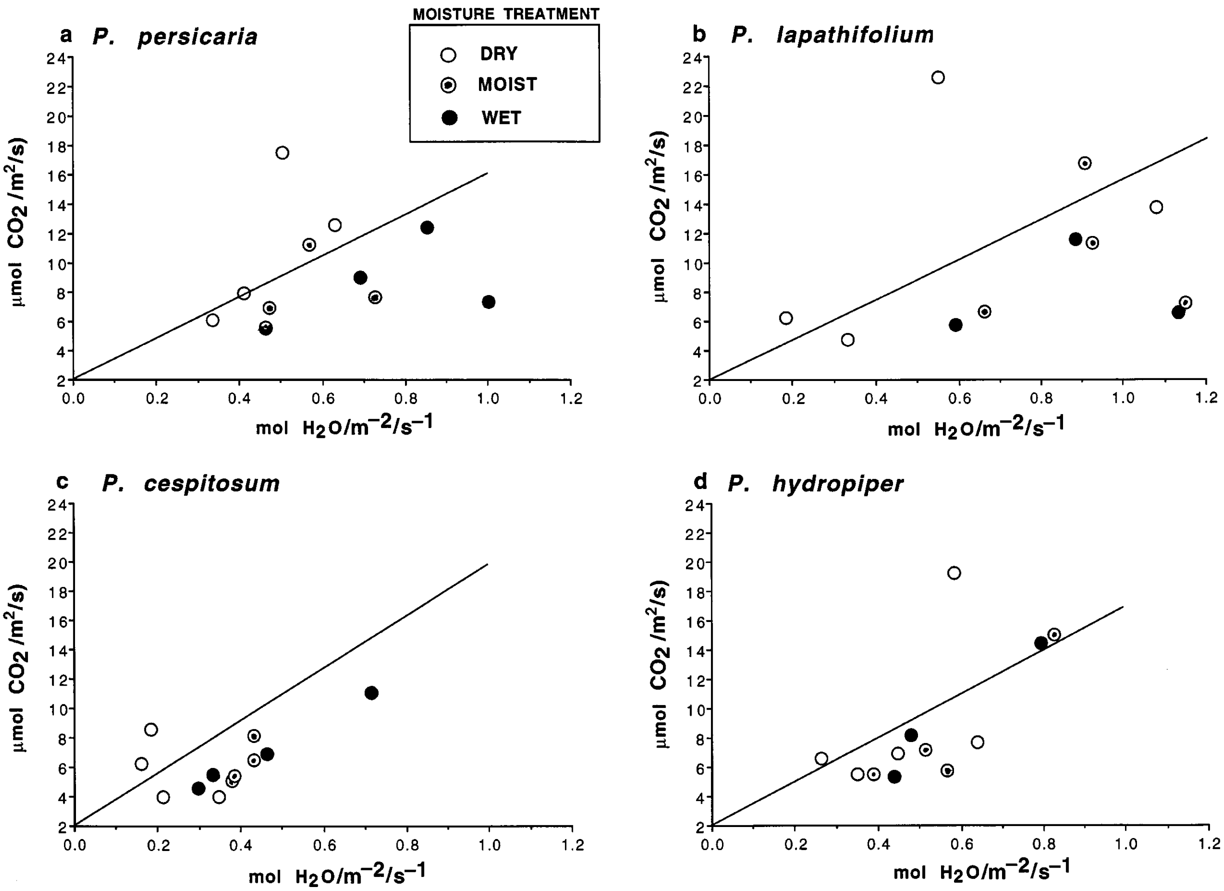


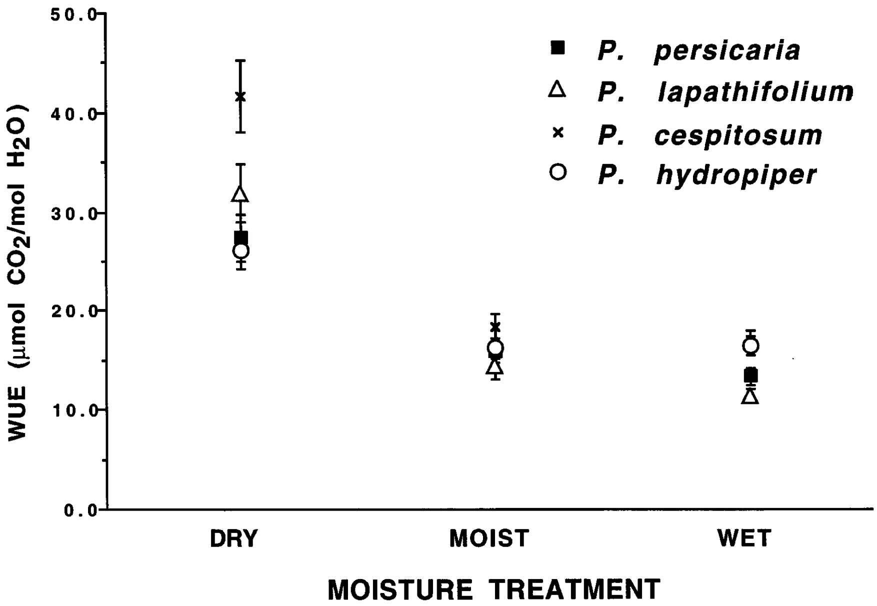
Fig. 6 Mean rates of photosynthesis versus conductance for four *Polygonum* species in twelve factorial environments. Mean photosynthetic rate in each factorial environment plotted against the mean conductance rate in that environment. *Solid line* predicts that species' overall (weighted) photosynthesis/ conductance ratio across environments (*open symbols* dry environments, i.e., high light/poor NPK, high light/rich Npk, low light/poor NPK, Low light/rich NPK, *dotted symbols* moist environments, *filled symbols* wet environments)

plasticity (Lewontin 1957; Baker 1965; Sultan 1987; see discussions in Sultan and Bazzaz 1993c; Schlichting and Pigliucci 1998).

A second example of complex species differences in photosynthetic response to environment is the differential effects of moisture treatment on response to high light (Fig. 3). Plants of *P. persicaria* and *P. lapathifolium* had significantly higher assimilation rates per unit leaf area in the dry treatment; *P. hydropiper* showed a similar (but non-significant) response. Since photosynthetic rate was measured per unit leaf area, this may reflect anatomical and biochemical differences in the much smaller leaves produced by plants in the dry treatment (S. Sultan, unpublished work). *P. cespitosum* plants increased photosynthetic rates slightly at high light only in the wet treatment (Fig. 3); in this species, leaf size decreased in flooded rather than droughted plants (S. Sultan, unpublished work). Furthermore, *P. persicaria* and *P. lapathifolium* steeply increased photosynthetic rates per unit leaf area in plants grown in the high light/dry/poor-nutrient environment (Fig. 4; note that plants in this stressful treatment produced little leaf area relative to the larger plants that developed in more favorable conditions). Interestingly, of the four species, only the latter two occur in open, dry, nutrient-poor sites in the field (Sultan et al. 1998). Increased rates of carbon gain per unit leaf area may largely reflect the anatomical effects of reduced cell size and hence leaf expansion rather than a specific adaptation to moisture stress (see Walters and Horton 1994); such developmental effects on gas exchange rates may be viewed as "genetic constraints" on natural selection for particular physiological responses (Dudley 1996b). Nonetheless, such increases will enhance the total carbon gain of small plants with low total leaf area, and thus partly offset the functionally deleterious developmental effects of either drought or flooding (see Sultan 1995 for discussion of adaptive versus inevitable aspects of phenotypic response).

