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Contrasting ecological breadth of co-occurring annual *Polygonum* species

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Summary

1 Understanding the relative distributions of ecological generalists vs. specialists requires precise characterization of the environmental ranges of closely related taxa. The ecological breadth of four annual species in the genus *Polygonum* was determined from field measurements taken from five natural populations per species in a common geographical range.
2 Significant early and late-season differences among the species were found for available light (photosynthetically active radiation) at canopy and mid-canopy levels, and for soil temperature, moisture availability, macronutrient content, pH, cation exchange capacity (CEC) and structure, at two depths. Field sites within each species also differed significantly for these variables.
3 The field distribution of *P. persicari*a covers the broadest range of habitats, from moderate shade with very dark microsites to full insolation, cool to very warm soils, flooded to dry moisture conditions, and organic, high-nutrient to nutrient-poor soils.
4 *Polygonum lapathifolium* is comparatively intolerant of shade, particularly early in the growth season. Although this species occurs in flooded to moderately dry conditions and in poor as well as rich soils, its moisture and nutrient ranges do not include such low extremes as those of *P. persicaria*, and its range of soil temperatures is also narrower.
5 *Polygonum cespitosum* is restricted to low-light habitats and to consistently moist soils that do not flood. The species is, however, found in a moderately broad range of soil types and macronutrient availabilities. *Polygonum cespitosum* occurs in extremely low-light habitats that are evidently beyond the shade tolerance of the other species.
6 *Polygonum hydropiper* is restricted to high-light sites with highly organic, consistently very moist or flooded soils. Unlike its congeners, this species can tolerate flooded soils during seedling establishment. The species is limited to soils with high early nitrate and calcium content, moderate CEC, and pH close to 6.0, but tolerates a broad range of soil temperatures.
7 The occurrence of spatial and temporal environmental variability within as well as among field populations of *Polygonum* species suggests that tolerance of such variability may result from individual phenotypic plasticity rather than from ecotypic adaptation of entire populations.

Keywords: environmental variability, generalists, niche breadth, *Polygonum*, specialists, species distribution

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Introduction

Successful and widespread colonizing species often occur in a diverse range of habitats, and hence are believed to be characterized by broad environmental tolerances (Baker 1965, 1974; Brown & Marshall 1981; Rice & Jain 1985; Bazzaz 1986). Such species are termed ecological 'generalists', in contrast to 'specialists' characteristic of particular habitats. The distinction between generalists and specialists is a critical element in theories about the evolution of

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phenotypic plasticity (Levins 1968; Sultan 1987; Crick & Grime 1987; Macdonald *et al.* 1988; Bradshaw & Hardwick 1989; Van Tienderen 1991) as well as in discussions of niche breadth and overlap (Colwell & Futuyma 1971; Macarthur 1972; Brown 1984; Silvertown 1984; Pianka 1988; Bazzaz 1991). Yet despite its fundamental importance, this distinction is generally based on non-quantitative, presumably self-evident differences in species distribution (Futuyma & Moreno 1988). Remarkably few studies have rigorously compared the realized ecological breadth of species (i.e. the range of environmental conditions in which they occur in the field, in the presence of competition and other stresses); fewer still have examined relative breadth for more than one environmental factor. Indeed, it is not known whether a species' ecological breadth for different resources or physical parameters is likely to be positively or negatively correlated (Futuyma & Moreno 1988). Hence, although the concept is widely employed, it is not known whether in fact certain species may be 'generalists' for many aspects of the environment, or whether this is an assumption based on their occupancy of several distinct types of habitat. Similarly, it is not known whether ecological 'specialists' are narrowly distributed with respect to just one or to several environmental factors, or indeed whether such species occur in particular habitats that generalists are unable to occupy (Silvertown 1984; Sultan 1992).

Clearly, a key initial step in understanding the ecology and ultimately the evolution of generalist vs. specialist species is to clarify the empirical basis of this distinction. This entails precise quantification in order to compare rigorously the range of conditions such taxa occupy along several different, ecologically important environmental axes (Colwell & Futuyma 1971; Rabinowitz 1981). To characterize a species' ecological breadth meaningfully, the critical information is the *range* of conditions the species may successfully occupy, i.e. the highest and lowest resource states that occur in sites inhabited by viable populations, rather than the mean or frequency distribution of environmental states. To determine this range accurately, it is essential to sample temporal and spatial environmental variation effectively *within* natural populations (Bazzaz & Sultan 1987), as well as variability among populations occupying different habitats (Quinn & Hodgkinson 1983; Baskauf & Eickmeier 1994; Blossey & Notzold 1995). In addition, the relative extent of within- and among-population environmental variability may in part explain the evolutionary response of the species with respect to phenotypic plasticity (Levins 1968; Via & Lande 1985; Sultan 1987).

Ideally, a comparative study of ecological breadth might consist of hundreds of field sites for each species of interest, intensively and repeatedly measured for all possible environmental parameters. A practicable alternative to this ideal design is to compare relative breadth for several major environmental parameters based on a sample of natural populations chosen to encompass each species' range of environmental conditions. Because the frequency distribution of environmental states is irrelevant, a sample of populations specifically designed to include environmental extremes is more informative with respect to ecological breadth than a random sample. Thus, each species' sample should cover the range of habitats in which the species forms viable populations (actual niche breadth; *sensu* Colwell & Futuyma 1971; i.e. populations that successfully reproduce as well as occupy a site due to seed inflow; Bengtsson *et al.* 1994). Such a sampling strategy for environmental range is critical, because it permits comprehensive measurement of the environmental variability within each of the field populations, as well as variation among populations in contrasting habitats.

In addition to an appropriate sampling design, several criteria have been specified for robust comparisons of species' ecological breadth. First, such studies will be most informative when they avoid confounding evolutionary differences by comparing closely related taxa (Rabinowitz 1981; Kruckeberg & Rabinowitz 1985; Harvey & Pagel 1991; Baskauf & Eickmeier 1994). Secondly, comparisons of environmental breadth must be made in a common geographical range, to avoid confounding the distribution history of taxa with their habitat specificity (Rabinowitz 1981). Thirdly, confounding differences among the species in life history or breeding system should be avoided if possible (Rice & Jain 1985; Bazzaz 1986, 1987). Finally, field sites where generalists and specialists co-occur are particularly useful to include in the population sample, since the most rigorous comparisons of relative ecological breadth can be made when the environmental range of the generalist(s) includes but extends beyond that of the narrower specialist(s) (Futuyma & Moreno 1988).

This study aimed to quantify and compare statistically the ecological breadth of four closely related species in the genus *Polygonum* L. (Polygonaceae) with respect to several key environmental variables. This genus contains some of the most common and widespread plants in Europe and North America (including several of the world's most ubiquitous and serious weeds), as well as species of extremely narrow habitat specificity (Löve & Löve 1956; Rejmanek *et al.* 1991). We compared two species considered to be of ecologically broad distribution, *P. persicaria* L. and *P. lapathifolium* L., and two species that appear to be specialists restricted to particular habitats, *P. hydropiper* L. and *P. cespitosum* Blume. This species group affords an extremely robust comparison according to the criteria described above. The four species are members of a single, monophyletic section of the genus (see Materials and methods). All four were introduced from Europe or Asia into North America, where their ranges now overlap substantially in the north-eastern region (Mitchell & Dean 1978; Staniforth & Cavers 1979). The species share an identical life history as obligate annuals with mixed breeding systems (Simmonds 1945a,b; Mulligan & Findlay 1970; Staniforth & Cavers 1979). Finally, many published accounts indicate that these species often co-occur at particular sites (e.g. Simmonds 1945a,b; Timson 1965), and hence meet the stringent comparative criterion of Futuyma & Moreno (1988).

We present an extensive data set, collected from field populations of the four *Polygonum* species in a common geographical range in north-eastern North America, to address three specific questions. (i) What is the range of conditions in which viable populations of the species occur with respect to light, moisture, soil nutrient levels, soil structure and soil temperature? (ii) Do certain species show a relatively broad distribution for several aspects of the environment, such that they may be considered ecological generalists? (iii) Do the ecological ranges of narrowly distributed species include conditions for which they are uniquely specialists, i.e. beyond the range of generalist congeners? The data consist of numerous environmental measurements taken both early and late in the growth season, at each of five field populations per species that were chosen to encompass its habitat range in the region. Because the four species share virtually identical phenologies, the range of environmental conditions they encounter during establishment and at reproductive maturity can be compared using synchronous measurements at the various field sites.

Materials and methods

STUDY SYSTEM

Polygonum persicaria, *P. lapathifolium*, *P. hydropiper* and *P. cespitosum* are closely related taxa known upon occasion to form (sterile) hybrids (Timson 1965; Mitchell & Dean 1978; Clapham *et al.* 1987). In all treatments of the genus, they are placed together within a single monophyletic section (*Persicaria*) that is distinguished on the basis of karyotype, pollen structure and plant architecture (Löve & Löve 1956); the section is clearly delineated and is elevated by many authors to generic rank (e.g. Weber & Wittman 1992). All four species are obligately annual herbs of disturbed habitats, with a common breeding system consisting of predominant self-fertilization with a low proportion of out-crossing (Stanford 1925; Simmonds 1945a,b; Mulligan & Findlay 1970; Staniforth & Cavers 1979; S. E. Sultan, unpublished data). They also share a common range as introduced species in north-eastern North America. *Polygonum persicaria*, *P. lapathifolium* and *P. hydropiper* are of European or Eurasian origin, and are now distributed circumboreally in temperate regions (Mitchell & Dean 1978; Gleason & Cronquist 1991). *Polygonum cespitosum* originated in south-east Asia and is now widely distributed in Asia, Europe and eastern North America (Gleason & Cronquist 1991; Hobbs 1992).

According to published reports, *P. persicaria* occurs in both open and partly shaded sites, in soils ranging from dry to flooded and from nutrient-poor to highly fertile (Simmonds 1945a; Staniforth & Cavers 1979; Lousley & Kent 1981; Preston & Whitehouse 1986; Staniforth & Bergeron 1990). *Polygonum lapathifolium* too is reported to have a broad ecological distribution, although this species is absent from shaded sites, and may be more confined to moist soils (R. Staniforth, personal communication; Simmonds 1945b; Lousley & Kent 1981; Staniforth & Bergeron 1990). In contrast, *P. hydropiper* is evidently confined to very moist to wet, nutrient-rich habitats (Timson 1966; Seymour 1969; Lousley & Kent 1981). Consequently, this species is not considered to be a potentially serious weed except in the case of paddy rice culture (Muenscher 1955; King 1966; Staniforth & Bergeron 1990). Like *P. hydropiper*, *P. cespitosum* is considered ecologically narrow, occurring only in damp, shaded situations (Wang 1990; Staniforth & Bergeron 1990). *Polygonum persicaria* may co-occur in the field with each of the three other species (Simmonds 1945a,b; Timson 1965; Voss 1985; S.E. Sultan, personal observation), and hence its habitat range appears to encompass those of the less generalist species.

