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DYNAMIC PHENOTYPIC PLASTICITY FOR ROOT GROWTH IN *POLYGONUM*: A COMPARATIVE STUDY[1]

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Species differences in patterns of phenotypic plasticity may be an important aspect of adaptive diversity. Plasticity for functionally important root traits was studied in inbred field lineages of *Polygonum persicaria* and *P. cespitosum* (Polygonaceae). Replicate seedlings were grown in plexiglass rhizotrons under a range of constant and temporally variable moisture treatments. Plasticity was determined for final whole-plant biomass, root biomass allocation, and absolute and proportional root length. The dynamic aspect of root plasticity was examined by digitizing weekly tracings of the proportional deployment of each plant's root system to different vertical soil layers. Plants of both species expressed significant functionally adaptive phenotypic plasticity in the relative allocation, length, and vertical deployment of root systems in response to contrasting moisture conditions. Plasticity patterns in these closely related species were in general qualitatively similar, but for most traits differed in the magnitude and/or the timing of the plastic response. Dynamic changes in root deployment were more marked as well as faster in *P. persicaria.* Species differences in patterns of individual plasticity were generally consistent with the broader ecological distribution of *P. persicaria* in diverse as well as temporally variable moisture habitats.

Key words: drought tolerance; flood tolerance; phenotypic plasticity; *Polygonum*; root allocation; root foraging.

Many studies have examined phenotypic plasticity as an individual mode of plant adaptation to environment (see reviews by Bradshaw, 1965; Schlichting, 1986; Sultan, 1987, 1995; Bradshaw and Hardwick, 1989; Travis, 1994; Via et al., 1995). The ability to alter root systems so as to maintain function and growth when soil resources are limiting may be a key aspect of individual adaptive plasticity (Grime, 1994). Since soil moisture and nutrients vary temporally as well as spatially (Bazzaz and Sultan, 1987; Caldwell, 1994; Fitter, 1994; Bazzaz, 1996), this aspect of adaptive response may involve dynamic readjustments in root allocation, morphology, and spatial deployment (Eissenstat and Caldwell, 1989; Jackson and Caldwell, 1989; Larigauderie and Richards, 1994, and references). Although such dynamic responses have been little studied to date by evolutionary ecologists (Bell and Lechowicz, 1994), the potential importance of such ''ontogenetic plasticity'' has been increasingly recognized (Travis, 1994; Pigliucci and Schlichting, 1995; Gedroc, McConnaughay, and Coleman 1996; Pigliucci et al., 1996). In species with indeterminate growth, these responses may be expressed continuously through the life of the individual (Winn, 1996). Thus, studies that measure traits at only one moment in the lifecycle may miss a key aspect of adaptive plastic response to environmental variation (Gates, 1968; Aphalo and Ballaré, 1995; Pigliucci and Schlichting, 1995; Sultan, 1995; Gedroc, McConnaughay, and Coleman, 1996; Pigliucci, Diorio, and Schlichting, 1997).

Because root growth and deployment are critical to maintaining function in different environmental conditions, plasticity for these traits may influence the ecological tolerance of individuals, and hence the field distribution of species. Functionally adaptive responses to low soil resource levels include increased biomass allocation and specific and total root length, which jointly determine uptake surface area (Fitter, 1987; Jackson, Manwaring, and Caldwell, 1990; Fitter and Hay, 1993; Rodrigues, Pacheco, and Chaves, 1995, and references). Plasticity in spatial deployment of roots is equally critical to resource acquisition (Fitter, 1994). Local proliferation into moist and/or nutrient-rich soil microsites allows plants to effectively exploit variable soil environments (Eissenstat and Caldwell, 1988; Grime, 1994; Larigauderie and Richards, 1994; Jackson and Caldwell, 1996, and references). The effectiveness of this response depends on its rapidity as well as its extent, especially in the presence of competing neighbors (Eissenstat and Caldwell, 1989; Jackson and Caldwell, 1989; Fitter, 1994). Similarly, the ability of plants in flooded soils to rapidly deploy roots to surface soil layers where oxygen remains available is critical to plant function in such environments (Jackson, 1955; Cook, Mark, and Shore, 1980; Sultan and Bazzaz, 1993a, and references). Although studies are available of ontogenetic change in root biomass allocation (Bazzaz and Morse, 1991; Gedroc, McConnaughay, and Coleman, 1996), very little is known about the timing of root deployment responses to changing distributions of soil resources (Jackson and Caldwell, 1989).

Differences among species in patterns of plasticity for root allocation, morphology, and spatial deployment may thus contribute to species differences in ecological breadth with respect to soil environment (e.g., Cook, Mark, and Shore, 1980). However, although a number of studies have demonstrated the existence of individual plasticity for these traits (references in Jackson and Caldwell, 1989; Berntson and Woodward, 1992; Sultan and Bazzaz, 1993a; Fitter, 1994; Grime, 1994), very little is

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known about differences in patterns of root plasticity in closely related but ecologically distinct taxa. In general, despite the centrality of this issue for our understanding of adaptive evolution (Sultan, 1995), we have little information regarding differences among closely related, naturally evolved taxa in patterns of plasticity for ecologically important traits (Schlichting and Levin, 1986; Roskam and Brakefield, 1996; Sultan et al., 1998b).

Moisture availability is a particularly critical aspect of soil environments (Kramer, 1983; Grime, 1994). Plant growth may decrease in dry soils due to tissue dehydration as well as reduced mineral availability (Fitter and Hay, 1993; Caldwell, 1994). Soil flooding also reduces plant growth by decreasing the availability of oxygen to roots (Etherington, 1984; Jackson and Drew, 1984; Ernst, 1990, and references). Soil moisture varies spatially among and within habitats according to soil properties and topography; variation occurs vertically among soil layers as precipitation percolates down or as the water table rises to cause flooding (Kramer, 1980, 1983). Hence, the amount and distribution of moisture in the soil show dramatic temporal variability within any given site or microsite (Bazzaz, 1996, and references). Although root systems in a number of species have been shown to proliferate locally in response to the addition of nutrients (Crick and Grime, 1987; Caldwell, Manwaring, and Durham, 1991; Gross, Maruca, and Pregitzer, 1992; Pregitzer, Hendrik, and Fogel, 1993; Grime, 1994; additional references in Fitter, 1994; Caldwell, 1994; Laurigauderie and Richards, 1994), surprisingly few studies address root deployment plasticity in response to the distribution of soil moisture (aspects of root response to moisture environment are treated by Lauenroth et al., 1987; Wan, Sosebee, and McMichaels, 1995; Holmes and Rice, 1996; see also Coupland and Johnson, 1965; Berntson and Woodward, 1992). Furthermore, available studies of root deployment responses (i.e., to nutrients) seldom address the timing of the proliferation response (Jackson and Caldwell, 1989), and they largely involve crop plants grown in water or sand culture rather than naturally evolved taxa growing in soil (Fitter, 1994).