Another major result of the study was that *Polygonum* species differed dramatically in individual photosynthetic response to light in ways that were consistent with their contrasting field distributions. The distinctively low response of the shade-distributed species, *P. cespitosum*, to increased light was confirmed in both experiments (Figs. 1 and 8a). In a previous study of field populations of these species in a common geographic range (Sultan et al. 1998), mean available PAR at canopy level ranged from 4% to 39% of full sun in

Fig. 7 Water use efficiency (WUE) of four *Polygonum* species in contrasting environments. Means and standard errors for instantaneous WUE of each species in dry, moist, and wet treatments (means in each moisture treatment include plants in all combinations of high light, low light, rich NPK, and poor NPK)



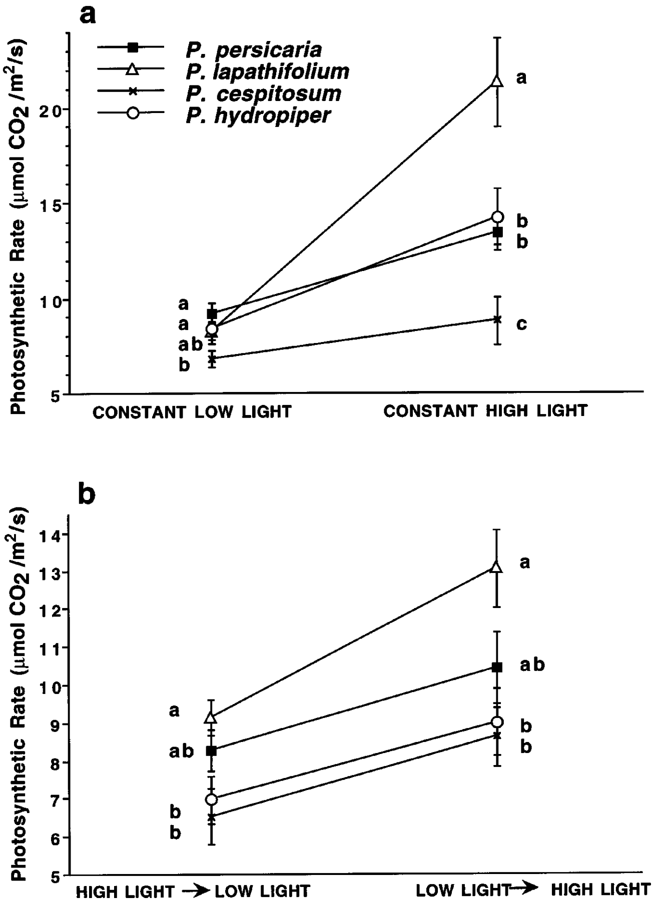


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Fig. 8a,b Photosynthetic rates of *Polygonum* species at low versus high light: plants measured in situ and after transfer to the contrasting light environment. **a** Mean photosynthetic rate and standard deviation of each species grown in low and high light, measured in situ . Species means in constant low light include plants grown and measured in low/moist/rich, low/dry/rich, and low/moist/poor treatments; same for species means in constant high light). Results are shown of Tukey's pairwise multiple comparison test for species differences within each growth/ measurement light level; species marked with the same *letter* do not differ at a probability of $P \leq 0.05$. **b** Mean photosynthetic rate and standard deviation of each species grown in low and high light, measured 1 h after transfer to the contrasting light environment (H–L means include plants grown in high/moist/rich, high/dry/rich, and high/moist/poor treatments measured after transfer to low light; L–H means include plants grown in low/moist/rich, low/dry/rich, and low/moist/poor treatments measured after transfer to high light). Results are shown of Tukey's pairwise multiple comparison test for species differences within each switching regime; species marked with the same *letter* do not differ at a probability of $P \leq 0.05$

P. cespitosum sites, compared with up to 99% in sites occupied by the other species. However, this species did not respond to low light with relatively high photosynthetic rates as a shade "specialist" might be expected to do (Gauhl 1976; Björkman 1980). Rather, *P. cespitosum* plants had the (significantly) lowest photosynthetic rates of the four species at low as well as at high light treatments. This type of constant, low response illustrates why performance equability is related to ecological amplitude only when a high level of function is maintained across environments. Thus, the distribution of *P. cespitosum* in shaded rather than open habitats may largely reflect the lower photosynthetic rates and hence growth and competitive ability of individuals of this species in open sites, relative to those of other annual colonizing species. Ecologists have increasingly recognized that many presumed "shade specialist" species are more accurately described as being restricted to shaded habitats due to limited physiological plasticity to exploit increased light levels (Gross 1984; Chow et al. 1988; Chazdon 1992; Sultan 1992; Chazdon et al. 1996; e.g., Boardman 1977; Bazzaz and Carlson 1982; Zangerl and Bazzaz 1983). The success of *P. cespitosum* at colonizing shaded sites (Sultan et al. 1998 and references) despite its relatively low per-unit area photosynthetic rates in low light may reflect other aspects of its growth and physi-

