Genotypic variation in *Polygonum pensylvanicum*: nutrient effects on plant growth and aphid infestation

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Abstract: Variation in the performance of 20 genotypes of *Polygonum pensylvanicum* under two nutrient treatments was studied in a garden experiment. Nutrient fertilization enhanced vegetative biomass and fruit biomass production, but did not result in significant genotype–environment interactions, suggesting that nutrient variation of the range used in the experiment has little potential as a microevolutionary factor in this species. Leaf nitrogen concentration was not affected by a nutrient pulse. The degree of transient aphid infestation that occurred during the experiment had a weak positive correlation with final reproductive biomass of plants. Mean density of aphids per leaf was negatively correlated with percent leaf nitrogen and was not affected by genotypic identity of host plants.

Key words: *Polygonum pensylvanicum*, genotype–environment interaction, phenotypic plasticity, aphids, nutrients.

Résumé : Dans un jardin expérimental, les auteurs ont étudié la variation de performance de 20 génotypes du *Polygonum pensylvanicum*, en présence de deux régimes nutritionnels. L'apport en nutriments augmente la biomasse végétative et la biomasse de la production en fruits, mais ne conduit pas à des interactions génoype–environnement significatives, ce qui suggère que la variation en nutriments, aux quantités utilisées pour l'expérience, comporte peu de potentiel comme facteur microévolutionnaire chez cette espèce. La teneur en azote foliaire n'est pas affectée par un apport ponctuel en nutriments. Le degré d'infestation transitoire par les pucerons, observée au cours de l'expérience, montre une faible corrélation positive avec la biomasse reproductive finale des plants. La densité moyenne des pucerons par feuille est en corrélation inverse avec le pourcentage d'azote foliaire et n'est pas influencée par l'identité génotypique des plants hôtes.

Mots clés : *Polygonum pensylvanicum*, génotype–environnement, interaction, plasticité phénotypique, pucerons, nutriments.
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Introduction

Owing to phenotypic plasticity, individual plant genotypes may not respond to consistent selection pressures resulting from spatial or temporal variability of edaphic or biotic conditions (Sultan 1995). It is therefore critical to assess the degree to which genotypes in natural populations exhibit phenotypic plasticity, as opposed to specialization, in response to environmental variation (Schlichting 1986). Despite important implications for our understanding of the ecological and evolutionary phenomena, there is little information on the genotypic variation in the performance of plants under different environmental conditions and on the genetic covariation of ecologically relevant traits (e.g., Geber and Dawson 1990; Sultan and Bazzaz 1993). For example, there is evidence for genetic variation in plant response to heavy metals, soil pH, and atmospheric pollution (Thomas and Jasieński 1996 and references therein). Genotypic variability in responsiveness to variation in soil nutrients (Sultan and Bazzaz 1993) has also been documented, but the extent to which such responsiveness depends on other environmental conditions, such as variation in abiotic variables (Bazzaz 1996), herbivory (Strauss 1990; Fritz and Simms 1992; Horner and Abrahamson 1992), or competition (e.g., Bazzaz et al. 1995), is poorly known.

We examined the responses of 20 genotypes of *Polygonum pensylvanicum* L. (Polygonaceae) to two nutrient regimes in an experimental garden. We focused on the detection of possible genotype–environment interactions that, if present, would indicate that different genotypes varied in their relative performance at low and high edaphic conditions. *Polygonum pensylvanicum* is suitable for experimental manipulation because it can be cloned, allowing the use of many replicates of genetically identical individuals exposed to different environmental conditions (e.g., Thomas and Bazzaz 1993). Furthermore, because it is an annual plant, reproductive performance of the different genotypes can be assessed over the plant's life span, allowing estimation of plant fitness.

A transient infestation of the plants by aphids in our experiment provided an opportunity to investigate impact of herbivory on genotypic variation in plant response to edaphic conditions. The suitability of plant tissues for aphids is dependent upon plant genotype (Painter 1958; Moran 1981; Service 1984*a*; Whitham 1989), the environment in which the plant is grown (van Emden 1966; Coleman and Jones 1988), and the interaction between genotype and environment (Maddox and Cappuccino 1986). Although several plant characteristics (e.g., secondary compounds, plant water status) may affect host plant suitability for aphids, the nitro-

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gen content of the phloem may be most influential (Kennedy 1958; Dixon 1970; Whitham 1978; Raven 1983; White 1984), indicating that nutrient fertilization may have an indirect effect on aphid infestation. We asked whether preferences of the aphid *Capitophorus hippophaes* Walker (Homoptera: Aphididae) during a naturally occurring infestation episode were influenced by the genotypic identity and nutrient fertilization of host plants and whether genotypes differed in their responses to aphid presence.

