POPULATION DIFFERENTIATION AND PLASTIC RESPONSES TO DROUGHT STRESS IN THE GENERALIST ANNUAL *POLYGONUM PERSICARIA*

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We tested the generalist annual plant *Polygonum persicaria* (Polygonaceae) for adaptive differentiation in drought responses. Populations from one consistently moist and two variably dry sites were grown in moist and drought conditions in a greenhouse. Physiological, morphological, and reproductive data were collected. All three populations maintained similar levels of fitness in both drought and moist conditions, indicating that these populations may be equally drought tolerant. Also, the three populations had similar water use efficiency and root biomass responses to soil moisture, indicating that substantial phenotypic plasticity is present in all the populations, including a population from a consistently moist site. The magnitude of plastic responses for specific traits varied among the populations; i.e., the physiological and morphological means by which these plants maintained reproductive homeostasis across moisture conditions was population dependent. In particular, the moist-site population had the greatest plasticity in water use efficiency, while the dry-site populations had greater plasticity in root biomass allocation. Selection analyses demonstrated that increased water use efficiency was adaptive in drought and that decreased root biomass allocation was adaptive in moist conditions. Overall, the maintenance of fitness in stressful conditions may involve population differentiation along different axes of functional plasticity.

Keywords: Polygonaceae, drought stress, phenotypic plasticity, water use efficiency, root allocation, generalists.

Introduction

Generalist plant species inhabit a wide range of habitats, including resource-poor and variable sites and may therefore be geographically widespread (Bazzaz 1986; Oliva et al. 1993). This ecological breadth can reflect individual phenotypic plasticity, genetic differentiation of populations to local environmental conditions, or a combination of both aspects of variation (Bradshaw 1965; Van Tienderen 1990; Rice and Mack 1991; Emery et al. 1994). Populations will differentiate if consistent selection pressures cause directional trait changes that erode genetic variation and fix population responses, resulting in locally specialized ecotypes (Endler 1986; McGraw 1987; Van Tienderen 1990; Donohue et al. 2001). However, selection pressures that vary through space and time can promote plastic trait responses to environmental conditions in individual genotypes rather than ecotypic differentiation (Blais and Lechowicz 1989; Sultan and Spencer 2002). Plasticity is expected to be selectively advantageous under more variable conditions (Via and Lande 1984; Moran 1992), in part because phenotypic flexibility may allow a species to capitalize on conditions conducive to reproduction as well as to tolerate stress (Sultan 2001). If individual adaptive plasticity confers

tolerance of diverse conditions, then populations in contrasting habitats may remain genetically similar (Novak et al. 1991; Rice and Mack 1991).

Accordingly, we might expect populations in variable sites to show similar, plastic responses to environmental conditions and populations in consistently different sites to differentiate into local ecotypes (Donohue et al. 2001). However, a more complex situation arises when sites differ in their degree of environmental variability. For instance, environmental factors such as soil moisture and nutrient availability vary to some extent in all mesic habitats, but the range and pattern of variation may differ consistently from one site to another. In such cases, individuals of all populations may show adaptive plasticity, but populations may differ genetically in the amount and precise pattern of plasticity their individuals express (Scheiner and Callahan 1999).

Because soil moisture availability is a critical factor in plant growth that can vary both among and within sites (Sultan et al. 1998*b*; Larcher 2003), studies of populations from contrasting moisture environments allow for a test of the evolutionary interplay between genetic differentiation and plastic responses to environmental variation. In particular, examining physiological and morphological responses to drought stress in generalist species is important for understanding how differentiation and plasticity contribute to environmental breadth. Two key soil moisture response mechanisms are water use efficiency (WUE = the ratio of carbon assimilation rate to stomatal conductance) and root biomass allocation (Van den Boogaard et al. 1996; Maliakal

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et al. 1999; Craine and Lee 2003). Both traits can vary plastically (Sultan et al. 1998*a* and references therein). Because increased WUE conserves water (Zangerl and Bazzaz 1984; Cowan 1986; Heschel and Hausmann 2001), it can contribute to higher fitness in drought conditions, even though it comes at the expense of lower carbon assimilation (Dudley 1996; Heschel et al. 2002). However, when water is plentiful, decreased WUE associated with maximum gas exchange can be adaptive (Geber and Dawson 1990; Donovan and Ehleringer 1992).