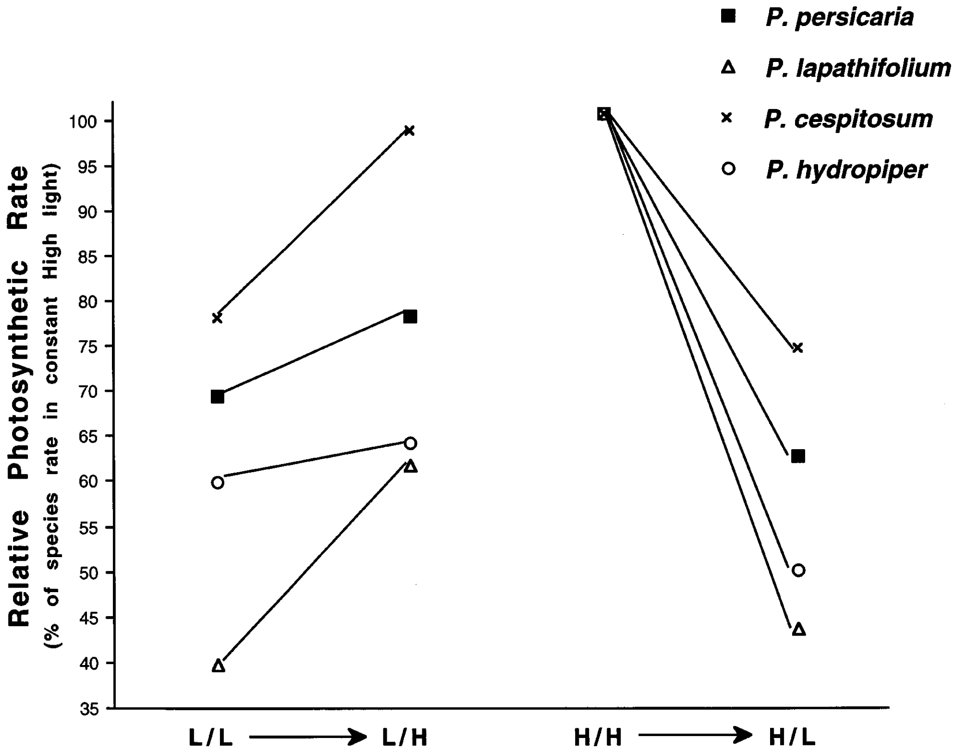

Fig. 9 Short-term photosynthetic plasticity of *Polygonum* species: photosynthetic rate relative to species maximum of plants switched to contrasting light environments. Mean photosynthetic rate of plants in each species transferred from low to high light (L/L–L/H) and from high to low light (H/H–H/L), expressed as a percentage of that species' mean in situ photosynthetic rate when grown and measured in high light (H/H). Means are based on *c*. 10 plants per species per transfer treatment; total $n = 83$ switched plants)

ology such as canopy architecture, biomass allocation, and high total leaf area (S. Sultan, unpublished work).

Both *P. hydropiper* and especially *P. lapathifolium* showed steeply reduced photosynthetic rates at low light relative to their assimilation rates in full sun (Figs. 1, 8a). Such "down-regulation" of carbon metabolism is not necessarily functionally adaptive to low light conditions (Givnish 1988; Walters and Horton 1994; Strauss-Debenedetti and Bazzaz 1996; Chazdon et al. 1996). These two species occur only in sites with high to very high light early in the season (canopy PAR means of 97–99% and 82–99% of full sun, respectively), and moderate to high light late in the season (over *c*. 50% of full sun; Sultan et al. 1998). The exclusion of these species from shaded sites may thus reflect in part an inability to maintain effective rates of net assimilation under strongly limiting light. In contrast, *P. persicaria* plants photosynthesized at a high rate (equivalent to *P. hydropiper*) in full sun, and maintained over fifty percent of that rate at low light; this species inhabits a wide range of light habitats (site means range from 25–99% of full sun at canopy level across the growth season). This response pattern exemplifies the kind of equable, high performance likely to be associated with ecological breadth. Individuals of this species apparently undergo the biochemical and ultrastructural changes in photosynthetic apparatus that enhance adaptive physiological plasticity in response to different light levels (Sultan and Bazzaz 1993a). These changes are known to occur in many taxa that inhabit both open and shaded sites (Björkman 1980; Fitter and Hay 1981; Berry and Downton 1982; Wulff 1987; Chow et al. 1988; Field 1988; Kitajima 1994; and references therein).