Here we present a comparative study of individual root system plasticity in response to both drought and flooding in two annual *Polygonum* species that have different ecological distributions with respect to soil moisture. *Polygonum persicaria* occurs in extremely dry to flooded microsites (from <1% to >200% of field capacity), while *P. cespitosum* is found only in moderately moist but not flooded soils (16–100% of field capacity; Sultan et al., 1998a). The species are closely related taxa within a monophyletic section of the genus (Löve and Löve, 1956), and share an identical life cycle as annual colonizers of disturbed habitats (Sultan et al., 1998a). This study system thus avoids confounding differences in plasticity with differences in either phylogeny or life history (Rabinowitz, 1981; Kruckeberg and Rabinowitz, 1985; Harvey and Pagel, 1991). To assess differences between the species in functionally adaptive aspects of root plasticity, we examined whole-plant traits such as root biomass allocation, total length, and morphology (specific length), as well as dynamic adjustment of root deployment over time in response to both constant and changing moisture conditions. We evaluated root deployment response to moisture in terms of adaptive plasticity by estimating the proportion of the plant's root system located in various vertical soil layers containing different amounts of moisture (see Fitter, 1994). Because root growth and deployment are strongly influenced by physical as well as chemical soil properties (Caldwell, 1994), we studied root growth in a naturalistic soil mix. We addressed the following specific questions: (1) How do *P. persicaria* and *P. cespitosum* plants alter root growth and deployment over time in response to different soil moisture conditions? (2) How do the two species differ in these patterns of plasticity? and (3) Do species differences in plastic response to specific moisture conditions correspond with differences in their field distribution?

MATERIALS AND METHODS

Experimental plant material—Experimental material was collected from two natural populations of each species, including one site where *Polygonum persicaria* and *P. cespitosum* co-occurred (Towle Paddock 1) and one additional site per species (Long Pond, *P. persicaria* and Arch Road Leeds, *P. cespitosum*; site details in Sultan et al., 1998a). Achenes from eight randomly chosen field parents from each population were grown under uniform greenhouse conditions and allowed to self-fertilize, to produce families of replicate inbred achenes (each family representing a different inbred field lineage). Five of these families were randomly chosen from each population, for an experimental sample of ten families per species (20 families total). Ten replicate achenes from each family were stratified at 4°C for 8 wk and germinated in flats of moist vermiculite on a greenhouse bench (21°–24°C day/19°–21°C night). Seedlings were fertilized once with 250 mL/flat of dilute Peters® 20:20:20 NPK (Grace-Sierra Horticultural Products Co., Milpitas, California) and grown to the second true leaf stage. Seedlings of approximately uniform size (both shoot and root systems) were used in the experiment.

Experimental treatments—One seedling from each of the 20 experimental families was randomly assigned to each of four moisture treatments ($N = 20$ plants per treatment; total $N = 80$). Seedlings were transplanted (28 May 1996) into individual flat 1.2-L containers designed for nondestructive root growth observations (''rhizotrons''; Berntson and Woodward, 1992). Each rhizotron was made from two clear, 6.35-mm plexiglass plates, bolted together through polyethylene side and bottom pieces and provided with drainage holes (Fig. 1). One plexiglass surface was painted white with waterproof marine enamel to maximize albedo and hence minimize soil temperature fluctuations (Berntson, Farnsworth, and Bazzaz, 1995). To promote root growth against the clear plate, rhizotrons were held in frames at an angle of 30° from the vertical (Gross, Maruca, and Pregitzer, 1992). To prevent light entry between adjacent rhizotrons, the clear surfaces were covered with white polyethylene foam sheets 2 mm thick. Each rhizotron was filled with a thoroughly moistened 2:2:1 mixture of coarse sand : sterilized topsoil : Turface™ calcined clay (Applied Industrial Material Corp., Deerfield, Illinois).

Seedlings in their individual rhizotrons were set in a randomized complete block design on two greenhouse benches, with one plant from each population (representing one of its five families) per treatment randomly assigned to each of five blocks. Soil was kept evenly moist for 7 d following transplanting, after which the following moisture treatments were imposed: moist (field capacity)—soil consistently moist throughout the container at all times; constant flooding—soil flooded at all times (containers submerged to within 4 cm of soil level); delayed flooding—soil initially moist throughout the container, then flooded as above after 4 wk; dry—soil initially moist throughout the container, then allowed to gradually dry down from upper to lower soil layers

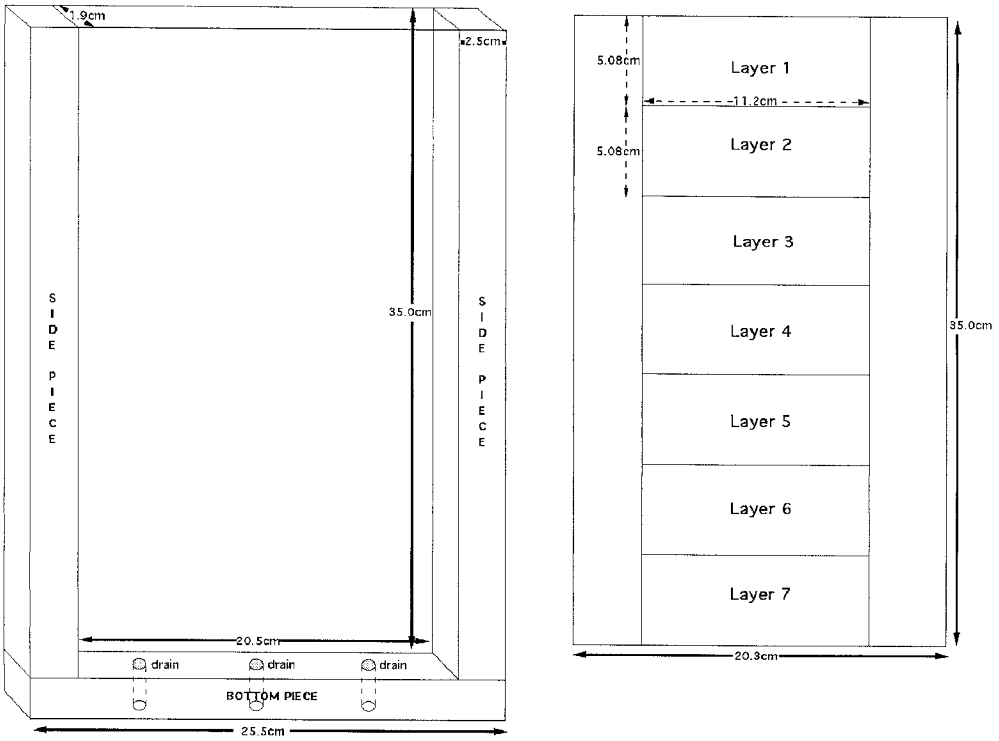

Fig. 1. Rhizotron container used for nondestructive observation of root growth (left); tracing field and its division into vertical layers to collect root deployment data (right).

(water added only when plants wilted and by bottom-watering only). Note that by the 3rd wk of the experiment, only the lowest soil layers in dry-treatment rhizotrons were moist (layers 5–7; Fig. 1). Plants were grown in the moisture treatments for 8 wk (4 June–1 August 1996) under ambient greenhouse light at 21°–24°C (day) and 19°–21°C (night). During the experiment two *P. cespitosum* plants died due to fungal infection.