Like WUE, increased biomass allocation to roots can promote drought tolerance. In dry conditions, greater proportional root biomass, and presumably uptake surface area, can increase water acquisition potential (Bell and Sultan 1999; Fitter 1999; Fitter and Hay 2002; Martre et al. 2003). Although increased allocation to roots comes at the expense of allocation to reproductive structures and to carbon-fixing organs such as leaves, this response may be adaptive when soil resources are low (Fitter and Hay 2002; Larcher 2003). Conversely, because of the cost of allocating biomass to roots, decreased root biomass proportion may be adaptive when soil resources are abundant (Fitter and Hay 2002). Thus, different levels of WUE and root allocation are likely to be functionally adaptive in drought versus moist conditions (Heschel et al. 2002). To date, however, few studies have experimentally examined relationships between fitness and these functionally important plastic traits (Blais and Lechowicz 1989; Farris and Lechowicz 1990; Dudley 1996; Arntz and Delph 2001; Geber and Griffen 2003).

Here, from a jointly evolutionary and functional perspective, we examine patterns of plastic responses to drought in populations of the generalist species *Polygonum persicaria* that inhabit contrasting moisture regimes. Because of this species' ecological breadth (Sultan et al. 1998*b*) and its affect on biodiversity as a widespread weedy colonizer (Bazzaz 1986), understanding how it tolerates environmental adversity provides an excellent model for comprehending the evolutionary strategies that promote both population persistence in stressful conditions and the ability to invade diverse habitats. In this study, we examined morphological, physiological, and reproductive responses to drought stress in three populations of the generalist *P. persicaria*. Two of the populations we studied experience variably dry conditions in the field, depending on measurement depth and date, and the third population experiences consistently moist soil conditions throughout the growing season. We manipulated soil moisture conditions experimentally in the greenhouse to test whether these populations have genetically differentiated in WUE and root allocation plasticity patterns and to determine the strength of correlations between these functional traits and fitness. Specifically, we addressed the following questions: (1) Do populations of the generalist *P. persicaria* from different soil moisture habitats show similar plastic responses to dry compared with moist soil conditions, or do they show ecotypic differentiation? (2) If the populations differ, do those from variable moisture habitats show greater plasticity than a population from a homogeneous, consistently moist, site? (3) For *P. persicaria*, are functional traits, such as WUE and root biomass proportion, important correlates of reproductive fitness in drought compared with moist conditions?

Material and Methods

Organism and Study Sites

Smartweed *Polygonum persicaria* (Polygonaceae) is an introduced annual, self-compatible herb of North American disturbed and agricultural sites (Gleason and Cronquist 1963). *Polygonum persicaria* populations are found in a diverse array of habitats, including partly shaded to open, nutrient poor to nutrient rich, and dry to flooded environments (Sultan et al. 1998*a*).

Achenes were originally collected from field parents in three well-established populations in eastern Massachusetts in 1995 (DFF = Dewitt Fish Farm, Amherst, Mass.; M = Daniel Webster Sanctuary, Marshfield, Mass.; NAT = Natick Farmyard, Natick, Mass.; see Sultan et al. 1998*b* for details) and were inbred under uniform conditions in the Wesleyan University research greenhouse for two generations. Significant differences in soil moisture availability have been documented across the study populations (fig. 1; Sultan et al. 1998*b*). On the basis of early and late measurements for a typical growing season, the DFF population is consistently moist, while the M and NAT populations encounter varying degrees of soil moisture stress, depending on soil depth (fig. 1).

Experimental Setup

Achenes (24) from eight inbred lines per population were stratified for 5 wk in distilled water at 4°C. On August 7 and 8, 2001, achenes were sown in the Wesleyan University greenhouse into flats filled with medium grade vermiculite (Country Cottage horticultural grade) and saturated with water. Achenes were sown equidistantly at a uniform depth of 7 mm, and flats were placed in randomized blocks. Germination began by August 15, and most seedlings had one true leaf by August 31. On September 3, each flat was fertilized with 15 mL of Peter's 20 : 20 : 20 NPK (Grace-Sierra Horticultural Products, Milpitas, Calif.) at a concentration of 1.30 mL/L to prevent nutrient stress.