FIELD SITES

The study was conducted in an area of north-eastern North America included within the geographical ranges of all four *Polygonum* species (from south-western Connecticut to the northern boundary and eastern Cape Cod peninsula of Massachusetts, *c.* 160 km × 230 km; Table 1). Five disjunct natural populations of each species were chosen to encompass the range of habitats occupied by viable populations of that species in the region, according to the criteria described below.

A set of 15–18 field populations of each species was randomly selected from numerous sites within the study area, covering a broad variety of naturally and artificially disturbed habitats likely to support annual species. (Initial examination of many potential field sites was essential to avoid confounding historical accidents of distribution into particular sites with exclusion from entire habitats.) The initial set of populations was characterized with respect to canopy light level, moisture at 0–10 cm soil depth, and plant community composition (as an indicator of edaphic conditions and overall habitat distinctness). To avoid possible bias in sampling the species' habitat ranges (e.g. due to prior expectations from qualitative reports of ecological breadth), the five most different sites from the initial set for each species were chosen as the final sample of sites (i.e. the sites of each species with the highest and lowest insolation and soil moisture,

Table 1 *Polygonum* species field sites. Each species is represented by a set of five sites at which the number and density of its individuals exceeds 40 in an area of *c.* 12 m^2 (established population). The species' sites were deliberately chosen to represent contrasting habitats. MA = Massachusetts; CT = Connecticut

Code	Site name and location	Description	Established population
M	Daniel Webster Sanctuary, Marshfield, MA	Sandy track through woods	*P. persicaria*/*P. lapathifolium*
MHF	Mount Herman Farm, Northfield, MA	Open, moist pasture	*P. persicaria*/*P. hydropiper*
TP1	Towle Paddock, section 1, Dover, MA	Shaded horse paddock	*P. persicaria*/*P. cespitosum*
NAT	Natick Farmyard, Natick, MA	Organically cultivated field	*P. persicaria*
LP	Long Pond, Brewster, Cape Cod, MA	Open sand shore of pond	*P. persicaria*
WP	Weston Pumpkins, Weston, MA	Organically cultivated field	*P. lapathifolium*
AD	Adams Ditch, Newington, CT	Open, muddy hollow	*P. lapathifolium*
EG	East Granby Site, E. Granby, CT	Old field embankment	*P. lapathifolium*
NBL	Northfield Barn Lot, Northfield, MA	Open waste land	*P. lapathifolium*
DFF	Dewitt Fish Farm, Amherst, MA	Field watered with effluent	*P. hydropiper*
NHP	Northfield Horse Pasture	Open wetland	*P. hydropiper*
TP2	Towle Paddock, section 2, Dover, MA	Open, moist horse paddock	*P. hydropiper*
RW	Rocky Woods Preserve, Medfield, MA	Shaded, moist trail	*P. hydropiper*/*P. cespitosum*
ARL	Arch Road, Leeds, MA	Shaded, moist bank	*P. cespitosum*
ORD	Katherine Ordway Preserve, Weston, CT	Shaded meadow	*P. cespitosum*
WEIR	Weir Farm, Wilton, CT	Roadside embankment	*P. cespitosum*

and with different main species of plant neighbours). Hence, the final sample for each species reflected the full range of habitat differences revealed in an initially large, random sample of its populations. For example, the five populations of *P. cespitosum in* the final sample included the sites with the lowest and highest mean available light at canopy level (ARL site and TP1 site; Fig. 2c) and the sites with the lowest and highest mean soil moisture availability (TP1 site and RW site; Fig. 8c) from among an initial sample of 18 field populations of the species; the five sites comprise five distinct plant communities including predominantly annual species (TP1), mixed forest understorey (RW), and distinct mixtures of herbaceous annuals, perennials and broadleaf vs. coniferous woody plants (ARL, Weir and Ordway sites; S. E. Sultan, unpublished data).

A further check against possible sampling bias was that sites were included only if they supported clearly viable populations rather than a few individuals: sites were included in a species' sample only if at least 40 reproductively mature plants of the species occurred within an area of approximately 12 m^2, a size and density typical of successfully established annual *Polygonum* populations (S. E. Sultan, unpublished data). Accordingly, one low-light site for *P. hydropiper* (RW) was dropped from the species' sample when the late-season visit showed that the initial dense seedling population had died out, indicating that this site could not support a viable population and thus could not be considered as part of the species' habitat range. Sites that included co-existing viable populations of more than one *Polygonum* species were deliberately included in the sample, resulting in a total of 16 field sites representing habitats ranging from the sand shore of a freshwater pond to cultivated fields, waste land, wooded trails and meadows (Table 1). Note that since the site sample was composed by design rather than at random, the site factor was tested as a fixed rather than random factor in all statistical comparisons (Bennington & Thayre 1994).

ENVIRONMENTAL MEASUREMENTS

For each of the 16 field sites, environmental measurements were taken on one day early in the 1994 growth season (between 23 June and 6 July) and on one day late in the season (between 25 August and 3 September). The early and late-season measurements correspond, respectively, to the period of seedling establishment and early growth, and the period of plant maturity and maximum fruit production in the study area. The early season data for *P. lapathifolium* included only two sites, due to the difficulty of correctly identifying very young seedlings of this species. Light and temperature data were collected between 10.30 and 16.00 hours on clear days to ensure comparable conditions among sites; the order of sites visited was randomized for both early and late collections. Sampling and measurement techniques are described below; environmental data means and their standard deviations (and, in some cases, data ranges) are presented for each species based on its set of five field sites, as well as separately for each of the species' sites.

Available light

At each site, two sets of measurements at the current *Polygonum* canopy level and two sets at the mid-canopy level (one-half current *Polygonum* height) were made along four transects across the site. Each set of measurements consisted of 16 instantaneous readings of photosynthetically active radiation (PAR) recorded simultaneously at 5-cm intervals along an Accupar PAR-80 Sunfleck Ceptometer with separably programmable sensors (Dekagon Devices, Pullman, WA). These quantum readings were converted to a percentage of total available PAR by dividing each reading by the amount of PAR received simultaneously by a separate quantum sensor (Licor Inc., Lincoln, NE) linked to the ceptometer, mounted on a 15-cm platform, and placed in the nearest fully insolated location. The total number of light measurements per site was 128 early season canopy (4 transects × 2 sets per transect × 16 samples per set), 128 early season mid-canopy, 128 late-season canopy, and 128 late-season mid-canopy, although in a few instances as few as 112 or as many as 160 measurements were collected. To describe the distribution of heavily shaded microsites in each field site, the proportion of measurements of available PAR $\leqslant 10\%$ was computed for each set of 16 measurements, to give eight early-season and eight late-season estimates of the relative frequency of dark microsites at canopy and mid-canopy levels.

Soil temperature

Soil temperature was measured at each site between 11.00 and 13.00 hours on a single day early in the season, at least 48 h after the most recent rain. Three temperature probes (Omega Microprocessor Thermometer model HH-23, Omega Engineering, Ontario, Canada) were placed at each of five random microsites per site: one buried 5 cm deep in the soil, one buried 1 cm deep, and one held 2 cm above the soil surface to record air temperature. To ensure comparable measurements among sites, soil temperature was normalized as departure from current air temperature by subtracting each reading from the average air temperature at that site during the five measurements.

Soil structural properties

Soil collections were taken early in the season at two soil depths (0–10 cm and 20–30 cm) from three microsites per field site, roughly evenly spaced across the site area. These samples were air-dried on a laboratory bench and used to determine the following soil properties for moisture and air retention following standard methods (Weeks 1975): field capacity (maximum soil moisture content of sieved soil held against gravity); permanent wilting point (soil moisture content at which a well-established *P. persicaria* seedling did not recover from previous wilting during 14 h of darkness); pore space (proportion of soil volume due to air pores); percentage organic matter (proportion of oven-dried soil weight lost under ignition at 375 °C for 24 h); and soil particle composition [percentage soil dry weight due to clay (< 0.002 mm diameter), silt (0.002–0.05 mm diameter) and sand (0.05–2.0 mm diameter), as determined by the pipette–hydrometer method]. Means for each of the two soil depths were calculated for each site.

Soil moisture availability

Soil moisture content was determined gravimetrically from soil samples taken both early and late in the season at two soil depths (0–10 cm and 20–30 cm) at each of eight microsites per field site, roughly evenly spaced across the site area. Soil collections were taken at least 3 days after the most recent rainfall. Moisture content was computed as the percentage of oven-dried soil weight due to water. To estimate soil water availability, the known field capacity of each site's soil at the two depths was used to convert each measurement of absolute soil moisture content to a proportion of field capacity (Sultan & Bazzaz 1993b).

Soil nutrient content and availability

Soil samples were taken both early and late in the season at two soil depths (0–10 cm and 20–30 cm) at each of six microsites per field site, roughly evenly spaced across the site area. When air-dried, the samples were analysed separately at the University of Massachusetts Soil Testing Lab using the Morgan extraction system (10% sodium acetate in 3% acetic acid). Early and late-season means for each of the two soil depths for each site were calculated for the following variables: soil pH, cation exchange capacity (CEC), and absolute content (p.p.m.) of phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), ammonium (NH_4) and nitrate (NO_3).

Results

LIGHT AVAILABILITY

The four species differed significantly in the mean amount of PAR available to plants at the sites they inhabited (Table 2). These differences were particularly pronounced early in the season, when *P. cespitosum sites* received an average of less than 18% of total PAR at canopy level, compared with 82% for *P. persicaria* and well over 90% for both *P. lapathifolium* and *P. hydropiper* (Fig. 1a). This species rank order remained consistent late in the season, when canopy light levels were reduced due to shading by mature neighbour plants (Fig. 1a), as well as at the mid-canopy level, where self-shading contributes to lower average light levels (Fig. 1b).