Data collection—*(1) Vertical root deployment*—Vertical distribution of root systems over time was measured by manually tracing the root system of each plant (visible through the clear plexiglass plate) onto an acetate sheet. Each plant was traced once weekly for 8 wk, for a total of 640 separate tracings. The tracing field on each acetate sheet was divided vertically into seven 5.1-cm layers extending from 2 to 3 cm above the soil surface to the bottom of the rhizotron (Fig. 1). To avoid edge effects on root growth, 3.8-cm margins were excluded (Fig. 1; G. Berntson, personal communication). Note that the top layer (layer 1) included the uppermost 2–3 cm of soil as well as the 2–3 cm space above, so as to include all roots produced at or near the air-soil interface. Root tracings were digitized as Adobe Photoshop™ LE images (Knoll et al., 1995) using a ScanJet 4c flatbed scanner (Hewlett-Packard Co., Camas, Washington). Root length within each layer of the digitized image was measured according to the calculations of Pan and Bolton (1991), using software Root Length+ (Berntson, 1997). The proportion of the traced root system within each soil layer was calculated weekly for each plant as: $h_{i\,x}$ = (traced root length in layer i at week x divided by Σ traced root length in layers $i - 7$ at week x) $\times$ 100%.

In order to test whether this root tracing technique accurately estimated vertical root deployment, the entire soil volume for a random subsample of eight plants (one plant per species per moisture treatment) was sliced at harvest into the seven vertical layers, and the total length of roots present in each layer was directly measured using a Comair Optical Root Length Scanner (Hawker de Havilland, Melbourne, Australia). Root proportion by layer was calculated for this subsample as: $h_{i,\,8}$ = (measured root length in layer i at week 8 divided by Σ measured root length in layers $i - 7$ at week 8) $\times$ 100%. According to one-way MANOVA (SYSTAT 5.2; Wilkinson, Hill, and Vang, 1992), there was no significant effect of measurement method (tracing vs. direct) on the estimated proportion of roots deployed to the seven soil layers (Wilks' lambda = 0.59; $F = 0.80$; $P \leq 0.61$).

(2) Final plant traits—Plants were harvested one block at a time (31 July–1 August 1996). The number of senescent leaves on each plant was counted, and the plant was then separated into roots, vegetative shoots, reproductive support structures, and achenes. Any adventitious roots produced were collected separately; each plant's production of adventitious roots was roughly scored as low, intermediate, or high, and the node(s) of origin from the plant base recorded. To determine total root length, the entire fresh root system of each plant (including any adventitious roots) was carefully washed and measured with a Comair Optical Root Length Scanner. (Any taproot over 2.5 mm in diameter was excluded from the sample [Hawker de Havilland User's Manual TM 0001]; this amount was $\ll 1\%$ of total root length in all cases.)

Both vegetative and reproductive support tissues were oven dried (1 h at 100°C and $\geq$72 h at 60°–65°C); roots were air dried and subsequently oven dried ($\geq$72 h at 60°–65°C); achenes were air dried on open greenhouse benches. For each plant, total root biomass included belowground root biomass, taproot biomass, and adventitious root biomass; total plant biomass was calculated as the sum of shoot, total root, reproductive support, and total achene mass. Based on direct (optically scanned) measurements of total root length (see above), the following ratios were calculated: specific root length (SRL, metres of root per gram root tissue = total root length/total root biomass), root biomass proportion (grams root per gram plant tissue = total root biomass/total plant biomass), and root length ratio (RLR, metres of root per gram plant tissue = total root length/total plant biomass).

Data analysis—*(1) Vertical root deployment*—Every week, mean

TABLE 1. Analysis of variance for final whole-plant traits of *P. persicaria* and *P. cespitosum* grown in four moisture treatments. *F* values are shown with their probability levels in parentheses. Boldface *P* values are significant at an experimentwide probability level of <0.05 according to a sequential Bonferroni procedure (details in Data Analysis). Squared multiple correlation statistic (r^2) for each ANOVA model is given at left (SYSTAT 5.2).

N	Trait	Species (df = 1)	Treatment (df = 3)	Species × treatment (df = 3)	Population (species) (df = 2)
74	Total plant biomass	14.320	108.502	3.099	7.762
	$r^2 = 0.863$	(≤**0.001**)	(≤**0.001**)	(≤0.033)	(≤**0.001**)
74	Root biomass proportion	8.267	79.857	4.779	13.599
	$r^2 = 0.837$	(≤**0.006**)	(≤**0.001**)	(≤**0.005**)	(≤**0.001**)
75	Total root length	25.265	55.971	0.278	6.335
	$r^2 = 0.780$	(≤**0.001**)	(≤**0.001**)	(≤0.841)	(≤**0.003**)
75	Specific root length	6.463	22.705	0.305	7.993
	$r^2 = 0.616$	(≤**0.014**)	(≤**0.001**)	(≤0.822)	(≤**0.001**)
74	Root length ratio	12.958	23.930	2.489	0.787
	$r^2 = 0.634$	(≤**0.001**)	(≤**0.001**)	(≤0.069)	(≤0.460)

root deployment to each soil layer was computed for plants of each species in each moisture treatment (SYSTAT 5.2; weekly means for each layer based on ten plants per species per treatment). These complex data for root deployment over time were analyzed in two ways. First, we analyzed the proportional distribution of roots to all seven soil layers at each measurement date (week 1, week 2, etc.) using MANOVA (SYSTAT 5.2) to test the effects of species, moisture treatment, species by moisture treatment interaction, and population (nested within species). A sequential Bonferroni procedure ($k = 32$), was used to protect tablewide probability levels at ≤ 0.100 (this alpha value was employed to avoid Type 1 error due to this large number of tests; Zar, 1984; cf. Nagy and Rice, 1997). Second, we used repeated-measures MANOVA (SYSTAT 5.2) to analyze changes over time in root deployment to each soil layer, and to the top layers (layers $1 + 2$) and bottom layers (layers $6 + 7$). Repeated-measures MANOVA was employed instead of univariate analysis due to the circularity of the within-subject factor, ''week'' (von Ende, 1993). The repeated-measures model tested the main effects of species, moisture treatment, and week, and the interaction effects of species by week, moisture treatment by week, and species by moisture treatment by week. We followed both analyses with separate MANOVA and repeated-measures MANOVA for plants in each moisture treatment, to test species differences within specific treatments. A significance level of $P \leq 0.1$ was used for these within-treatment tests since total *N* was only 20 (Sultan and Bazzaz, 1993b). Full details of all statistical tests are reported by Bell (1997).

(2) Final plant traits—For each trait, species means and standard errors for each moisture treatment were calculated, using measurements of the same ten inbred lines of each species grown in all four treatments. These means are presented as norm of reaction plots to facilitate comparison of species plasticity patterns across environments, but note that the order of treatments in these plots is arbitrary. Two-way nested Model I ANOVA was performed for each trait to test the effects of species, moisture treatment, species by moisture treatment interaction, population (nested within species), and block (SYSTAT 5.2; Wilkinson, Hill, and Vang, 1992). Total root length was square root-transformed (Steele and Torrie, 1960); all other traits met the normality and homoscedasticity assumptions of ANOVA without transformation. Block effects were nonsignificant in all cases ($P > 0.05$). For each trait, this analysis was followed by separate one-way nested ANOVA for the effect of species within each moisture treatment (see section 1 above). In all analyses, the species effect was tested over the error term, since population was considered a fixed, rather than random, effect (Winer, 1971; see Sultan et al., 1998a). A sequential Bonferroni procedure was used to correct probability levels for multiple, simultaneous tests (alpha = 0.050, $k = 5$; Rice, 1989). Planned pairwise treatment contrasts were performed following ANOVA (SYSTAT 5.2). Three plants that developed abnormally were omitted from the analysis, and the total biomass value for one plant was lost due to experimental error (final sample $N = 75$). No statistical outliers were deleted.