On September 8 and 9, eight healthy seedlings from each line were transplanted into individual clay pots (130 mm diameter) filled with a 1 : 1 : 1 mix of sterilized local topsoil (Turface fritted clay: medium grade sand, mixed with 1.5 g of 15 : 8 : 12 N : P : K fertilizer [Agway, Middlefield, Conn.]) and watered to field capacity. The pots were randomly positioned across four greenhouse benches. Each bench (135×335 cm) held 60 plants, evenly spaced. The soil was kept moist for 7 d to allow the plants to establish before treatments were imposed. Supplemental light, from high-intensity mercury halide lights, was used between 7:00 AM and 7:00 PM if ambient light fell below ca. 760 μmol m^{-2} s^{-1} for more than 15 min.

The plants produced reproductive structures early in the life cycle, possibly resulting from seedling nitrogen stress or late-season growth cues. Precocious reproductive buds were excised every 2 d during the second and third weeks of September. Bud removal does not affect subsequent growth in annual *Polygonum* species (M. Geber, personal communication). To provide a covariate to account for initial seedling size differences, the area of each plant's longest leaf was
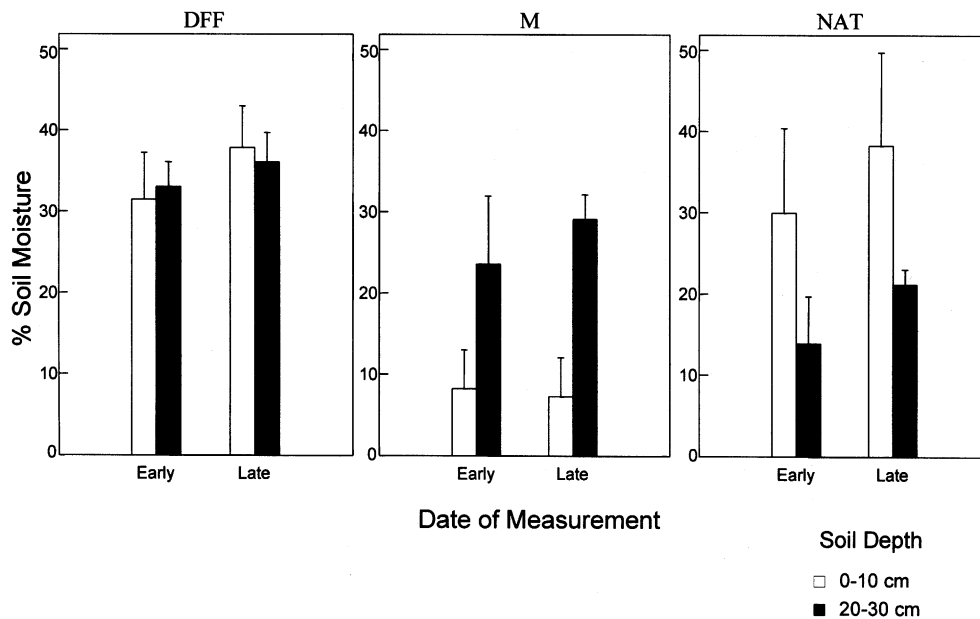
Fig. 1 Soil moisture availability as a percentage of field capacity in each population site at 0–10 and 20–30 cm soil depths. Soil moisture was determined gravimetrically both early (June 1994) and late (August 1994) in the growing season (data are taken from Sultan et al. 1998*b*). Field capacity is equivalent to a soil water potential of zero. Means ± 1 SD are shown.

measured at the time of bud removal using a Li-3100 leaf area meter (LI-COR, Lincoln, Nebr.). This metric also accounts for any nutrient stress effects before transplanting.

Experimental Design

On September 20, one individual per line was randomly assigned to either a dry (hereafter referred to as drought) or moist treatment on each of four greenhouse benches or blocks (60 plants per block). This resulted in a total of 192 plants (three populations × eight lines per population × two water treatments × four replicates). Plants were watered automatically using Chapin watering tubes by a computer-controlled solenoid valve on each bench. Drought-treatment plants were given 24 mL of water daily, and moist-treatment plants received 72 mL of water. Supplemental water was added to individual pots as required to maintain uniform treatment conditions, such that soil water availability was similar across plants within a given treatment.