The species also differed in the range of light conditions in which they occurred. *Polygonum persicaria* had the broadest field distribution with respect to light: this species inhabited sites that range from moderately low to extremely high levels of available PAR at the plant canopy, both early and late in the growth season (site means range from 39% to 99% early, and from 25% to 97% late in the season; Fig. 2a). Both

Table 2 Variation in light availability among *Polygonum* species and among sites within species. Analysis of variance for the fixed effects of species and site nested within species on available light, measured as the instantaneous percentage of available PAR recorded at 128 microsites per field site and tested over the MS error (Winer 1971, p. 361; see Materials and methods above). Data were square-root transformed to meet assumptions of ANOVA. All results significant at $P < 0.001$

	Source of variation	d.f.	*F* ratio	*P*
Early season				
Canopy:	Species	3	2184.5	0.000
	Site within species	12	118.0	0.000
	Error	2016		
Mid-canopy:	Species	3	582.6	0.000
	Site within species	12	93.6	0.000
	Error	2000		
Late season				
Canopy:	Species	3	1287.8	0.000
	Site within species	15	102.9	0.000
	Error	2397		
Mid-canopy:	Species	3	714.7	0.000
	Site within species	15	121.7	0.000
	Error	2365		

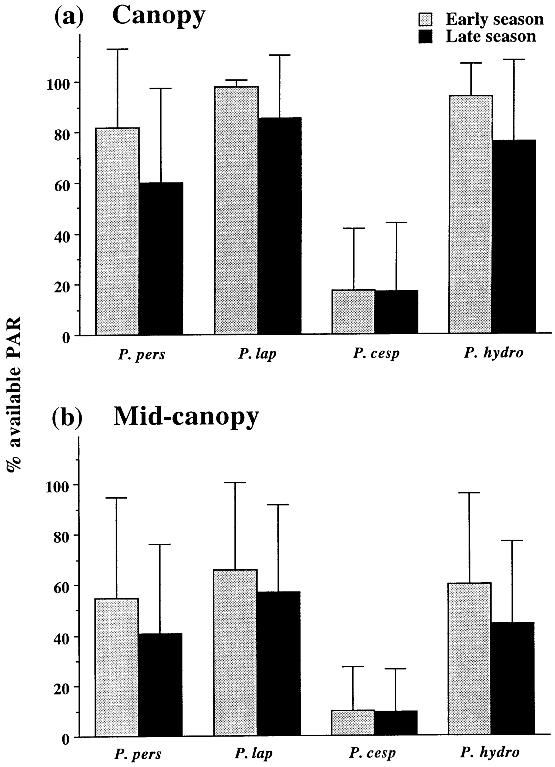

Fig. 1 Mean available PAR (% of full sun) ±SD encountered by each species early and late in the growth season. Means are based on 128 instantaneous PAR measurements taken on one day early and one day late in the growth season at each of five field sites per species. $n = 640$ for *P. persicaria* (*P. pers*), *P. lapathifolium* (*P. lap*), *P. cespitosum* (*P. cesp*); $n = 512$ for *P. hydropiper* (*P. hydro*). *Polygonum* canopy level = 10–15 cm at most sites; mid-canopy level = 5–8 cm at most sites.

P. lapathifolium and *P. hydropiper* occurred only in sites with high to very high light early in the season (97–99% and 82–99%, respectively), although both tolerated somewhat lower light levels late in the season (site means as low as 42% in *P. lapathifolium*, but no lower than 62% in *P. hydropiper*; Fig. 2b, 2d). The distribution of *P. cespitosum* was quite distinct: this species is evidently limited to low-light habitats. Thus, although *P. persicaria*, *P. lapathifolium* and *P. hydropiper* all inhabited sites where plants receive virtually full sun at the canopy level both early and late in the season, *P. cespitosum* did not occur in any site with a mean canopy light level of more than 39% of full sun (Fig. 2c). Furthermore, this species may establish populations in extremely dark sites (site means for available PAR at canopy level may be as low as 4% of full sun both early and late in the season; Fig. 2c).

The frequency within each site of sensor readings below 10% of available PAR provides an index of species' tolerance for habitats that contain extremely dark microsites. Species differed significantly in this aspect of light habitat as well (Table 3). The sites inhabited by *P. cespitosum* consisted predominantly of such dark conditions: this species occupied sites at which over 59% of microsites received less than 10% of PAR at canopy level early in the season, and between 70 and 80% of microsites less than this amount late in the season and at mid-canopy (Fig. 3a). *Polygonum persicaria* also occurred in habitats that included these very dark microsites at the canopy level: the mean percentage of dark microsites for its five field sites was 8% early and 15% late in the season (Fig. 3a). In contrast, *P. lapathifolium* and *P. hydropiper* populations were not found in field habitats that included such dark microsites: there was not a single early season measurement of less than 10% light at the canopy level in sites of either species, and such conditions were extremely infrequent even late in the season (6% for *P. hydropiper* and 0 for *P. lapathifolium*; Fig. 3a). Even at mid-canopy, the fre-

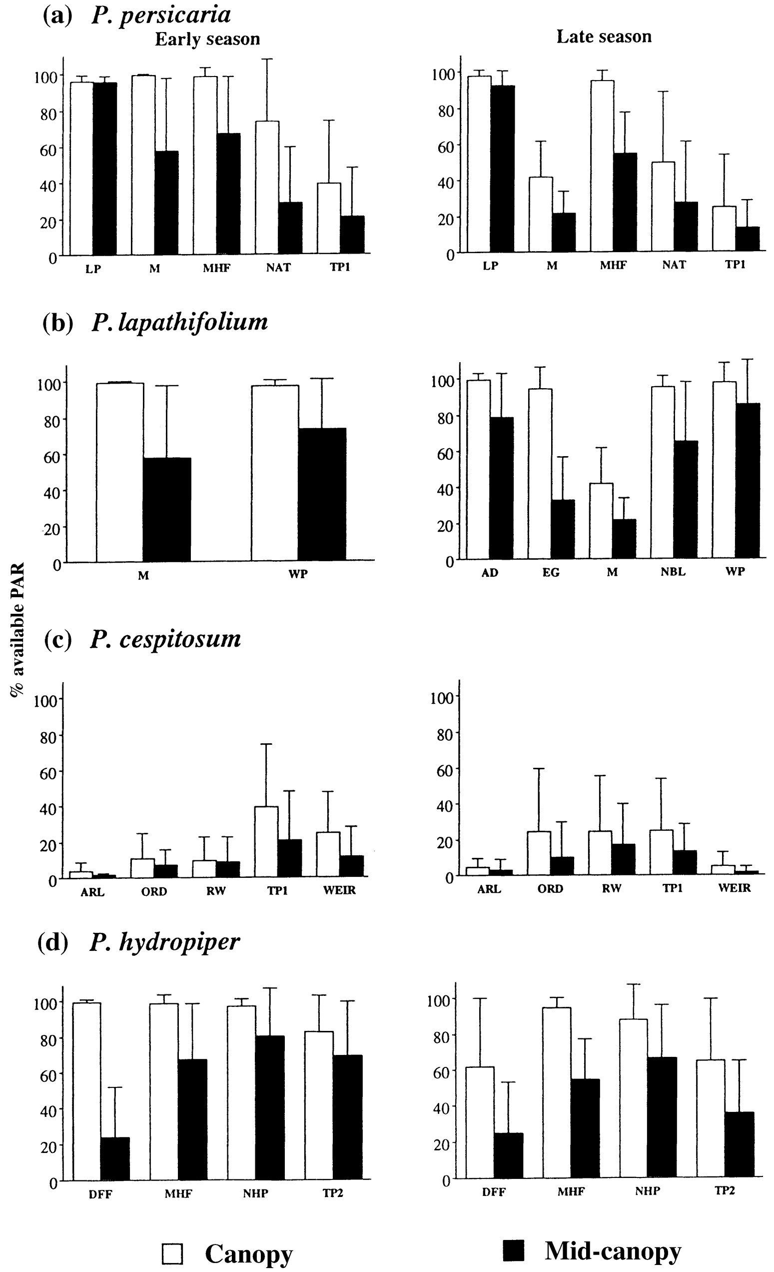

Fig. 2 Mean available PAR (% of full sun) ± SD at each species' field sites early and late in the growth season at *Polygonum* canopy and mid-canopy levels.

quency of dark microsites was very low in these two species compared with their congeners (Fig. 3b).

SOIL TEMPERATURE

Species differed significantly in early season soil temperature at both 1 cm ($P \leqslant 0.001$, $n = 79$) and 5 cm ($P \leqslant 0.001$, $n = 80$), according to one-way fixed ANOVA. *Polygonum cespitosum* and *P. hydropiper* occurred in cooler soils, averaging *c.* 3 °C and 5 °C below air temperature at 1 cm and 5 cm below the soil surface, respectively (Fig. 4). *Polygonum persicaria* and *P. lapathifolium* occurred in sites with average soil temperatures closer to ambient (Fig. 4). The species temperature ranges also differed: *P. cespitosum* populations did not encounter soil temperatures above air temperature, even at the 1 cm depth; in the remaining three species soil at this shallow level could be *c.* 2 °C above air temperature, and in *P. persicaria*, deeper soil could be even warmer (Fig. 4). *Polygonum cespitosum* showed the narrowest range of soil temperatures (0.1–6.1 °C below ambient; Fig. 4). *Polygonum lapathifolium* also showed a relatively narrow range (Fig. 4). In contrast, both *P. hydropiper* and *P. persicaria* occupied a broad range of soil temperatures. In *P. hydropiper*, soils could be either higher or substantially lower than air temperatures (cf. a minimum of 9.2 °C below air at 5 cm; Fig. 4). This variation occurred largely among microsites within *P. hydropiper* populations, which (like populations of *P. lapa-*

Table 3 Variation in frequency of dark microsites among *Polygonum* species and among sites within species. Analysis of variance for the fixed effects of species and site nested within species on the proportion of instantaneous light readings of less than 10% of total available PAR, tested over the MS error (Winer 1971, p. 361; see Materials and methods above). Data were square-root transformed to meet assumptions of ANOVA. All results significant at $P < 0.001$

	Source of variation	d.f.	*F* ratio	*P*
Early season				
Canopy:	Species	3	68.50	0.000
	Site within species	12	5.71	0.000
	Error	111		
Mid-canopy:	Species	3	48.10	0.000
	Site within species	12	9.33	0.000
	Error	110		
Late season				
Canopy:	Species	3	96.50	0.000
	Site within species	15	4.60	0.000
	Error	132		
Mid-canopy:	Species	3	57.60	0.000
	Site within species	15	8.58	0.000
	Error	130		