Note that total plant biomass rather than achene biomass was used as an estimate of plant performance (fitness), since *P. persicaria* plants had not completed reproduction by the time of harvest. The correlation between total achene biomass and total plant biomass for these species is extremely high (Pearson pairwise correlation $r = 0.941$ for plants of both species grown in 12 experimental light, moisture, and nutrient environments; S. E. Sultan, unpublished data).

RESULTS

Overall patterns of plasticity—Plants of both species showed significant phenotypic plasticity for all measured root traits. Effects of moisture treatment on all whole-plant traits were highly significant (and greater than species effects; Table 1); and significant treatment effects on vertical root deployment were apparent from week 1 and in all subsequent weeks (Table 2). With respect to plant performance, *P. persicaria* and *P. cespitosum* plants produced similar total biomass in the favorable moist treatment, and reduced biomass by $\sim 80\%$ when grown in dry soil (Fig. 2; Table 3). Plants of *P. persicaria* had significantly lower total biomass in constant but not delayed flooding compared to moist soil (Table 3). In contrast, *P. cespitosum* plants produced significantly lower total biomass in both the constant and delayed flooding treatments than in the moist treatment (Table 3).

The two species showed similar patterns of change in total root length in response to moisture treatment (nonsignificant species × treatment effect, Table 1). Plants of both species produced the longest root systems in the moist treatment and significantly shorter root systems in the dry, delayed flooding, and constant flooding treatments (Fig. 2). (Relative to plants in the moist treatment, these changes in absolute root length primarily reflect reduced plant biomass in the dry treatment, reduced allocation to roots in the delayed flooding treatment, and both effects in the constant flooding treatment.) The two species also showed very similar response patterns for specific root length, although *P. persicaria* plants produced slightly higher SRL in every treatment (Table 1; Fig. 2).

The species patterns of allocational plasticity were qualitatively similar but differed quantitatively (signifi-

TABLE 2. MANOVA on vertical root deployment to seven soil layers, at each of eight measurement intervals. Wilks' Lambda F statistics are shown with probability levels for multivariate tests on species, treatment, species × treatment, and population (nested within species). Boldface P values are significant at a tablewide probability level of ≤0.100 according to sequential Bonferroni procedure to avoid Type I error due to $k = 32$ (details in Data Analysis).

	Week							
Source	1	2	3	4	5	6	7	8
Species	1.65	2.67	2.293	3.37	3.33	3.16	1.58	2.45
	(≤0.174)	(≤0.023)	(≤0.039)	(≤**0.004**)	(≤**0.005**)	(≤**0.007**)	(≤0.160)	(≤0.029)
Treatment	3.99	10.28	9.176	12.20	2.90	11.52	12.98	13.23
	(≤**0.001**)	(≤**0.001**)	(≤**0.001**)	(≤**0.001**)	(≤**0.001**)	(≤**0.001**)	(≤**0.001**)	(≤**0.001**)
Species × treatment	0.85	1.33	0.88	1.06	2.00	1.40	1.04	1.38
	(≤0.596)	(≤0.177)	(≤0.616)	(≤0.402)	(≤**0.008**)	(≤0.125)	(≤0.422)	(≤0.135)
Population (species)	1.72	2.79	3.16	1.93	1.57	0.81	1.25	1.13
	(≤0.101)	(≤**0.002**)	(≤**0.001**)	(≤0.030)	(≤0.099)	(≤0.656)	(≤0.249)	(≤0.343)

cant species × treatment effect, Table 1). In plants of both species, root biomass proportion was highest in dry soil, and lowest under constant and delayed flooding (Fig. 2). However, plants of *P. persicaria* more sharply increased root allocation in dry soil (Fig. 2). Root length ratio plasticity patterns, which reflect both root biomass proportion and SRL, were likewise qualitatively similar in the two species. Plants of both species produced the highest root length per unit plant biomass in dry soil, a moderate ratio in both moist and constantly flooded soils, and a low ratio under delayed flooding, where root death in newly flooded soil layers evidently proceeded more rapidly than the production of new roots at the surface (Fig. 2). However, this plastic response was stronger in *P. persicaria* plants, which unlike *P. cespitosum* significantly increased RLR in dry compared with moist soil (significant species effect within dry treatment; Fig. 2; due to the high variability of this ratio trait the overall species × treatment interaction effect for RLR was marginally nonsignificant; Table 1).

The two *Polygonum* species showed qualitatively similar root deployment responses to moist and flooded but not to dry soil (Figs. 3–6). Plants of both species distributed roots evenly throughout moist soil layers (Fig. 3) and solely to the uppermost layers of constantly flooded soil (Fig. 4). As expected, root deployment patterns in the delayed flooding treatment were initially similar to those in the moist treatment (compare Figs. 5 and 3, week 4); both species responded to the flooding event by increasing root deployment to surface soil layers (Fig. 7). However, only *P. persicaria* significantly increased root deployment to lower soil layers in dry soil compared with moist soil (compare Figs. 6 and 3; effect of dry vs. moist soil on vertical root deployment in week 8 significant at $P \leq 0.002$), while final root distribution patterns in *P. cespitosum* did not differ in the two treatments (Figs. 3, 6; effect of dry vs. moist soil on deployment pattern nonsignificant at $P \leq 0.270$). Furthermore, the species differed in the timing of deployment responses to the four moisture treatments (significant effect of species × treatment × week interaction on proportion of roots in layers 1, 4, 6, and 7, $0.002 \geq P \leq 0.02$).

Comparison of species responses to specific moisture treatments—*Moist treatment*—Total plant biomass in this favorable treatment was equally high in both species (Fig. 2). These similar final growth levels were associated with slightly (nonsignificantly) higher total allocation to roots and hence total root length and RLR in *P. persicaria* than *P. cespitosum* (Fig. 2). The two species also showed very similar, even patterns of root distribution to the seven soil layers (Fig. 3), such that their final patterns of vertical root deployment were statistically indistinguishable (species effect on root deployment in week 8 nonsignificant at $P \leq 0.277$).

Dry treatment—After 8 wk of growth in the dry treatment, *P. persicaria* and *P. cespitosum* plants had produced similar total biomass, although root allocation and therefore total root length and RLR were significantly higher in *P. persicaria* (Fig. 2). The two species also differed in both timing and final patterns of root deployment in response to the drying-down of upper soil layers (Fig. 6). Recall that by week 3 moisture was available only in layers 5–7 and the top two soil layers were very dry. *Polygonum persicaria* plants rapidly and increasingly deployed roots to moist lower layers and reduced root proportion in the uppermost layers, compared with a slower and less pronounced response in *P. cespitosum* (species × week interaction effect on root proportion in layers 6 + 7 in the dry treatment significant at $P \leq 0.020$; species × week effect on deployment to layers 1 + 2 significant at $P \leq 0.054$; cf. Fig. 6). Final patterns of root deployment differed significantly in the two species (species effect on vertical root deployment at week 8 significant at $P \leq 0.030$). After 8 wk in the dry treatment, *P. persicaria* plants had deployed ~65% of roots to the lowest two soil layers, compared with ~44% in *P. cespitosum* (Fig. 6).