To determine whether there was a difference in soil moisture between drought and moist treatments, eight additional "dummy" pots containing *P. persicaria* plants were placed in random positions in the experimental setup. Half of these pots were randomly assigned to the drought treatment, and the other half were assigned to the moist treatment. At harvest, soil samples were collected from each pot, weighed, dried at 65°C for 72 h, and reweighed to gravimetrically determine soil moisture content (Pearcy et al. 1989). The watering regime resulted in significantly drier pots in the drought treatment (mean drought pot water content as a percent of dry soil mass ± SE = 11.45% ± 0.38%, mean moist pot water content as a percent of dry soil mass ± SE = 19.89% ± 38%; $t_6 = 15.72, P < 0.0001$).

Data Collection

Carbon assimilation rate ($A = \mu$mol CO_2 m^{-2} s^{-1}) and stomatal conductance ($g_{st} = $ mol H_2O m^{-2} s^{-1}) were measured with a LI-COR Infrared Gas Analyzer (IRGA), model 6250 (LI-COR), and WUE (A/g_{st}) was calculated for each plant. On partially sunny to sunny days, between 10:00 AM and 3:00 PM, measurements were taken on the most recent fully expanded leaf under a Q-Beam (blue and red diode) light source set at 900 μmol m^{-2} s^{-1} (Quantum Devices, Barneveld, Wis.). This light level was found to be saturating for *P. persicaria* (Sultan et al. 1998*a*). Leaf temperature was always kept cooler than the ambient temperature, and humidity never varied more than 3% from ambient conditions. Plants were measured in a random fashion with respect to population and line and in even numbers each day with respect to treatment and block. Effects of time of measurement and date were factored out by adjusting IRGA values with residuals from linear regression models (Type I sums of squares) that included time and date (Farris and Lechowicz 1990; Dudley 1996). Boundary-layer conductances were estimated with moist Whatman filter paper leaf mimics (Parkinson 1985). To correct for different leaf areas in the IRGA chamber during measurements, individual areas of the most recent fully expanded leaves were determined using a LI-COR (LI-3100) leaf area scanner (this trait is hereafter referred to as "leaf size").

Plants were harvested during the early stages of senescence in the second week of November. The perianth was removed from achenes, and the achenes and floral structures were weighed separately. Subsamples of 20 achenes per replicate were weighed to estimate total achene number. The remaining aboveground biomass was dried at 100°C for 1 h, then at

65°C for ≥48 h before weighing (Pearcy et al. 1989). The pots, soil, and roots were kept in a cold room until root biomass was measured. The roots were washed, dried for at least 72 h at 65°C, and weighed.

Statistical Analyses

ANOVA and ANCOVA were used to test for population differences in physiology, morphology, and reproduction. For the physiological traits, models included effects of block (greenhouse bench), treatment, line (nested within population), population, population by treatment, and line (population) by treatment. For all other traits, models incorporated these effects as well as initial leaf size as a covariate. For all models, block, treatment, and population were fixed effects, and line was a random factor (Sultan 2001). Block was considered a fixed factor on the basis of a priori knowledge of differences in environmental conditions among greenhouse benches (Sultan 2001). The effects of drought treatment, line, and population by treatment were tested over a synthetic denominator comprised of the treatment by line mean squares; the population term was tested over the line mean squares (Heschel et al. 2002). Because of limited sample size and consequent lack of power we report tests significant at $P \leq 0.10$. All models were examined to confirm homoscedasticity of error variances and normality of residuals. WUE and total achene number were $\log_{10}$-transformed to meet normality assumptions. To examine where population differences lie within a particular interaction term, planned comparisons were constructed using the line by treatment mean squares in the denominator of these across-treatment contrast statements (SAS Institute 1994; Heschel et al. 2002).