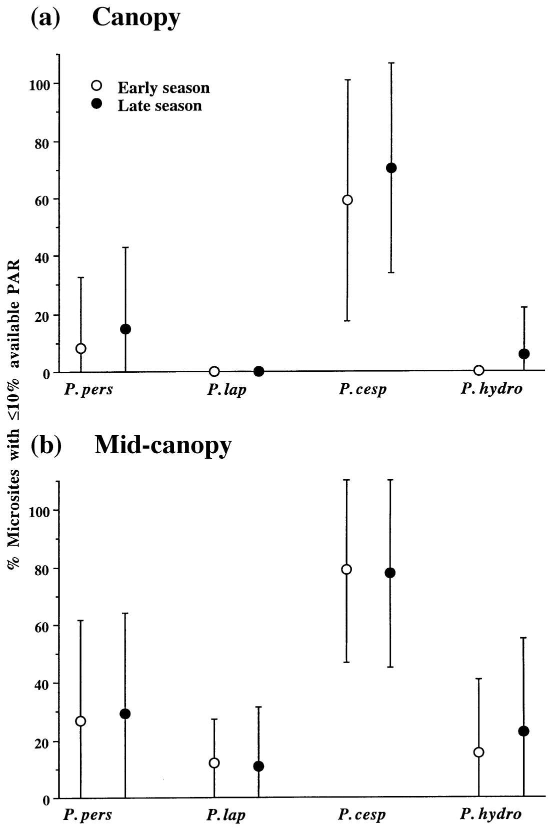

Fig. 3 Percentage of microsites with less than 10% of full sun measured at field sites of *P. persicaria*, *P. lapathifolium*, *P. cespitosum*, and *P. hydropiper*: species means ± SD based on eight early season and eight late-season transects for five sites per species ($n = 16$ measurements/transect).

thifolium and *P. cespitosum*) had generally similar mean temperatures (Fig. 5d,b,c). *Polygonum persicaria* occurred in soil temperatures ranging from over 6 °C below to more than 3 °C above ambient, the highest soil temperatures found in any species' site (Fig. 4). This range reflects the dramatic differences in habitat types among *P. persicaria* populations, from moist pasture (MHF site; Fig. 5a) to freshwater pond shore (LP site; Fig. 5a).

SOIL COMPOSITION

The fractional composition of site soils at both depths differed significantly among the four species, as well as among sites within each species (multivariate tests; Table 4). The relative proportions of sand, silt and clay each differed significantly among both species and sites, but the species did not differ significantly in percentage organic matter, probably because *P. persicaria* occupied the soils that were both highest and lowest in organic matter (univariate tests; Table 4). This species occupied the greatest range of soil types, from the exceptionally rich soil at the Natick organic farm, with 23% organic matter and only 45% sand, to the Long Pond site with over 99% sand (Fig. 6a). *Polygonum cespitosum* and *P. lapathifolium* also occurred on a wide range of soils, including poor soils with up to 83% sand and less than 2% organic matter (Fig. 6b,c). *Polygonum hydropiper* occurred only on relatively rich soils with high organic matter content (over 8% on average) and less than 75% sand (Fig. 6d). The minimum organic matter proportion measured at any *P. hydropiper* site was 4.7%, compared with minima of less than 1% for the other three species.

SOIL MOISTURE RETENTION PROPERTIES

Species and sites within species differed significantly at both soil depths in soil porosity (% pore space by

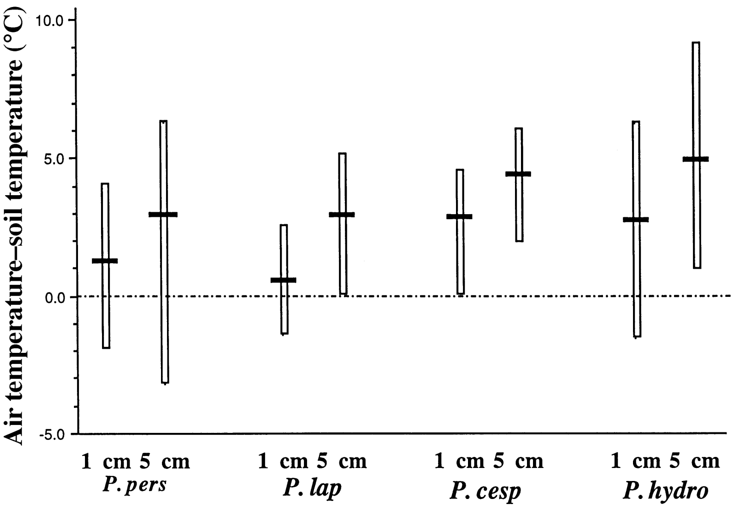

Fig. 4 Soil temperatures encountered by *P. persicaria*, *P. lapathifolium*, *P. cespitosum* and *P. hydropiper* early in the growth season, expressed as the difference between air and soil temperature. Means (horizontal bars) and ranges at 1 cm and 5 cm are shown based on five measurements at each soil depth at each of five field sites per species. Higher values signify cooler soils; values below zero indicate soil temperatures above ambient.

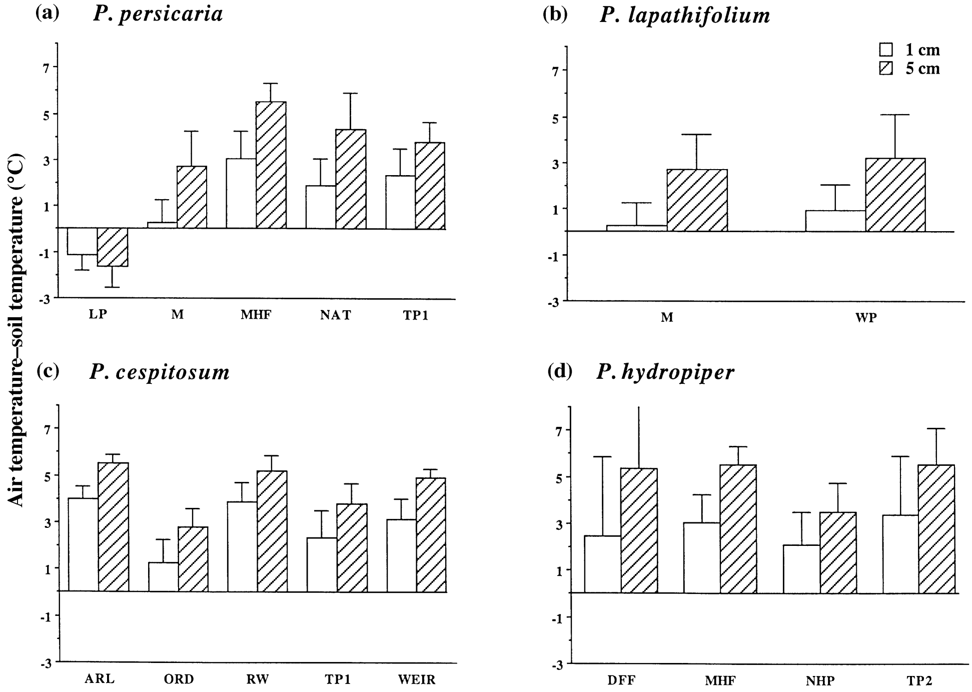

Fig. 5 Soil temperatures (mean difference between soil and air temperature and SD of the mean) at field sites of each species early in the growth season. Field sites nested within species differ significantly at 1 cm depth ($P \leqslant 0.001$) and at 5 cm depth ($P \leqslant 0.001$) according to one-way ANOVA.

volume), field capacity moisture content, and moisture content at permanent wilting point (except for borderline significance of species effect on field capacity at 20–30 cm depth; Table 5). In accordance with the range in soil composition noted above, *P. persicaria* occurred in soils that ranged widely in field capacity, permanent wilting point, and soil pore space (cf. standard deviations; Table 5). *Polygonum cespitosum* sites showed the next greatest range of values for these soil properties among sites, as well as the highest variability within sites for field capacity. *Polygonum lapathifolium* sites were consistently low in soil field capacity and permanent wilting point among as well as within sites, particularly at the shallow depth (0–10 cm; Table 5). Note, however, that the range of *P. persicaria* included soils with lower field capacities at both soil depths than occurred in any of the other species (samples of 15 measurements per species included minima of 20.4% and 14.9% for *P. persicaria* at the two soil depths, compared with 22.3% and 38.1% for *P. lapathifolium*, 26.2% and 29.1% for *P. cespitosum*, and 48.9% and 29.4% for *P. hydropiper*).

Table 4 Variation in soil composition among *Polygonum* species and among sites within species. Multivariate analysis of variance (MANOVA) for the fixed effects of species and site nested within species on soil fractional composition (percentage organic matter, sand, silt and clay; see Materials and methods above). *F*-statistics for multivariate tests on all soil fractions were calculated as Wilks' Lambda and tested over the error MS (Winer 1971, p. 361)

	d.f.	*F* ratio	*P*
0–10 cm depth			
EFFECT OF SPECIES ON			
All soil fractions (multivariate test)	12, 34	1762.0	**0.000*****
Percentage organic matter	3	1.43	0.272 NS
Percentage sand	3	6.82	0.004**
Percentage silt	3	21.79	0.000***
Percentage clay	3	7.66	0.002**
EFFECT OF SITE (WITHIN SPECIES) ON			
All soil fractions (multivariate test)	48, 52	439.0	**0.000*****
Percentage organic matter	12	3.86	0.007**
Percentage sand	12	91.54	0.000**
Percentage silt	12	69.80	0.000***
Percentage clay	12	9.33	0.000***
20–30 cm depth			
EFFECT OF SPECIES ON			
All soil fractions (multivariate test)	12, 34	16839.2	**0.000*****
Percentage organic matter	3	1.79	0.189 NS
Percentage sand	3	11.30	0.000***
Percentage silt	3	9.8	0.001**
Percentage clay	3	3.36	0.045*
EFFECT OF SITE (WITHIN SPECIES) ON			
All soil fractions (multivariate test)	48, 52	2621.1	**0.000*****
Percentage organic matter	12	3.71	0.008**
Percentage sand	12	79.82	0.000**
Percentage silt	12	65.97	0.000***
Percentage clay	12	10.05	0.000***

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.
NS, not significant.

Polygonum hydropiper occurred in sites with consistently high porosity (Table 5).