Delayed flooding treatment—The species differed dramatically in fitness under delayed flooding, where plants of *P. persicaria* produced on average ~60% more biomass than those of *P. cespitosum* (Fig. 2). This marked fitness difference was not associated with differences in either allocation to roots or RLR (Fig. 2), and plants of both species appropriately increased the proportion of roots in the uppermost soil layer in response to the flooding event (Fig. 5). However, the species differed significantly in both the magnitude and the timing of this plastic response to flooding. Before flooding was imposed at the end of week 4, the species had similar vertical root deployment patterns (Fig. 5). After flooding, *P. persicaria* plants rapidly increased roots at the soil surface, but *P.*

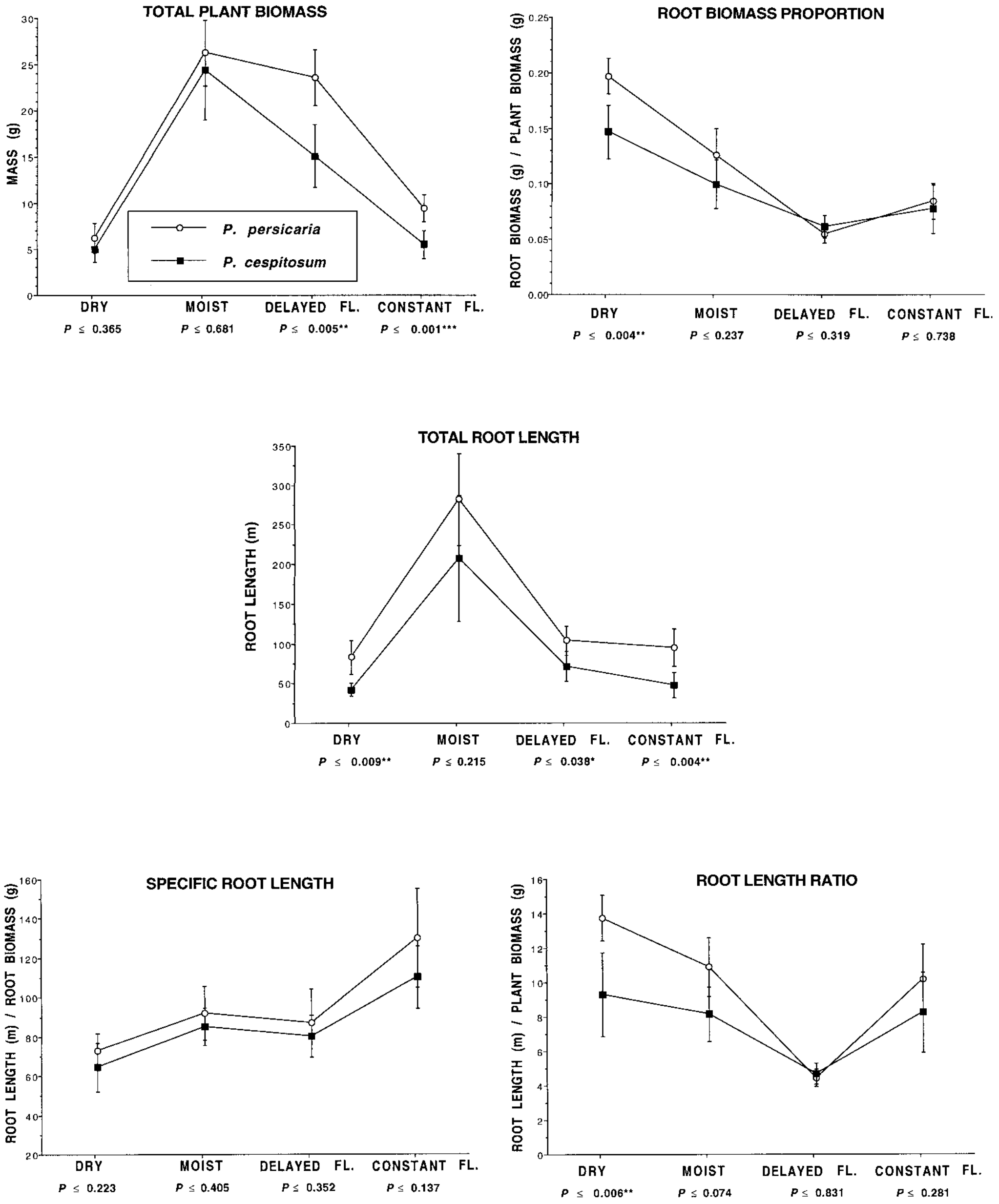

Fig. 2. Effect of moisture treatment in *P. persicaria* and *P. cespitosum* on total plant biomass, root biomass proportion, total root length, specific root length, and root length ratio. For each trait, means ± 2 SE are shown of 9–10 plants per species in each treatment. Probability levels indicate significance test for the effect of species within each treatment according to separate one-way ANOVA (details in Data Analysis section).

TABLE 3. Mean reductions in total plant biomass under dry, constant flooding, and delayed flooding treatments compared with the favorable moist treatment in *P. persicaria* and *P. cespitosum. F* values and their significance levels are shown for linear contrasts based on ANOVA for effect of treatment within each species (details in Data Analysis).

	P. cespitosum			*P. persicaria*		
	% Biomass reduction	Contrast *F*	*P*	% Biomass reduction	Contrast *F*	*P*
Moist vs. dry	−81	199.2	≤0.001	−77	121.9	≤0.001
Moist vs. constant flooding	−78	199.5	≤0.001	−65	85.5	≤0.001
Moist vs. delayed flooding	−39	48.7	≤0.001	−10	2.28	≤0.143

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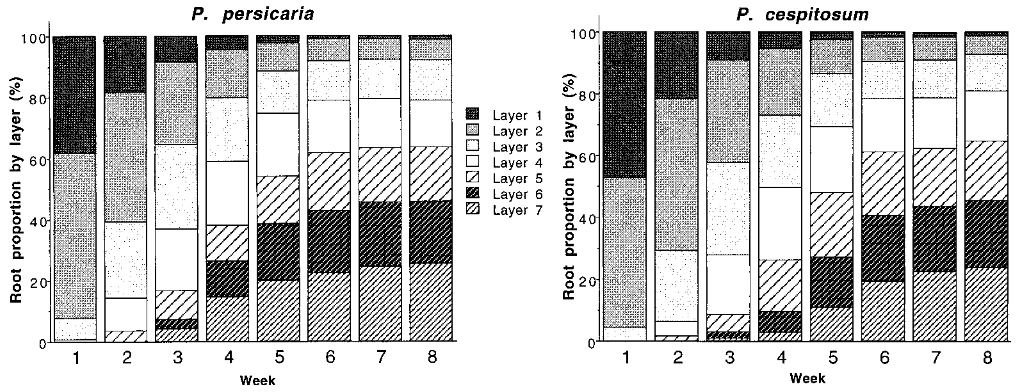