Phenotypic selection analyses were performed by examining the relationship between total reproductive fitness and physiological/morphological traits within each soil moisture treatment (Lande and Arnold 1983; Heschel et al. 2002). Simple linear regression of each trait on fitness generated estimates of treatment-specific selection differentials; multiple regression of all the traits simultaneously on fitness generated estimates of treatment-specific selection gradients (Lande and Arnold 1983). All traits were standardized to their respective standard deviations, and relative fitness of each plant was calculated with respect to the mean number of achenes produced in each treatment. A block term was included in both the simple and multiple regression models to control for microenvironmental effects on fitness across all populations. A population term was also included in all models to control for population differences in fitness resulting from unmeasured traits (Heschel et al. 2002). Population by trait terms were initially included in all models, but in every case, these effects were found to be nonsignificant and were therefore dropped from all models. Quadratic terms were initially included in all models to test for nonlinear selection, but no stabilizing/disruptive selection was detected, so these terms were also dropped.

Results

Physiological Traits

In response to drought conditions, all three study populations significantly increased their WUE by more sharply reducing stomatal conductance than carbon assimilation (fig. 2; table 1). For WUE as well as carbon assimilation rate and stomatal conductance, a highly significant drought-treatment effect was observed but not a population by treatment interaction, indicating that the observed responses of gas exchange
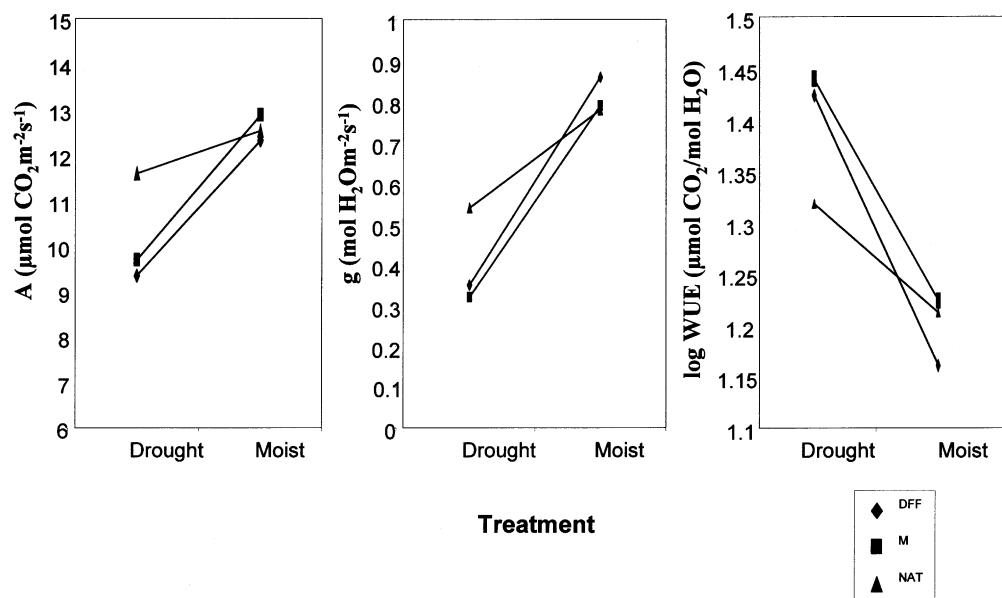

Fig. 2   Carbon assimilation rate (A), stomatal conductance (g_{st}), and water use efficiency (WUE = A/g_{st}) values for all populations in drought and moist conditions. Least square means are shown. DFF = Dewitt Fish Farm, Amherst, Mass.; M = Daniel Webster Sanctuary, Marshfield, Mass.; NAT = Natick Farmyard, Natick, Mass.

Table 1

ANOVA for Population and Drought Treatment on Physiological and Morphological Traits

	Block	Drought treatment	Line (population)	Line (population) × treatment	Population	Population × treatment	Initial leaf area
A	0.84	15.38***	1.33	0.97	0.94	1.32	…
g_{st}	2.16+	20.59***	1.21	1.67*	0.43	0.83	…
WUE	0.92	6.12*	1.13	1.88*	0.08	0.18	…
Leaf size	0.09	0.004	7.04***	0.42	2.04	0.46	9.64**
Root biomass proportion	1.52	36.007***	3.21**	1.27	0.88	2.36+	0.83
No. achenes	2.67*	0.0012	1.93*	3.05***	7.19**	0.98	3.14+

Note. F statistics and P values are reported. A = carbon assimilation rate; g_{st} = stomatal conductance; WUE = water use efficiency; ellipses = no covariate used in the analysis.