SOIL MOISTURE AVAILABILITY

The four species differed significantly in available soil moisture at shallow and deep levels, both early and late in the season (moisture content as a percentage of field capacity; Table 6). *Polygonum hydropiper* occurred in consistently very moist soils, and *P. cespitosum* in consistently moderately moist soils, while mean soil moisture varied in *P. persicaria* and *P. lapathifolium* (Fig. 7a). The minimum and maximum moisture conditions in which the species occurred indicated very different species distributions with respect to both flooded and dry soils. *Polygonum persicaria*, *P. lapathifolium* and *P. hydropiper* all inhabited sites where soil flooding may occur, but only *P. hydropiper* occupied sites that may be flooded close to surface level early in the season (Fig. 7b). The ecological range of *P. cespitosum* does not include flooded soils (Fig. 7b). *Polygonum hydropiper* is evidently far less tolerant of drought than the other species: the minimum recorded soil moisture for either depth at any site was 30% of field capacity, compared with minima of *c.* 15% for *P. cespitosum* and *P. lapathifolium*, and a minimum of less than 1% of field capacity for *P. persicaria* at the Long Pond site (Fig. 7c), a value barely above permanent wilting point for that soil. Although late in the season the shallow soil at this site was extremely dry, concurrently *P. persicaria* also had the lowest minimum value for shallow soil early in the season (Fig. 7c), suggesting relatively high seedling drought tolerance in this species. Both *P. persicaria* and *P. lapathifolium* occupied soils where moisture availability at the surface varied strongly among and within sites; the deeper soils varied less (Fig. 8a,b). In contrast, soil moisture conditions were less variable among and within field sites for *P. cespitosum* and *P. hydropiper* (Fig. 8c,d). *Polygonum cespitosum* sites were uniformly moderately moist (site means ranged from 30% to 60% of field capacity), and *P. hydropiper* sites were all moist to very moist across the season (all site means were over 42% for both soil depths; Fig. 8d).

SOIL NUTRIENT CONTENT AND AVAILABILITY

Species as well as sites within species differed significantly in macronutrient content at shallow and

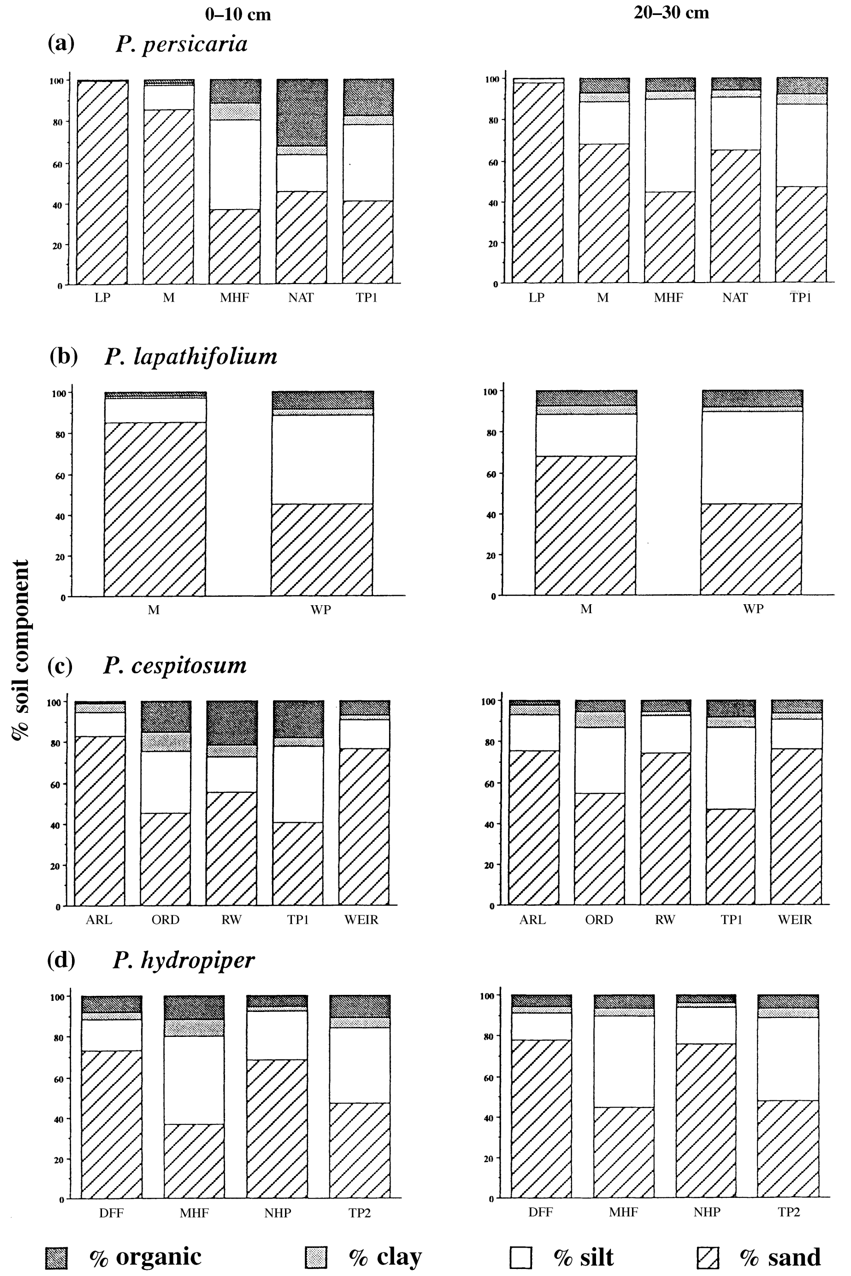

Fig. 6 Soil fractional composition (% dry mass in organic matter, clay, silt and sand) at sites occupied by *Polygonum* species. Means are shown for field sites of each species at 0–10 cm depth and 20–30 cm depth, based on three soil samples per depth per site.

deeper soil depths, both early and late in the growth season (multivariate tests, Table 7), although differences among species in individual minerals tended to be non-significant early in the season due to very high among-site variance (Table 7). In particular, high variation in nitrate content among sites early in the season obscured the lower average levels in *P. cespitosum* (species mean at 20–30 cm depth of 3.9 p.p.m. ± 0.92, compared with 11–18 p.p.m. ± up to 34.2 in the remaining species). Although early in the growth season all species included sites with both low and high macronutrient levels, the range was greatest among *P. persicaria* sites (Fig. 9). This resulted not from differences in minimum nutrient levels (which were very low in all four species), but from the fact that the range within *P. persicaria* (and to a lesser extent *P. hydropiper*) included extreme high-nutrient microsites (e.g. phosphorous; Fig. 10). This explains the generally higher mean nutrient values for *P. persicaria*. *Polygonum hydropiper* was limited to moderately high nitrate levels early in the season. For instance, at the lower soil depth, all sites of this species had mean levels of at least 8.3 p.p.m. of nitrate, which was higher than any *P. cespitosum site* (maximum of 4.3 p.p.m.) and substantially higher than the minimum site means of 3.7 for *P. lapathifolium* and 3.0 for *P. persicaria* (Fig. 9). *Polygonum hydropiper* also had higher minimum early season site

Table 5 Moisture retention properties of soils occupied by *Polygonum* species. Means ± SD are shown based on three measurements per depth from each of five sites per species (see Materials and methods). Probability levels are reported for the fixed effects of species and site nested within species for each soil property, based on one-way fixed ANOVA for untransformed data for each variable at each soil depth. All *F*-ratios tested over MS error; Winer (1971), p. 361. NS = not significant at $P \leqslant 0.05$. Permanent wilting point and field capacity are reported as percentage of dry soil mass due to water; *P. pers.* = *P. persicaria*; *P. lap.* = *P. lapathifolium*; *P. cesp.* = *P. cespitosum*; *P. hydro.* = *P. hydropiper*

	P. pers.	*P. lap.*	*P. cesp.*	*P. hydro.*	Species	Site
0–10 cm depth						
% pore space	55 ± 11.5	52 ± 5.2	60 ± 6.8	64 ± 2.5	0.000	0.000
Permanent wilting point	3.1 ± 2.1	1.9 ± 1.0	3.7 ± 2.0	3.7 ± 1.4	0.000	0.000
Field capacity	73 ± 67.7	38 ± 11.5	74 ± 31.8	67 ± 13.2	0.000	0.000
20–30 cm depth						
% pore space	55 ± 10.2	57 ± 3.9	56 ± 5.2	61 ± 3.3	0.005	0.000
Permanent wilting point	2.3 ± 1.3	3.1 ± 1.1	2.7 ± 1.2	2.7 ± 1.1	0.008	0.000
Field capacity	46 ± 15.0	48 ± 6.9	47 ± 12.7	52 ± 9.4	0.056 NS	0.000

Table 6 Variation in moisture availability among *Polygonum* species and among sites within species. Analysis of variance for the fixed effects of species and site nested within species on available soil moisture, measured as soil moisture content expressed as a percentage of soil field capacity (tested over the MS error; Winer 1971, p. 361). Data were arc-sine transformed to meet assumptions of ANOVA. Identical ANOVA results were achieved for soil moisture content (g moisture per g soil; see Materials and methods). All results significant at $P < 0.001$

	Source of variation	d.f.	*F* ratio	*P*
Early season				
0–10 cm depth	Species	3	11.6	0.000
	Site within species	12	4.3	0.000
	Error	96		
20–30 cm depth	Species	3	16.3	0.000
	Site within species	12	23.4	0.000
	Error	96		
Late season				
0–10 cm depth	Species	3	21.7	0.000
	Site within species	15	11.8	0.000
	Error	126		
20–30 cm depth	Species	3	16.9	0.000
	Site within species	15	10.5	0.000
	Error	124		

means for calcium and phosphorous at both soil depths (Figs 9 and 10), and higher early and minimum late-season site means for magnesium (Fig. 11). Differences among species in soil nutrient content were more pronounced later in the season, particularly in nitrogen compounds (Table 7). Ammonium and nitrate content were most strongly depleted at *P. lapathifolium* sites; this species also had the lowest late-season levels of potassium and magnesium (Fig. 11). *Polygonum persicaria* included the greatest among-site range in all macronutrients, late as well as early in the season (Figs 9 and 11).