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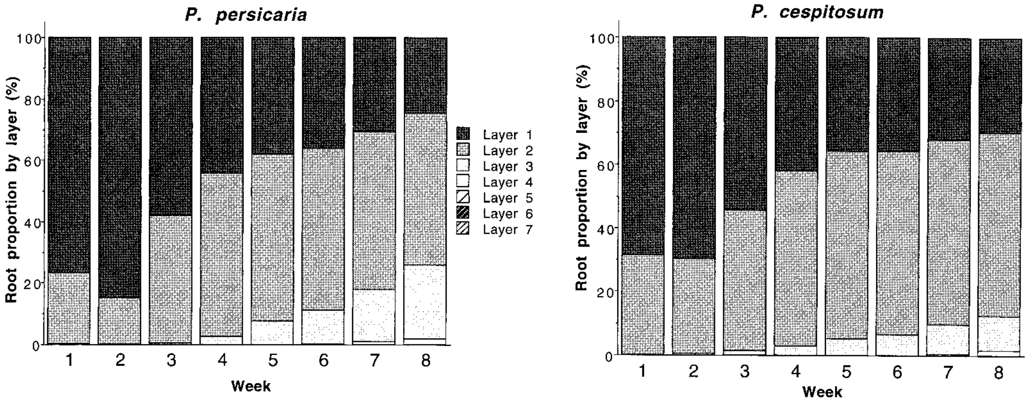

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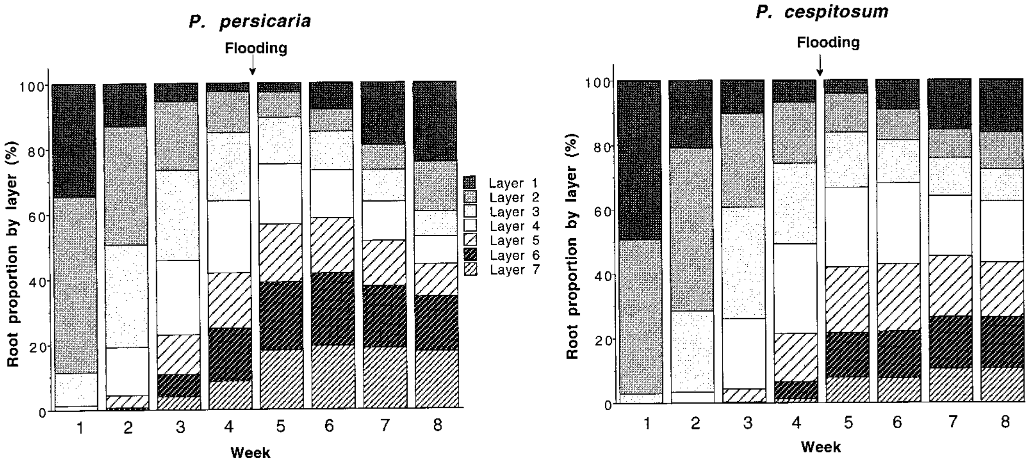

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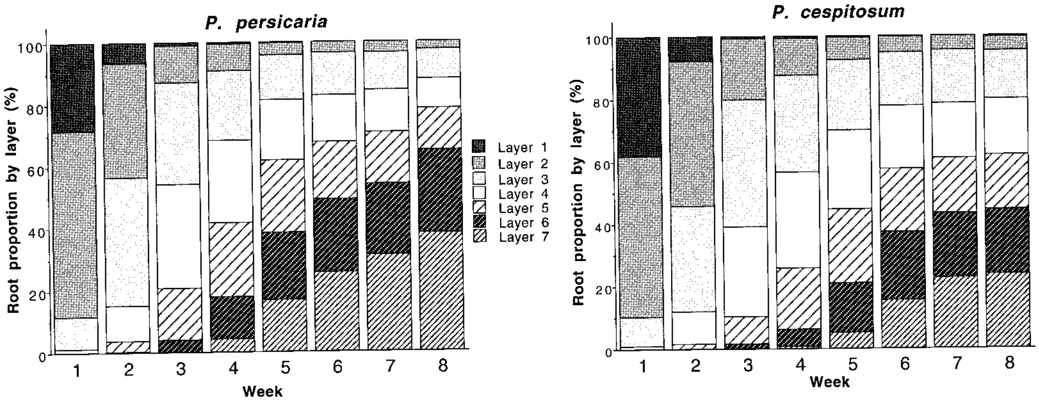

Figs. 3–6. Vertical root deployment patterns over time of plants grown in four moisture treatments. Each column shows the mean proportion of roots located in each soil layer for a given week based on 9–10 plants per species measured at weekly intervals (details in Materials and Methods). **3.** Moist soil. **4.** Constant flooding. **5.** Delayed flooding. **6.** Dry soil.

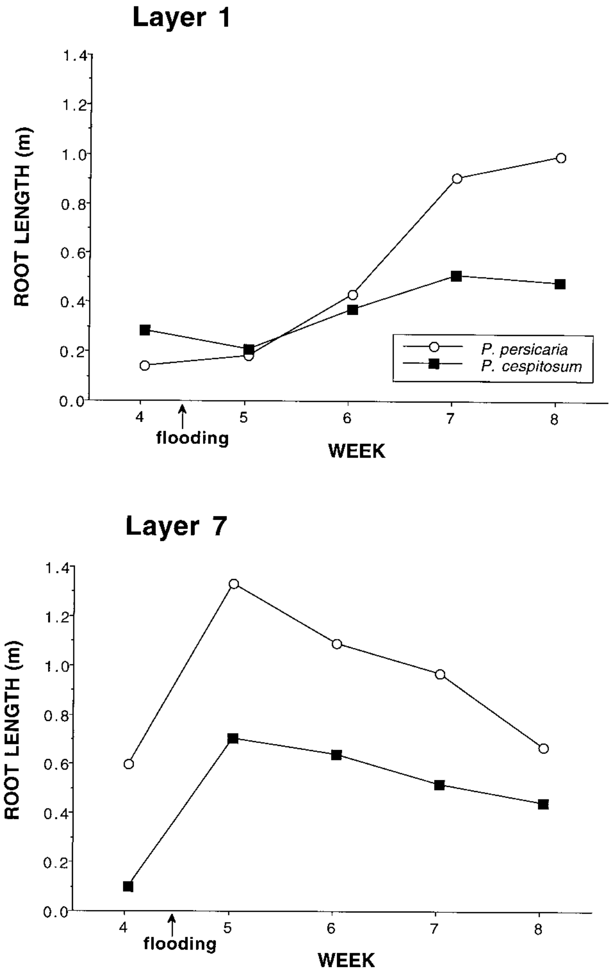

Fig. 7. Mean change in absolute root length in response to delayed flooding in *P. persicaria* and *P. cespitosum.* (Top) Length of traced roots in surface soil layer (layer 1). (Bottom) Length of traced roots in lowest soil layer (layer 7).

cespitosum plants showed a significantly slower and less marked change in root deployment (species × week interaction effect on root proportion in layer 1 significant at $P \leq 0.075$; cf. Fig. 5). Compared with root distribution just prior to flooding, *P. persicaria* plants increased root deployment to layer 1 by 9, 113, 612, and 803% in weeks 5–8, respectively, while in contrast *P. cespitosum* plants reduced root deployment to layer 1 in week 5, and then increased deployment by 32, 119, and 131% in weeks 6–8, respectively. In both species, this increase in proportional deployment to layer 1 reflected both root death in flooded lower layers and the production of new roots at the top layer (Fig. 7). *Polygonum persicaria* plants increased root production at the surface area sixfold compared with a twofold change in *P. cespitosum* (Fig. 7). In addition, by week 8 *P. persicaria* plants had reduced the proportion and absolute length of (presumably useless) roots in the bottommost soil layer more markedly than had plants of *P. cespitosum* (Figs. 5, 7).