   + $P \leq 0.10$.
   * $P < 0.05$.
   ** $P < 0.01$.
   *** $P < 0.001$.

to drought stress were in the same direction for all the populations (table 1). However, differences were observed in the magnitude of these responses (fig. 2). In particular, the DFF population (consistently moist site) exhibited the greatest plasticity for WUE in response to drought (fig. 2). Thus greater soil moisture variability within a site did not translate into greater WUE plasticity. Across the three populations, genetic variation among lines was detected for stomatal conductance and WUE response (significant line by treatment interaction; table 1).

Morphological Traits

The proportion of total biomass allocated to roots increased in drought and decreased in moist conditions for all the study populations (highly significant treatment effect; table 1; fig. 3). In addition, a marginally significant population by treatment interaction was detected (table 1), reflecting a reduced drought response of the DFF population (fig. 3). The plants from the M and NAT populations (variably dry sites) had the strongest root biomass responses to soil moisture and converged on a significantly higher root proportion in the drought
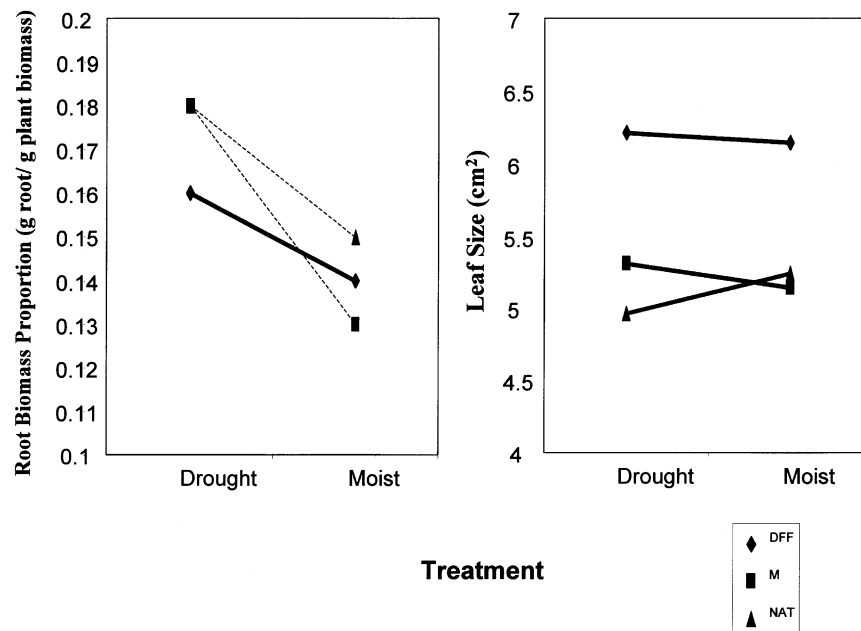

Fig. 3   Population responses to drought and moist conditions for root biomass proportion (grams root/grams whole-plant biomass) and the area of the most recently fully expanded leaf (leaf size). Least square means are shown. Dashed lines indicate a significant contrast between the two treatment levels at $P = 0.05$. DFF = Dewitt Fish Farm, Amherst, Mass.; M = Daniel Webster Sanctuary, Marshfield, Mass.; NAT = Natick Farmyard, Natick, Mass.

treatment (fig. 3). All the populations responded similarly to drought conditions by decreasing aboveground biomass from 11% to 20% percent (*t*-test, $F_1 = 8.56$, $P = 0.004$), indicating that drought conditions were stressful.

Only a significant effect of line was observed for leaf size (table 1). There was no significant main effect of drought treatment on leaf size (table 1). Also, each of the population's leaf responses to drought was nonsignificant (fig. 3).

For each population, achene number did not vary in drought versus moist conditions (fig. 4; table 1, nonsignificant treatment effect), indicating that all the populations tolerated drought stress. Significant population differences in achene production were detected regardless of treatment (fig. 4; table 1), with plants from the M population producing the greatest number of fruits in both treatments. Genetic variation was detected for achene production across all the populations (table 1).