In addition to soil nutrient content, nutrient availability is influenced by soil properties such as pH and CEC. *Polygonum cespitosum* showed the greatest range in pH (from 4.8, a level at which macronutrient deficiency may occur, to 8.0, a level at which trace elements may become unavailable, compared with a range of 5.1–6.8 in the remaining three species). *Polygonum hydropiper* had a consistently narrow distribution very close to pH 6.0. On average, CEC was highest in *P. cespitosum* soils, with *P. persicaria* and *P. hydropiper* at moderate levels (but with extreme variability in *P. persicaria*) and *P. lapathifolium* consistently lower. *Polygonum hydropiper* again had the narrowest range, appearing limited to soils with moderately high CEC (e.g. site means for late-season CEC at 0–10 cm ranged from 12.5 to 14.8 in *P. hydropiper*, compared with 2.2–12.4 in *P. lapathifolium*, 2.0–28.1 in *P. cespitosum*, and the widest among-site range, 0.3–24.1, in *P. persicaria*).

Discussion

Polygonum persicaria, *P. lapathifolium*, *P. hydropiper* and *P. cespitosum* showed significant differences in

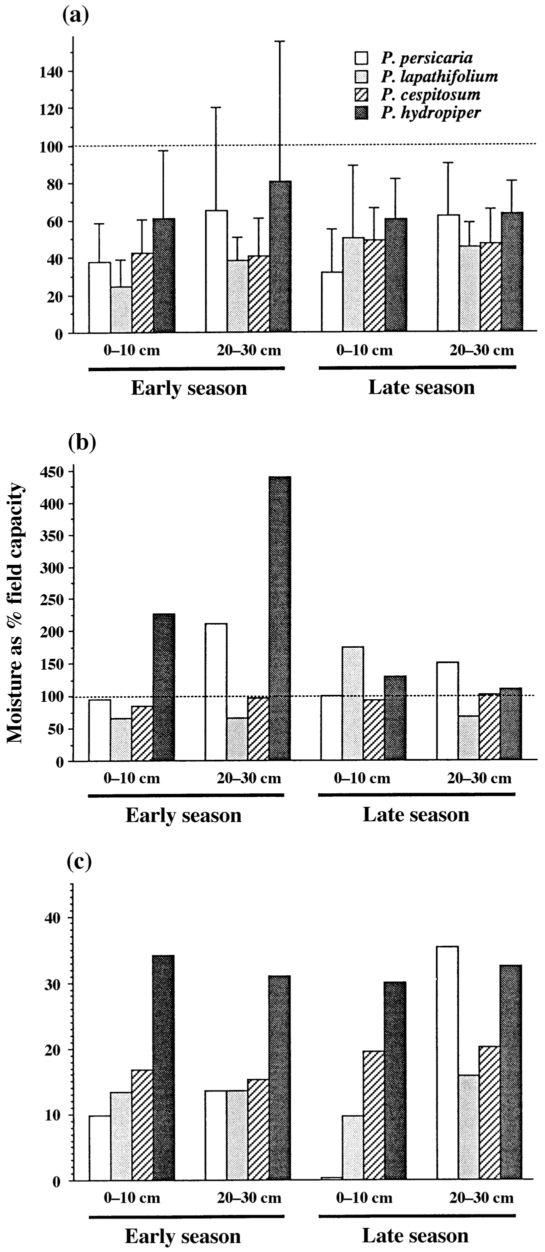

Fig. 7 Differences among *P. persicaria*, *P. lapathifolium*, *P. cespitosum* and *P. hydropiper* in soil moisture availability (expressed as percentage of field capacity), based on eight early season and eight late-season measurements from each of two soil depths at five field sites per species. Values greater than 100% of field capacity indicate soil flooding. (a) Mean moisture availability ± SD for each species. (b) Maximum moisture availability measured at any field site occupied by the species. (c) Minimum moisture availability measured at any field site occupied by the species.

ecological distribution in a contiguous area of north-eastern North American in which all four species occur. Based on a sample of natural populations chosen to encompass the species' respective habitat ranges in the region, the species differed in the relative breadth of their ranges in light, moisture, macronutrient, soil structure, and soil temperature conditions. Since the species' measured ranges for these factors were based on field distribution, they reflected realized tolerance for these environmental states in the presence of competition and other biotic and abiotic stresses (Colwell & Futuyma 1971). Although the relative ecological breadth of the species varied from one resource to another, *P. persicaria* emerged as a species with broad realized tolerance for all of the environmental variables examined. This result supports the view that certain species, such as *P. persicaria*, may be ecological generalists for numerous environmental parameters.

Any attempt to quantify realized ecological breadth confronts certain inherent limitations, since it is not possible to measure all populations (and microsites) of a species to determine with certainty the extremes of its environmental distribution. Furthermore, adequate within-site sampling is only feasible for a limited number of field sites in a multispecies study. In the present study, each species' ecological distribution was represented by a sample of five populations, drawn from an initially random set of *c.* 75 field sites for all four species. Although the strategy employed (see Field sites above) provides reasonable confidence that these population samples reflect the range of habitats for the four species in this region, the possibility remains that the extreme levels of a particular parameter of interest may not have been encompassed by the study sample for a given species. This possibility may be greater with respect to soil nutrients and temperature, since these factors were not used directly as sampling criteria (see Field sites above). Sampling environmental variation among microsites as well as entire populations (e.g. Fig. 7b,c) provides a partial safeguard against such underestimates, since it makes the identification of each species' absolute environmental extremes more likely. Moreover, a species' environmental breadth will be at least as great as is revealed by field sampling: despite the possibility of underestimates, the environmental ranges revealed for any species are a robust minimum for that species. However, this inherent sampling limitation remains a possible source of bias in this and other such studies, such that comparisons of relative ecological breadth must be made with some caution.

Despite these caveats regarding possible underestimation of environmental breadth, the data clearly demonstrate that *P. persicaria* inhabits an extremely broad habitat range with respect to light, soil temperature, soil type, macronutrient content and moisture. This species occupies sites with full to relatively low average canopy insolation, as well as extreme within-site variability, both early and late in the growth season. *Polygonum persicaria* individuals evidently may establish as well as reproduce successfully under both low and high light levels. The species occurs in a broad range of soil temperatures early in the season, indicating the ability of seedlings to establish root systems in soils ranging from very cool to well above air temperature. *Polygonum persicaria* also occupies the broadest range of soil types, from

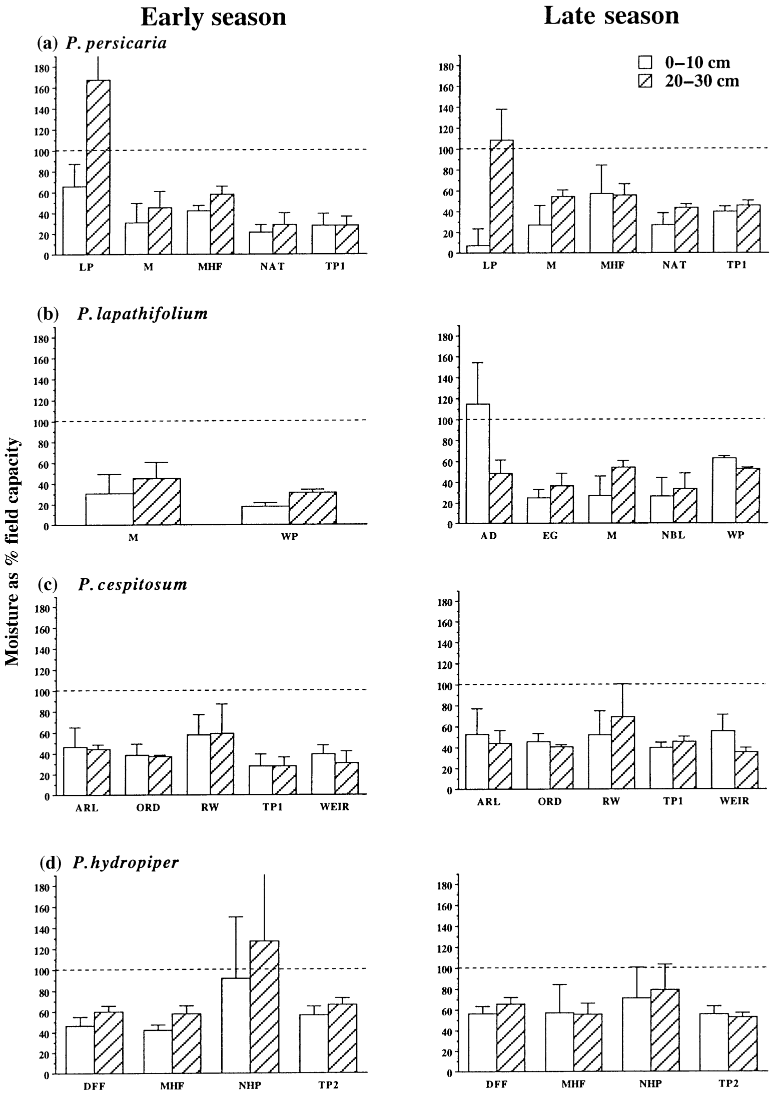

Fig. 8 Moisture availability (expressed as a percentage of field capacity) at two soil depths at field sites of each species early and late in the growth season. Means ± SD are shown based on eight measurements per depth at each site.

extremely rich, organic soils to nearly pure sand, with correspondingly great variation in porosity, moisture retention, cation exchange capacity, and macronutrient content. Finally, the species tolerates moisture conditions from near permanent wilting point to flooded soil, both among and within sites. This moisture range is greater at the soil surface than deep within the soil, suggesting that the ability to tolerate extreme variation in surface moisture may reflect flexibility in the deployment of roots (D. L. Bell & S. E. Sultan, unpublished data).