Constant flooding treatment—Polygonum persicaria plants also had dramatically higher fitness under constant flooding than plants of *P. cespitosum* (~75% more total biomass; Fig. 2). As in the delayed flooding treatment, there were no associated species differences in root allocation or RLR, and only a slight (nonsignificant) difference in SRL (Fig. 2). Although constantly flooded plants of both species placed ~99% of their roots in the top three soil layers (Fig. 4), the species differed significantly in the timing of this deployment response to flooding (effect of species × week interaction on root deployment to layer 1 significant at $P \leq 0.050$). *Polygonum persicaria* plants more quickly deployed a higher proportion of roots to the soil/air interface layer (77% of roots in week 1 and 86% of roots in week 2, compared with 68 and 70%, respectively, in plants of *P. cespitosum*; Fig. 4). As a result, by week 2 the species differed significantly in vertical root distribution patterns (species effect on root deployment in week 2 significant at $P \leq 0.094$). Following this initial lag, in the subsequent weeks of the experiment patterns of root deployment were similar in the two species (Fig. 4).

DISCUSSION

Patterns of plasticity in P. persicaria and P. cespitosum—Individuals of both species expressed considerable phenotypic plasticity for the absolute and relative size (length and biomass), structure, and vertical placement of root systems in response to different soil moisture environments. Root deployment responses were rapid and labile, showing significant treatment differences within one week. The direction and magnitude of these responses depended on both the trait measured and the environmental treatment. This kind of highly specific developmental adjustment may constitute adaptive phenotypic plasticity: specific phenotypic responses to environmental conditions that are functionally advantageous to those conditions (Bradshaw, 1965; Schlichting, 1986; Sultan, 1987, 1995; Bradshaw and Hardwick, 1989; West-Eberhard, 1989; Travis, 1994; Via et al., 1995).

Changes in absolute root length and mass reflect the inevitable growth limits of suboptimal moisture environments, while functionally appropriate changes in proportional traits, such as an increased ratio of root length and mass to total plant biomass in dry soil, indicate adaptive plastic adjustment in the context of such limits (Sultan, 1995). Preferential deployment of roots to moist or aerated soil layers under conditions of drought and flooding, respectively, also comprise functionally adaptive plastic response (cf. Justin and Armstrong, 1987). Plants of both species expressed these specific, appropriate root growth and deployment responses. Hence, the precise patterns of plasticity expressed by *P. persicaria* and *P. cespitosum* plants (along with their ability to survive and reproduce in all four contrasting moisture treatments) indicate that both species possess adaptive plasticity for several aspects of root growth. This type of individual adaptability is expected to be relatively high in annual plants of variable environments such as these colonizing species (Bazzaz, 1996, and references).

Although it is clear that congeneric species may differ in patterns of individual phenotypic response to environment (Schlichting and Levin, 1986; Carter and Grace, 1990; Laan et al., 1989; Aerts and de Caluwe, 1994; Blom et al., 1994; Pigliucci, Diorio, and Schlichting, 1997), little is known about the specific ways that closely related species are likely to differ in patterns of plasticity. In this study, plastic changes in functionally important aspects of root systems generally occurred in the same direction in plants of both *Polygonum* species: patterns of plasticity in response to moisture environment were qualitatively similar in the two species (as indicated by the generally slight species × treatment effects). In one trait (specific root length), plastic changes were similar in magnitude as well as direction, such that the species' patterns of response were parallel across the range of environments. However, for most of these traits, the species' patterns of plasticity differed quantitatively (reflected in significant species differences within particular treatments). Individuals of *P. persicaria* generally showed a more pronounced change in response to moisture environment (e.g., in root biomass proportion, root length ratio, and vertical deployment to appropriate soil layers).

The species also differed in a subtle but ecologically critical aspect of plastic root response—the timing of root deployment responses to changes in soil resources. *Polygonum persicaria* and *P. cespitosum* showed significantly different root deployment changes over time in response to both dry soil and delayed flooding. Because the adaptive impact of plasticity in maintaining function depends in part on timely response to environmental change, differences between species in the timing of plastic adjustments may have important ecological consequences (Tilman, 1988; Schmitt and Wulff, 1993; Aphalo and Ballaré, 1995; Pigliucci and Schlichting, 1995). A temporal delay can render ineffectual an appropriate plastic response (Sultan, 1995; e.g., equivalent but delayed shoot elongation in a flood-intolerant rice cultivar; Eiguchi et al., 1993). Hence, despite the qualitatively similar response patterns of *P. cespitosum* and *P. persicaria* to delayed and constant flooding and their quantitatively equivalent final deployment patterns under constant flooding, the slower response of *P. cespitosum* may strongly limit flood tolerance in this species (see next section). Generally, the ability to rapidly proliferate active roots in response to resource availability is likely to enhance plant success at capturing fluctuating, mobile soil resources (e.g., Lauenroth et al., 1987), especially under competitive conditions (Fitter, 1994) or in the event of soil gaps (Eissenstat and Caldwell, 1989). The rapid, adaptive root deployment responses of *P. persicaria* individuals revealed in this experiment may thus contribute to the species' success in resource-rich as well as resource-poor conditions (Sultan et al., 1998a). Plastic changes over time in response to environment have been documented for a number of growth and reproductive traits in response to such external and internal environmental cues as light (Novoplansky, Cohen, and Sachs, 1994; Jones, 1995; Pigliucci and Schlichting, 1995), nutrients (Gersani and Sachs, 1992; Pigliucci, Diorio, and Schlichting, 1997), temperature regime (Winn, 1996), flooding (Van der Smam, van Tongeren, and Blom, 1988; Van der Smam, Blom, and Barendse, 1993), neighbors (Turkington, 1983; Novoplansky, Cohen, and Sachs, 1990), and maternal investment (Diggle, 1994). To our knowledge, this study documents for the first time differences among closely related taxa in temporal (or ''ontogenetic'') plasticity patterns of potential adaptive significance.

The species' root responses did differ qualitatively in one important respect: *P. persicaria* plants showed markedly different vertical root deployment patterns in every moisture treatment, while *P. cespitosum* did not alter root deployment in dry vs. moist soils. This result suggests that closely related species may differ in their ability to sense and respond to a given environmental stress. This may reflect different sensitivities of the two species to low soil water potentials as an environmental cue; alternatively, both species may perceive the cue, but only *P. persicaria* subsequently produce the appropriate developmental response (Fitter, 1987; Aphalo and Ballaré, 1995). An analogous difference was found at the population level by Wan, Sosebee, and McMichaels (1995), who showed that certain *Gutierrezia sarothrae* populations failed to alter root deployment in response to drying of upper soil layers. Both sensitivity to variation in soil moisture and the capacity for associated plastic response may be critical to plant tolerance of habitats that are subject to microspatial and temporal drought stress. In general, the capacity to sense environmental change may be of great ecological importance in temporally variable habitats (Bazzaz, 1996).