The *Polygonum* species also responded differently to short-term changes in light intensity (Figs. 8b, 9). The capacity for rapid photosynthetic adjustment to such changes is a distinctive aspect of physiological response necessary to occupy variable light environments, and hence important to ecological distribution (Pearcy 1988; Strauss-Debenedetti and Bazzaz 1991; Chazdon et al. 1996; Bazzaz 1996). Individuals of *P. lapathifolium* and *P. hydropiper* showed relatively low short-term adjustment: after one hour, photosynthetic rates remained severely reduced in plants switched from low to high light, as well as in high-light grown plants transferred to low light (Fig. 9). In contrast, individuals of both *P. persicaria* and the shade-distributed *P. cespitosum* reached close to their maximum assimilation rates within one hour after switching into high light, and maintained over 60% of maximum rates when transferred to low light. These contrasting patterns of short-term photosynthetic response are broadly consistent with the field distributions of the four species. The two less plastic species are evidently restricted to extremely open sites, where light intensity will be relatively consistent over time (see above; details in Sultan et al. 1998). Furthermore, the high short-term adjustment ability of *P. cespitosum* (relative to its limited maximum assimilation rate) may contribute to its tolerance of shaded habitats. Plants in such habitats experience much of their daily irradiance in brief sunflecks, so that the ability to rapidly maximize assimilation rate in previously shaded leaves may be critical to efficiently utilizing the light available (Pearcy 1988; Fitter and Hay 1987; Dong 1995). Likewise, the ability of *P. persicaria* to both maintain high assimilation rates under short-term shade, and to utilize short-term intense light, may contribute to this species' tolerance of partly shaded and hence temporally variable light environments. Because this ability to respond quickly to increased irradiance apparently depends on leaf nutrient status (Thompson et al. 1988; Osmond and Chow 1988; Chazdon et al. 1996), it will differ among species depending on their individual abilities to acquire and flexibly re-allocate minerals in various environmental conditions (Field and Mooney 1986).

A third striking result was that photosynthesis and stomatal conductance changed independently in response to certain conditions, again in species- as well as environment-specific patterns (Fig. 6). Photosynthetic rates are usually highly correlated with stomatal conductance, since reduction of stomatal density or aperture (e.g., in response to tissue drought stress) will reduce all gas exchange (Givnish 1988). However, in three of the four *Polygonum* species, leaves of droughted plants increased photosynthetic rates while significantly reducing stomatal conductance (*cf.* Figs. 3 a,b, d and Fig. 5). This result suggests that physiological response to environment in these species entails biochemical changes in the photosynthetic apparatus, rather than simply mechanical adjustment of stomatal aperture. These photosynthesis and conductance adjustments resulted in sharply increased instantaneous WUE in dry relative to moist and wet soils in all four species (Fig. 7), presumably an adaptive response (Dudley 1996a).

The consistently low conductance rates of *P. cespitosum* plants may reflect lower stomatal density or size in leaves of this species, a possible cause of their constrained photosynthetic rates (note that all four species have stomates on both adaxial and abaxial leaf surfaces as well as similar stomatal structure; Lersten and Curtis 1992). This causal interpretation cannot be assumed, however, as plants may also reduce conductance to match photosynthetic capacity that is limited by other factors, to avoid unnecessary water loss (Pearcy et al. 1987; Chapin 1991). Thus, the significantly reduced conductance rates of low-light grown plants of *P. lapathifolium* and *P. hydropiper* may represent a functionally appropriate stomatal response to an existing photosynthetic constraint, rather than a stomatal constraint on photosynthesis in those environments. Indeed, in *P.lapathifolium*, assimilation rate dropped less steeply at low light than did conductance, such that shaded plants had greater instantaneous WUE.