Note that *P. persicaria* accommodates great temporal and spatial environmental variability within as well as among distinct field sites (Sultan & Bazzaz 1993a,b,c). *Polygonum lapathifolium* too inhabits sites in which soil moisture varies widely, and *P. hydropiper* tolerates the broad within-site range of soil temperatures that results from a combination of high insolation and wet soil. In cases of within-population variability, genetic tracking of environmental conditions is unlikely. Hence, in such cases a species' broad environmental tolerance may derive from the plasticity of individuals, rather than from ecotypic specialization of entire populations under local selection pressures (Sultan 1987 and references therein). Indeed, it has long been hypothesized that the success of widespread weed species is due to the great adaptive plasticity of their individuals, which allows them to colonize a variety of habitats successfully (Baker 1965, 1974; Bazzaz 1986) and hence wide geographical ranges as well (Rabinowitz 1981). The results of several recent studies support this hypothesis (Oliva *et al.* 1993; Williams *et al.* 1995; Hermanutz & Weaver 1996). Conversely, restricted endemics tend to have inherently narrow ranges of environmental tolerance (Baskauf & Eickmeier 1994). The relation of individual plasticity to realized ecological breadth for light, soil moisture and soil nutrients is currently

Table 7 Variation in soil nutrient content and availability among *Polygonum* species and among sites within species. Results of multivariate analysis of variance (MANOVA) for the fixed effects of species and site nested within species on soil macronutrient content (P, K, Ca, Mg, NH_4 and NO_3) and one-way fixed analysis of variance (ANOVA) for species and site effects on soil pH and CEC; see Materials and methods). *F*-statistics for multivariate tests on all soil fractions are calculated as Wilks' lambda and tested over the MS error (Winer 1971, p. 361)

	Early season		Late season	
	Species	Site	Species	Site
0–10 cm depth				
EFFECT OF				
All macronutrients (multivariate test)	0.001**	0.000***	0.000***	0.000***
Phosphorous	0.062 NS	0.000***	0.166 NS	0.109 NS
Potassium	0.071 NS	0.001**	0.000***	0.000***
Calcium	0.072 NS	0.000***	0.060 NS	0.000***
Magnesium	0.057 NS	0.000***	0.002**	0.000***
Ammonium	0.505 NS	0.000***	0.000***	0.000***
Nitrate	0.519 NS	0.001**	0.000***	0.000***
pH	0.000***	0.000***	0.019*	0.000***
Cation exchange capacity	0.011*	0.000***	0.000***	0.000***
20–30 cm depth				
EFFECT OF				
All macronutrients (multivariate test)	0.000***	0.000***	0.000***	0.000***
Phosphorous	0.005**	0.006**	0.083 NS	0.010**
Potassium	0.889 NS	0.000***	0.000***	0.000***
Calcium	0.090 NS	0.000***	0.896 NS	0.000***
Magnesium	0.057 NS	0.000***	0.504 NS	0.000***
Ammonium	0.411 NS	0.447 NS	0.040*	0.003**
Nitrate	0.265 NS	0.229 NS	0.013*	0.017*
pH	0.001**	0.000***	0.339 NS	0.000***
Cation exchange capacity	0.480 NS	0.000***	0.379 NS	0.001**

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
NS, not significant.

under investigation in the *Polygonum* system (Sultan 1995; Sultan *et al.* 1998; D. L. Bell & S. E. Sultan, unpublished data; S. E. Sultan, unpublished data).

Although, like *P. persicaria*, *P. lapathifolium* is a geographically widespread weed long associated with agroecosystems (Staniforth & Cavers 1979), the field distribution data reveal that this species has somewhat narrower habitat breadth on several resource axes. These observations are not necessarily contradictory: the cultivated fields that both species so successfully colonize may represent a more or less uniform habitat with respect to light, moisture and macronutrients, well within the ecological range of both species for these resources. It is interesting that, although both *P. persicaria* and *P. lapathifolium* are considered to be serious cropland weeds in many temperate regions (Muenscher 1955; Holm *et al.* 1979; Staniforth & Cavers 1979), *P. persicaria* is often characterized as more aggressive and/or abundant (Simmonds 1945a; Mitchell & Dean 1978; Preston & Whitehouse 1986). This greater invasiveness and abundance may reflect the wider range of habitats and microhabitats that *P. persicaria* successfully occupies.

The most pronounced difference revealed between these two species is in breadth of distribution for light levels: *P. lapathifolium* tolerates moderate shade at maturity, but does not establish populations in sites lacking high available light early in the life cycle, or in sites with deeply shaded microsites. Thus, this species has markedly lower realized shade tolerance than *P. persicaria*, particularly during initial growth when pre-emption of light may be a key to competitive success. This may explain why, unlike *P. persicaria*, *P. lapathifolium* is not found in woodland sites (Simmonds 1945b; Staniforth & Cavers 1979; S. E. Sultan, personal observation). With respect to both soil moisture and nutrient availability, the ranges of tolerance in *P. lapathifolium* are broad, but do not extend to such low levels as those of *P. persicaria*. *Polygonum lapathifolium* tolerates poor as well as rich edaphic conditions, and indeed is largely found in such conditions, but not in the extremely poor soils occupied by *P. persicaria* populations such as at Long Pond. *Polygonum lapathifolium* tolerates moisture conditions from flooded to moderately dry. Like *P. persicaria*, it occupies habitats in which moisture conditions vary widely, especially at the soil surface. The results of this study are consistent with the reported distribution of the two species in Ontario, where they both occupy many soil types and soil moisture conditions (Staniforth & Cavers 1979). The occurrence of *P. lapathifolium* in sites that experience flooding is

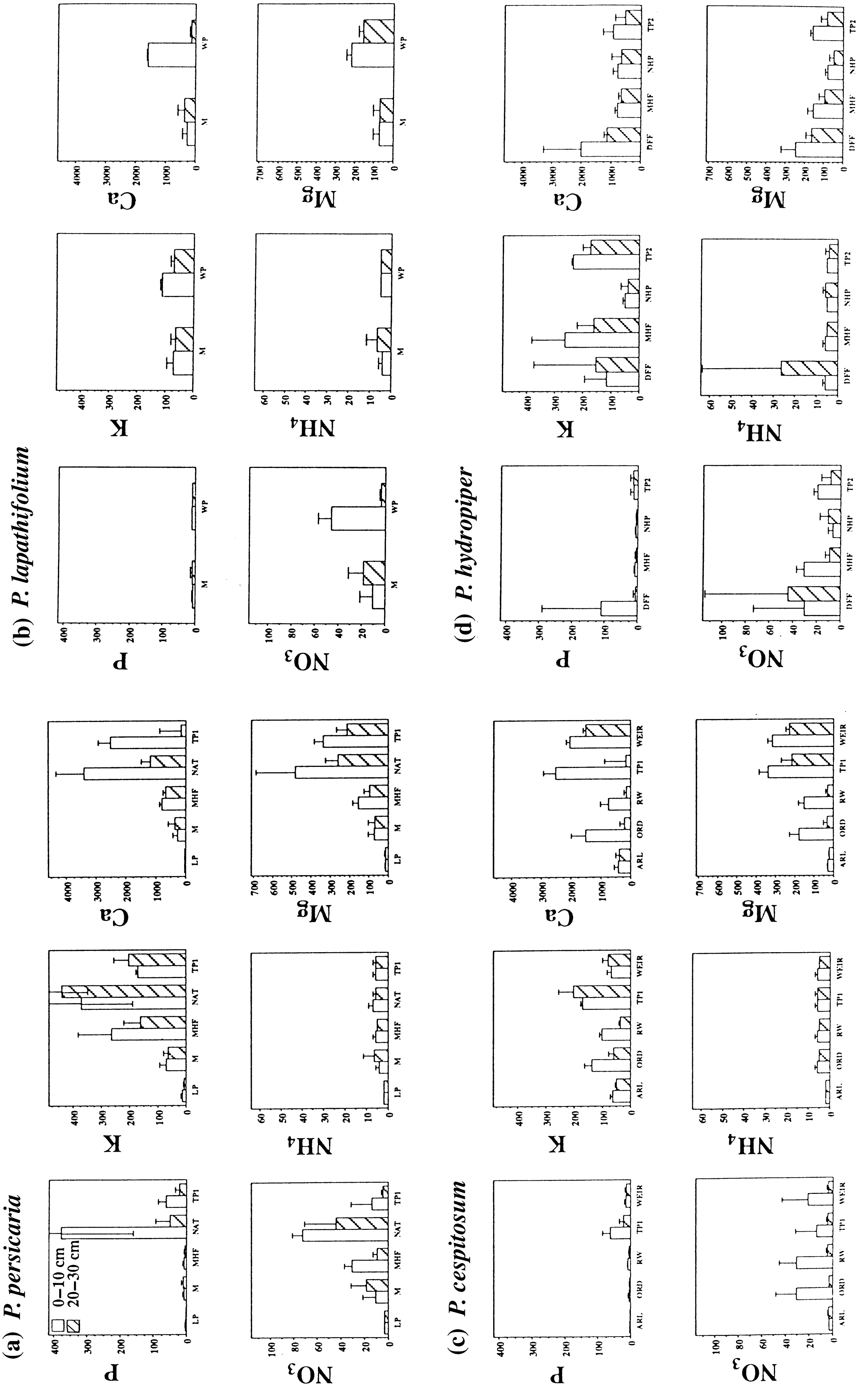

Fig. 9 Early season macronutrient content at two soil depths at field sites of each species. Means ± SD are shown based on three measurements per depth at each site for six macronutrients.

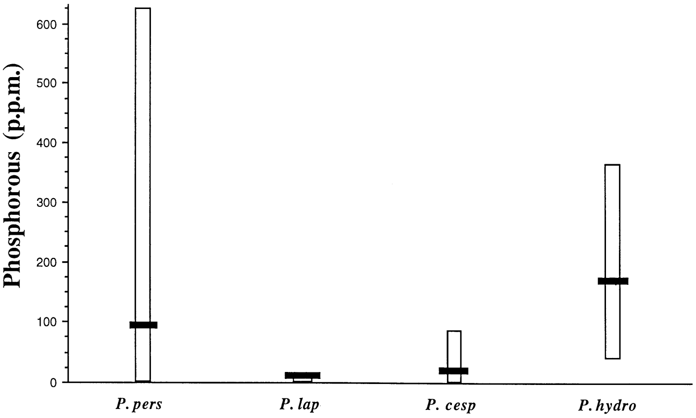

Fig. 10 Early season phosphorous content of soils occupied by *P. persicaria*, *P. lapathifolium*, *P. cespitosum* and *P. hydropiper*. Means (horizontal bars) and ranges for each species are shown based on three measurements at 0–10 cm depth from five field sites (species $n = 15$). Note extremely high maxima in both *P. persicaria* and *P. hydropiper*.

consistent with the observation that this species, like *P. persicaria*, occurs in poorly drained or winter-flooded habitats in England (Preston & Whitehouse 1986).