Preferential deployment of roots to the precise location(s) of soil resources is considered a critical aspect of functionally adaptive plant plasticity (Eissenstat and Caldwell, 1988; Grime, 1994; Laurigauderie and Richards, 1994; Caldwell, 1994, and references). Although the timing of these responses is not known, plants of many species have been shown to proliferate roots in the precise locations where nutrients or both nutrients and water are available (Crick and Grime, 1987; Tilman, 1988; Eissenstat and Caldwell, 1989; Caldwell, 1989; Eissenstat, 1991; Pregitzer, Hendrik, and Fogel, 1993; additional references in Hutchings and de Kroon, 1994; Aphalo and Ballaré, 1995). Other plant species have been found to alter root deployment patterns in response to such environmental cues as the presence of neighboring roots (McConnaughay and Bazzaz, 1992) and oxygen availability (Laan, Clement, and Blom, 1991). The mechanisms underlying these highly specific root deployment responses are not well known (Kramer, 1988). With respect to drought response, it has been suggested that root caps are able to directly sense and respond to moisture gradients (Takahashi and Scott, 1993), and/or to sense chemical or hormonal signals produced by roots of droughted (neighboring) plants (Davies and Zhang, 1991; Aphalo and Ballaré, 1995). Unfortunately, with the exception of the phytochrome cue system for perceiving light quality (references in Schmitt and Dudley, 1996), mechanisms whereby individual plants perceive environmental stress remain poorly understood (Geiger and Servaites, 1991).

Functional significance of species responses to specific moisture treatments—In consistently moist soil, both species produced root systems of moderate length and mass in proportion to total plant size that were evenly deployed throughout the soil layers. When resources such as moisture or nutrients are distributed throughout the soil, such a vertically homogeneous root deployment pattern maximizes their effective collection by the plant (Coupland and Johnson, 1965; Crick and Grime, 1987; Berntson and Woodward, 1992; Gross, Maruca, and Pregitzer, 1992; Berntson, Farnsworth, and Bazzaz, 1995). Note that both species occupy moist sites in the field (Sultan et al., 1998a).

When upper soil layers were allowed to dry down, total plant growth was severely reduced in both species (see Kramer, 1980, and references on inevitable growth reductions due to limited soil moisture). In *P. persicaria*, these smaller plants preferentially proliferated roots in the lower soil layers where moisture remained available, increasing the proportion of roots to lower layers over time as upper soil layers became increasingly dry. This progressive root deployment response may enhance tolerance of dry soils in the field, where (depending on rainfall) upper soil zones may become quite dry as the season progresses (e.g., Sultan and Bazzaz, 1993a). Several species have been shown to deploy roots to lower, moist soil layers in the field (Mambani and Lal, 1983; Wan, Sosebee, and McMichaels, 1995; Gallardo, Jackson, and Thompson, 1996; Holmes and Rice, 1996). In addition, by increasing biomass allocation to roots, droughted *P. persicaria* plants also significantly increased the length of root produced per unit of plant tissue. Since root length is directly related to absorptive surface area (Fitter and Hay, 1993; Rodrigues, Pacheco, and Chaves, 1995), such a response would appropriately increase the relative availability of soil moisture as well as mineral nutrients (Viets, 1972; Caldwell, 1994). Numerous studies have indirect evidence for this type of plasticity in response to limited soil moisture (e.g., Mooney and Gulmon, 1979; Meyer and Boyer, 1981; Sultan and Bazzaz, 1993a; Pell et al., 1993; Rodrigues, Pacheco, and Chaves, 1995; Holmes and Rice, 1996; Zhang, 1996). This allocational plasticity may contribute to the realized tolerance of *P. persicaria* for habitats subject to severe drought at surface levels (Sultan et al., 1998a).

In contrast, *P. cespitosum* plants in the dry treatment showed neither plastic increases in root length ratio, nor increased deployment of roots to lower, moist soil layers. Despite the absence of these presumably adaptive plastic root responses, *P. cespitosum* plants produced the same total biomass in this experimental treatment as did those of *P. persicaria*. This result suggests that individuals of *P. cespitosum* may maintain moisture availability and hence growth in dry soil in other ways, possibly through low transpiration rates or extraction water potentials (cf. Meyer and Boyer, 1981; Fitter and Hay, 1993). Indeed, *P. cespitosum* plants have consistently lower stomatal conductances than *P. persicaria* (Sultan et al., 1998b), and hence may more effectively conserve water. Note however that unlike *P. persicaria*, *P. cespitosum* does not occur in dry, high light habitats (Sultan et al., 1998a) where transpiration demands are likely to be quite high. Hence, despite similar levels of performance in dry soils in the greenhouse (where the drought syndome is modulated by high humidity), the species' contrasting root plasticity responses to drought may contribute to this difference in their realized ecological breadth.

Plants of *P. persicaria* maintained higher growth in both delayed and constant flooding than did plants of *P. cespitosum*. These performance differences were associated with significant differences in both the timing and extent of root deployment to surface soil layers in both flooding treatments. The production of a dense root system at the soil/air interface and uppermost, aerated soil layers is a well-understood, functionally appropriate response to soil flooding, since roots cannot respire in lower, anoxic soil zones (Cook, Mark, and Shore, 1980; Justin and Armstrong, 1987). Species' differences in the ability to produce such root systems may help explain differences in their ecological distribution (e.g., Cook, Mark, and Shore, 1980). In response to both constant and delayed flooding, *P. persicaria* individuals were quicker to develop appropriate superficial root systems than plants of *P. cespitosum*. Such rapid response to soil flooding is likely to be a key aspect of realized flood tolerance (Blom et al. 1990, 1994; Visser et al., 1995). The significantly lower fitness of *P. cespitosum* plants under both constant and delayed flooding (despite equally high final levels of root allocation, extent, and surface deployment) suggests that their slower plastic deployment response may contribute to the exclusion of this species from flooded habitats. Conversely, the ability of *P. persicaria* plants to quickly produce functionally appropriate root systems may contribute to this species' tolerance of habitats that experience flooding (Sultan et al., 1998a).

Plants of both species increased specific root length in response to constant flooding. Such a response is contrary to theoretical expectations (Eissenstat, 1992) since a relative increase in surface area might promote excessive loss of oxygen to the soil (Justin and Armstrong, 1987). Note, however, that such expectations are based on the assumption that root tissue density is constant across environments, such that increased specific root length necessarily indicates a narrower root diameter (cf. Eissenstat, 1992). This assumption may well be invalid for plants in flooded soils, which may have lower tissue density due to the production of aerenchyma tissue containing large, air-filled spaces or lacunae (Cook, Mark, and Shore, 1980; Smirnoff and Crawford, 1983). Aerenchyma promotes oxygen diffusion below the water level through internal air spaces, and thus maintains oxygen supplies to submerged tissues (Crawford, 1982; Smirnoff and Crawford, 1983; Justin and Armstrong, 1987; Heathcote, Davies, and Etherington, 1987; Blom et al., 1990). The high specific root length in flooded plants of both *P. persicaria* and *P. cespitosum* may reflect appropriate anatomical plasticity, rather than a maladaptive increase in relative surface area. Direct anatomical studies are required to determine whether plants of *P. cespitosum* and *P. persicaria* do indeed produce aerenchyma in response to flooding, and whether the species differ in this type of anatomical plasticity.

It has long been recognized that species may differ in characteristic rooting depths and that such differences may influence ecological distribution (Coupland and Johnson, 1965; Parrish and Bazzaz, 1976; Cody, 1986). The results of this study demonstrate that species' differences in functionally important aspects of root growth and deployment may be far more complex than this view suggests. Such species' differences must be seen to include variation for patterns of individual plasticity in response to soil environments. This variation may entail differences in the direction of plastic response, the magnitude of the response, or the precise timing of the response. Comparative studies that incorporate all three aspects of individual plasticity will contribute substantially to our understanding of adaptive diversity and its ecological consequences.

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