Selection Analyses

Different associations with fitness were detected for functional traits within each soil moisture treatment. In drought conditions, plants with higher WUE were more fit (when holding the effects of block, population, leaf size, and root biomass proportion constant; table 2). In moist conditions, no selection was detected on WUE; however, plants that allocated less biomass to roots and that had larger leaves were more fit (table 2). Since selection on root biomass proportion and leaf size was not detected when other measured traits were included in the analyses, these trends were probably due to indirect associations of root biomass and leaf size with fitness
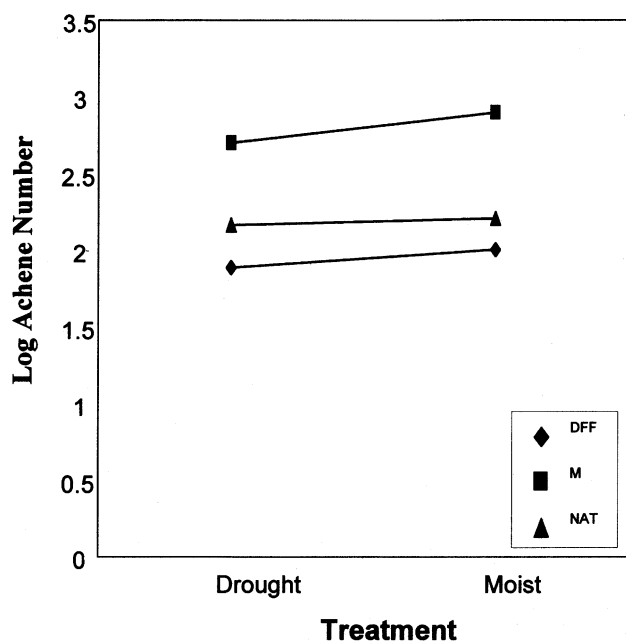
Table 2
Results of Phenotypic Selection Analysis, Controlling for the Effect of Population and Block

Trait	Drought		Moist	
	S	β	S	β
WUE	0.036	0.058[*]	0.015	−0.006
Leaf size	0.012	−0.13	0.18[*]	−0.071
Root biomass proportion	−0.20	0.0002	−0.21[+]	0.080

Note. Standardized selection differentials (S) and selection gradients (β) are shown for each water treatment. S reflects direct and indirect associations between a given trait and fitness, whereas β reflects the direct association between a given trait and fitness, holding the associations of the other traits with fitness constant.

[+] $P < 0.10$.

[*] $P < 0.05$.

through correlations with WUE. When holding the effects of WUE and leaf size constant, no selection was detected on root biomass proportion in moist conditions (table 2). Likewise, no selection was detected on leaf size after holding the effects of WUE and root biomass proportion constant (table 2).

Discussion

Population Differentiation and Plasticity

Polygonum persicaria from two variably dry sites and one consistently moist site showed similar patterns of functional plasticity in response to soil moisture: all three populations increased WUE and root biomass allocation in drought compared with plants grown in moist greenhouse conditions. Moreover, drought-stressed plants did not make smaller leaves, so carbon uptake potential may not have been reduced; in each population, reproduction was maintained at equivalent levels across the moist and drought treatments. Thus, populations of this ecologically widespread species shared broadly similar plastic responses despite site differences in moisture level and variability. Plants from the *P. persicaria* populations were also equally able to maintain fitness under drought stress (i.e., equivalently flat responses of fitness to drought stress), regardless of their native moisture habitat. Interestingly, this fitness homeostasis was maintained despite overall decreases in plant size in drought conditions, indicating that plants were allocating more biomass to reproduction and root tissue in dry conditions. These results support the view that similar, functionally plastic populations may successfully occupy diverse sites in generalist species. This indicates that highly plastic species may consist of adaptively similar, generalist populations in diverse field habitats rather than narrowly specialized ecotypes (Oliva et al. 1993; Williams et al. 1995).