Polygonum cespitosum, the most recently introduced of the species (Harger 1930; Mitchell & Dean 1978; Hobbs 1992 and references therein), reveals both broad and narrow environmental ranges depending on the environmental factor. This species occurs in a broad range of soil types, from poor and sandy to highly organic, and occupies soils with a wide range of pH levels. Thus, although nutrient content of its site soils is generally moderate, the species colonizes sites with variable levels of available nutrients. However, *P. cespitosum* inhabits only a narrow range of both light and moisture conditions. In striking contrast to its congeners, this species is excluded from high light habitats. Although *P. persicaria* often co-occurs with this species in moderately shaded habitats (Voss 1985; S. E. Sultan, personal observation), *P. cespitosum* is the only species found in sites that are extremely dark throughout the season. With respect to moisture availability, *P. cespitosum* occupies soils that offer consistent, moderate or slightly dry moisture levels: very little soil moisture variation occurs either among or within sites of this species. This suggests that the restriction of *P. cespitosum* to shaded sites may be due to intolerance of drought, rather than to intolerance of high light *per se*: preliminary results of factorial experiments that independently varied moisture and light support this interpretation (S. E. Sultan, unpublished data). The species may also be excluded from open sites due to indirect effects of light levels on herbivore distribution or other biotic factors (Huffaker 1957; Louda & Rodman 1996). A further interesting result is the absence of flooding in any microsites of the species, a result which is consistent with existing qualitative accounts of its field distribution (e.g. Hobbs 1992). Thus, *P. cespitosum* may differ from its congeners in being intolerant of flooding either early or late in its life cycle (D. L. Bell & S. E. Sultan, unpublished data). The range of soil temperatures measured at *P. cespitosum* sites is relatively narrow; this may simply be a result of the shaded, moist conditions rather than a factor that in itself influences the species distribution.

According to floristic records, *P. cespitosum* was introduced into North America from south-east Asia as recently as the late 1920s, and since that time has spread rapidly across the north-east, south-east and mid-western regions, establishing extremely dense populations along shaded roadsides and damp woodland trails (Harger 1930; Seymour 1969; Hough 1983; Hobbs 1992; Weatherbee 1996). Despite its narrow habitat specificity, the species has become widespread in the region, and has recently come to be listed as a fully naturalized weed (Mitchell & Dean 1978; Gleason & Cronquist 1991; Carr & Hernandez 1993). Possibly the favourable combination of disturbance, low light and moderate moisture is a rarer habitat in its native subtropical Asian range than in this highly industrialized temperate region, where shaded road-cuts abound. The species may also be undergoing rapid evolutionary change in the absence of its native competitors and herbivores that enhances its competitive ability and hence invasive spread (Blossey & Notzold 1995).

Polygonum hydropiper is the only one of the four species that has a distinctly narrow ecological range on most resource axes. This species is limited to sites with consistently high light availability and moisture levels throughout the growth season, as well as highly organic, porous soils. *Polygonum hydropiper* also appears to have certain specific mineral requirements: although it occupies sites with very low to very high macronutrient content, it occurs only in sites with high early nitrate and calcium levels, and does not occur in sites with low cation exchange capacities. The fact that all sites of this species were found to have similar pH levels close to 6.0 is also suggestive of restriction to a particular type of soil solution. Because *P. hydropiper* is restricted to sites that share

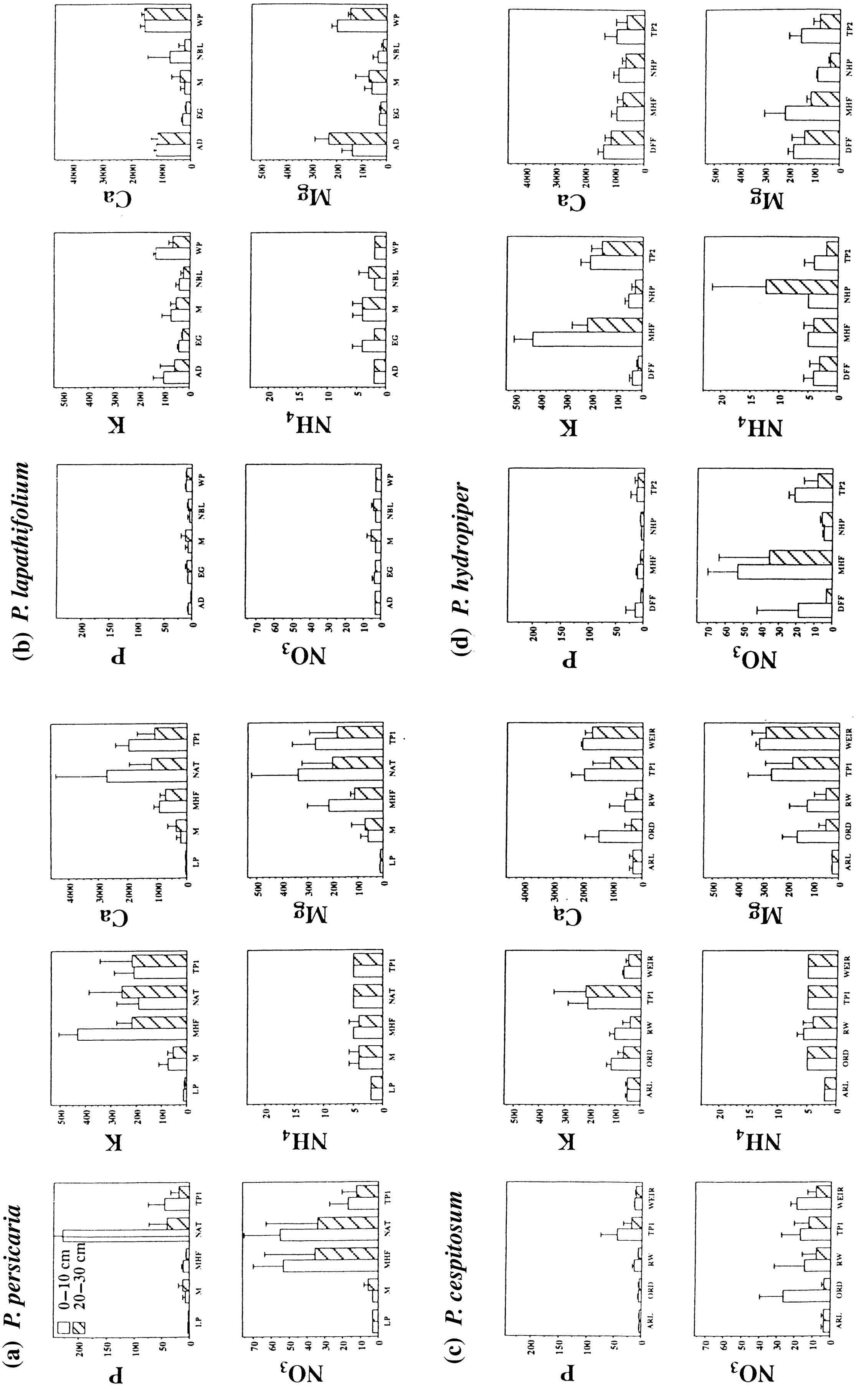

Fig. 11 Late-season macronutrient content at two soil depths at field sites of each species. Means ± SD are shown based on three measurements per depth at each site for six macronutrients.

this complex of edaphic traits, further studies are required to elucidate which environmental factor(s) limits the species' distribution. For instance, soil moisture availability is positively correlated with field capacity and hence organic matter, soil porosity, cation exchange capacity and macronutrient content (Wilson & Keddy 1985; Gaudet & Keddy 1995). In general, when environmental states are correlated, conclusive determinations of environmental tolerance for particular factors ('fundamental niche'; *sensu* Futuyma & Moreno 1988) require controlled, single-factor studies (Sultan 1995).

However, the results also indicate that the ecological range of *P. hydropiper* may exceed that of the two more generalist species with respect to seedling flood tolerance: only this species occurs in sites where shallow as well as deeper soils were flooded early in the growth season. Even if juvenile and mature plants of species such as *P. persicaria* and *P. lapathifolium* were equally flood tolerant as those of *P. hydropiper*, such a difference in seedling tolerance would effectively exclude the former species from wetland habitats in which early flooding occurred (Grubb 1977). The fact that *P. hydropiper* achenes are significantly larger than those of the other species suggests that these highly provisioned propagules may be able to develop branched and possibly adventitious root systems earlier in development, and thus ensure access to surface or soil oxygen.

It is often assumed that the generalist 'Jack of all trades is master of none', and that more narrowly distributed species are 'more efficient on their own ground' (Pianka 1988). In this view, species that are found only in particular habitats are assumed to be specially adapted to, and hence competitively superior, in those habitats (see references and critique in Futuyma & Moreno 1988). An alternative view postulates that in many cases putatively specialist taxa are simply restricted to a narrower range of environmental conditions than are inhabited by broadly tolerant generalists (Sultan 1992 and references therein). The distribution data presented here support the latter view: *P. persicaria* successfully colonizes a wide diversity of habitats and microhabitats, including those inhabited by its less broadly distributed congeners. Thus, the co-existence of *P. persicaria* with ecologically narrower *Polygonum* species in their characteristic habitats may result from niche overlap in those habitats combined with stochastic environmental variability, rather than from resource partitioning according to the classical, animal-based model (discussion and references in Zobel 1992; for discussion of 'lottery' models of species co-existence see Chesson & Huntley 1989; Goldberg & Barton 1992; Bengtsson *et al.* 1994; and references therein). The ecological ranges of the two most narrowly distributed species, *P. cespitosum* and *P. hydropiper*, do, however, extend to unfavourable environmental states (constant deep shade and early season flooding, respectively) not found in the realized distribution of *P. persicaria*. Thus, despite substantial ecological overlap, specific extreme conditions or microsites associated with certain habitats may be outside the environmental range of generalist species such as *P. persicaria*.

Conclusions

The results of this study support the notion that plant species may have a broad realized distribution for several key environmental variables, and hence be considered ecological generalists. *Polygonum persicaria* is evidently such a species, possibly due to the great phenotypic plasticity of its individuals (Sultan & Bazzaz 1993a,b,c). A second widespread agricultural weed in this group, *P. lapathifolium*, has broad tolerance for moisture and nutrient variability but evidently has narrower requirements for available light, and accordingly occurs in a narrower range of habitats than *P. persicaria*. Based on samples of five populations for each species, *P. cespitosum* and *P. hydropiper* occur only in a specific and narrow range of conditions: these species are characteristic of shaded, moist habitats and bright, moist, high-nutrient habitats, respectively. Overlap in the realized distribution of *P. cespitosum* and *P. hydropiper* with that of *P. persicaria* suggests that the former species may not be functional specialists in these habitats, but rather may be restricted to them due to intolerance of other types of environment. Ongoing comparative studies of individual phenotypic plasticity and environmental tolerance under controlled conditions (Sultan 1995; Sultan *et al.* 1998; D. L. Bell & S. E. Sultan, unpublished data; S. E. Sultan, unpublished data) should clarify the causal basis of these differences in realized ecological breadth among *Polygonum* species.

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