Note however that adaptive interpretation of the WUE ratio is quite problematical: the existing literature indicates that the association of WUE to relative fitness or biomass varies in sign as well as strength, depending on species and growth conditions (Donovan and Ehleringer 1994; Dudley 1996a). In other words, high WUE is not always functionally adaptive. In many taxa and environments, high photosynthesis and growth rates are associated with high conductance and hence low WUE (e.g., Geber and Dawson 1990); this is the case with *P. lapathifolium* plants at high light conditions (similar to those which they inhabit in nature). Thus, low WUE may contribute positively to fitness in plants such as these annual species, in which rapid growth is critical (Donovan and Ehleringer 1994 and references therein). Indeed, low WUE is associated with high growth rates and early fecundity in many crops (references in Geber and Dawson 1990). Conversely, the high WUE of *P. cespitosum* plants in moist, high light conditions, due to their limited rates of both photosynthesis and conductance, is unlikely to confer functional or competitive superiority in such environments, where indeed the species does not occur (Sultan et al. 1998; see Donovan and Ehleringer 1994; Farris and Lechowicz 1990). High WUE due to stomatal closure may also be associated with functional disadvantages not reflected in instantaneous measurements, such as leaf overheating (Berry and Downton 1982; Rice and Bazzaz 1989; Sims and Pearcy 1991).

Moreover, the water costs and carbon gains quantified by this ratio are not comparable across either environments (Lechowicz and Blais 1988; Geber and Dawson 1990) or taxa. A mole of water "costs" more in an environment where water is limiting; increased WUE may positively correlate with fitness in dry conditions but have no adaptive value in moist environments (Berry and Downton 1982; Dudley 1996a). Likewise, a mole of carbon has greater "value" in light- or nutrient-limited conditions. Finally, relatively low WUE may not represent an appreciable cost to those individuals best able to maintain water supplies (e.g., by means of appropriate root morphology and deployment or osmotic adjustments; Levitt 1980; Lechowicz and Blais 1988; Sultan and Bazzaz 1993b). For example, the relatively steep WUE decrease in shaded plants of *P. persicaria* may indicate either a maladaptive inability of shaded plants to reduce conductance, or an adaptive ability of these plants to acquire sufficient soil moisture to keep stomates open and hence maximize photosynthesis. As with other functional costs and benefits, WUE must be interpreted in the context of both environmental circumstances and interacting phenotypic traits.

In conclusion, this multifactorial study demonstrates the extraordinary complexity of physiological response to environment in the *Polygonum* model system. First, the effects of independently varied environmental factors on rates of photosynthesis and conductance may be interactive rather than additive. Second, closely related species may respond differently not only to changes in the availability of single resources, but to specific multivariate combinations of resource levels. These results underscore the importance of multifactorial studies of plant response to environment (Chapin 1991). They further point to the need to incorporate this complexity into ecological and evolutionary studies of niche differentiation and community structure in variable environments.

The extremely complex differences among *Polygonum* species in patterns of physiological response were largely consistent with specific environmental differences in the species' field distributions. Compared with its ecologically narrower congeners, individuals of the species with the broadest ecological distribution maintained relatively high rates of carbon gain at the greatest range of high and low resource levels and when transferred to contrasting light environments. *P. persicaria* thus expressed an equable, high photosynthetic response across the broad range of factorial light, moisture, and nutrient treatments. This type of functional constancy reflects high underlying plasticity for the myriad allocational, anatomical, biochemical, and ultrastructural traits that influence assimilation rates. These results support the view that individual long- and short-term physiological plasticity may be an important element in the realized distribution of species and hence their relative ecological breadth. This interpretation is particularly robust because the species comparison is confounded by neither phylogenetic, geographical, or life-history differences.

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