Although functional responses to soil moisture were generally similar across all three *P. persicaria* populations (no significant population by trait interactions; table 1), differences in degree of response were detected for specific traits. In particular, DFF plants (consistently moist-site population) responded to soil moisture variation with greater plasticity in WUE and less plasticity in root biomass allocation, while the

Fig. 4 Reproductive fitness (log total achene number) for all populations in drought and moist conditions. Least square means are shown. DFF = Dewitt Fish Farm, Amherst, Mass.; M = Daniel Webster Sanctuary, Marshfield, Mass.; NAT = Natick Farmyard, Natick, Mass.

populations from variably dry field conditions (M and NAT) more sharply increased root allocation in response to drought. These populations evidently have genetically differentiated for the strength of different aspects of plastic response to drought. These results indicate that selection on morphological and physiological modes of stress response may reflect compensatory interactions among traits. Functionally, plants that allocate less biomass to roots might require higher WUE for persistence in drought conditions because of the lower water acquisition capacity of plants with smaller root surface areas. Conversely, plants that have greater water acquisition potential from high biomass allocation to roots may not require sharply increased WUE to persist in drought conditions. Thus, populations may achieve similar levels of stress tolerance through different underlying combinations of responses (Griffith et al. 2004).

Within-site differences in moisture variability did not necessarily translate into differences in degree of response. *Polygonum persicaria* populations from variable soil moisture conditions were not always more plastic than the population from a consistently moist site. Although the variably dry-site populations responded to soil moisture deficit with greater plasticity in root biomass allocation than the consistently moist-site population, the dry-site populations responded with less WUE plasticity. Our results thus indicate that increased environmental variation does not necessarily lead to a greater degree of functional plasticity. Indeed, the moist-site population expressed the steepest increase in WUE in response to drought, even though this population does not experience moisture deficits in nature. This result may reflect episodic selection during an anomalous drought year in the past or the founding of the population by achenes from a dry or variable site. Alternatively, the greater stomatal sensitivity to drought could have resulted from selection to rapidly open stomata in response to excess soil water and anoxia (Larcher 2003).

The high drought plasticity of the moist-site population is intriguing and indicates that once plasticity has evolved it can be maintained even in the absence of ongoing selection pressures. This may be particularly likely in the case of drought plasticity because the same types of response affect adjustment to both fine-scale and severe soil moisture deficits. In such cases, the ability to strongly express plasticity may bear no substantial cost to the organism (Sultan 1992; see DeWitt et al. 1998 for a general discussion of this issue). Lack of genetic variation in *P. persicaria* populations is unlikely to be a significant constraint on population differentiation, given the ample variation revealed (line and/or line by treatment interaction effects; table 1) even in our relatively small genotypic sample.

Selection Analyses

The complex contributions of stress-related, functional traits to fitness have rarely been examined (Blais and Lechowicz 1989; Farris and Lechowicz 1990; Donovan and Ehleringer 1994; Dudley 1996; Arntz and Delph 2001; Geber and Griffen 2003). In our experimental drought conditions, direct selection favored increased WUE (for similar results, see Dudley 1996 and Heschel et al. 2002). In moist conditions, indirect selection was detected for increased leaf size and decreased root biomass proportion. Therefore, the types of plastic responses to drought stress that we observed do indeed contribute to reproductive fitness. In drought, physiological adjustments of WUE contributed the most to fitness, but in moist conditions, morphological adjustments in leaf and root traits were favored (albeit indirectly). This indicates that, in drought conditions, WUE may functionally outweigh morphological adjustments to water uptake capacity. In other words, the evolution of drought tolerance strategies may involve population responses at loci that influence WUE, but in moist conditions, differentiation is predicted to occur for root and leaf allocation patterns. These results further indicate that for generalist species, the ability to invade dry habitats may require plasticity in WUE, while the invasibility of moist habitats may rely more on plasticity in root allocation.

Conclusions

The drought response of the weedy generalist *Polygonum persicaria* reflects a complex interplay between phenotypic plasticity and local differentiation. The three study populations were from a diversity of soil moisture habitats but expressed roughly similar patterns of functional plasticity that maintained fitness in dry compared with moist conditions. Such plasticity evidently contributes to tolerance of the range of moisture variability that occurs within source sites; strong expression of these plastic responses may allow for tolerance of contrasting sites as well. Although all three *P. persicaria* populations shared significant plasticity, the populations expressed different patterns of plasticity for specific aspects of functional response, reflecting genetic differentiation as well. These responses evidently interact functionally to result in similar levels of environmental stress tolerance.

Acknowledgments

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