Materials and methods

Plant propagation and experimental protocol

The seeds of randomly chosen individuals of *P. pensylvanicum* were collected at a 2-ha area in Phillips Tract of the University of Illinois Experimental Area, Urbana, Illinois in November and December 1987. After a natural stratification treatment over the winter, seeds were sent to Native Plants Inc. (NPI), Salt Lake City, Utah for propagation using an axillary bud enhancement technique. This technique begins with a single seed per genotype; the single individual grown from this seed is then used to produce a clonal line of genetically identical daughter plants. To reduce initial variability, all genets were trimmed to uniform height and leaf number prior to transplantation. Plants were transplanted directly to an experimental garden in Cambridge on July 15, 1988, and 1 week later, five plants from each of the genotypes received either a nutrient pulse of 0.80 g Peter's 15:30:15 N−P−K (125 mg nitrogen) or were left unfertilized. The nitrogen dosage corresponded to a moderate fertilization intensity used in other experiments in our laboratory on the same sample of genotypes. Replicates were planted 0.75 m apart in parallel strips with genotype positions randomized within each strip.

Aboveground parts of all plants were harvested 76 days after transplanting (September 21, 1988) and then dried at 55°C to constant weight. Each plant was separated into reproductive and vegetative structures, and then vegetative dry weight biomass (shoots and leaves) was determined. Fruits were sorted from infructescences to determine mature fruit biomass. Fruit counts were made on a random subsample of nine genotypes, using two replicates per treatment per genotype (36 plants in total). Mature fruit number for the remaining genotypes was estimated by total fruit weight; total mature fruit biomass was divided by the weight of 100 fruits, as estimated from the subsample; multiplying by 100 then gave an estimate of total fruit number.

Aphid counts

Capitophorus hippophaes Walker is a common aphid species in the United States; it is host alternating, utilizing *Eleagnus* spp. or *Hippophae rhamnoides* L. (Sea Buckthorn) as its primary hosts, and various species of *Polygonum*, including *P. pensylvanicum*, as summer hosts. The aphid overwinters as eggs (holocyclic) on the primary hosts and completes the remainder of its life cycle on the secondary hosts (Bei-Bienko 1967). Aphids began colonizing plants from a naturally occurring local population 1 week after transplantation (July 21) and were observed feeding on the underside of leaves of all ages.

To relate aphid population size to plant performance, whole plant aphid counts were conducted from July 26 to July 29. Aphids were counted on every leaf of 2 plants per genotype randomly selected within each nutrient treatment (80 plants in total). While such allocation of effort enabled characterization of all 20 plant genotypes, it inevitably reduced the power of inference about individual genotypes and genotype−nutrient interaction. However, the amount of labor involved in aphid counting precluded higher within-genotype replication. Mean aphid number per leaf (on an individual plant) and interleaf variance in aphid numbers were used to compute a coefficient of dispersion that indicates the degree to which aphid distribution deviated from a random pattern (Poisson distribution) (Sokal and Rohlf 1981). To remove the effects of differences in leaf number among plants, we computed also mean aphid densities on the 20 most densely infested leaves on each plant.

We believe populations peaked at the time of our census because daily visual surveys thereafter did not indicate increasing densities, and populations declined sharply within a week of our survey. However, to be certain that our measures of aphid density were not influenced by aphid numbers that peaked on different genotypes at different times, we conducted a second nonrandom census on 17−19 August. We selected six genotypes representing a range of infestation levels at the time of the initial census. This second census indicated that mean densities of aphids per leaf had declined by an average of 86% (range: 78−93%); daily surveys of the plants gave no indication of staggered aphid population peaks among genotypes. Following these censuses, aphid numbers continued to decline, and populations had disappeared by the time plants were harvested. Since we were able to conduct aphid population counts for all genotypes only once, aphid numbers reported in our experiment are likely to be a composite function of both aphid settling preference and their performance after settling.

Nitrogen analysis

The first two youngest fully expanded leaves per plant were collected for nitrogen analysis on July 30. Young leaves were chosen because they generally have higher concentrations of nitrogen than older leaves and because aphids are phloem feeders known to concentrate on new and senescing leaves (Kennedy 1958; Dixon 1970). Percent nitrogen was analyzed by an ammonia distillation process using a semimicro Kjeldahl-steam distillation unit (Bremner 1965) following an aluminum block digestion technique (Gallaher et al. 1976).

Statistical analyses

Interactive effects of fertilizer and genotype on total fruit biomass and total vegetative biomass were tested in a mixed-model, multivariate analysis of variance, with genotype as the random factor. Genotype−environment interactions in both traits were investigated in more detail using a bootstrap-based test of qualitative crossover changes in genotypic ranks (Thomas and Bazzaz 1993), with 1000 iterations. The procedure tests the null hypothesis of perfect correlation in genotypic ranks ($r = 1$), i.e., when there are no significant changes in ranks between nutrient levels.

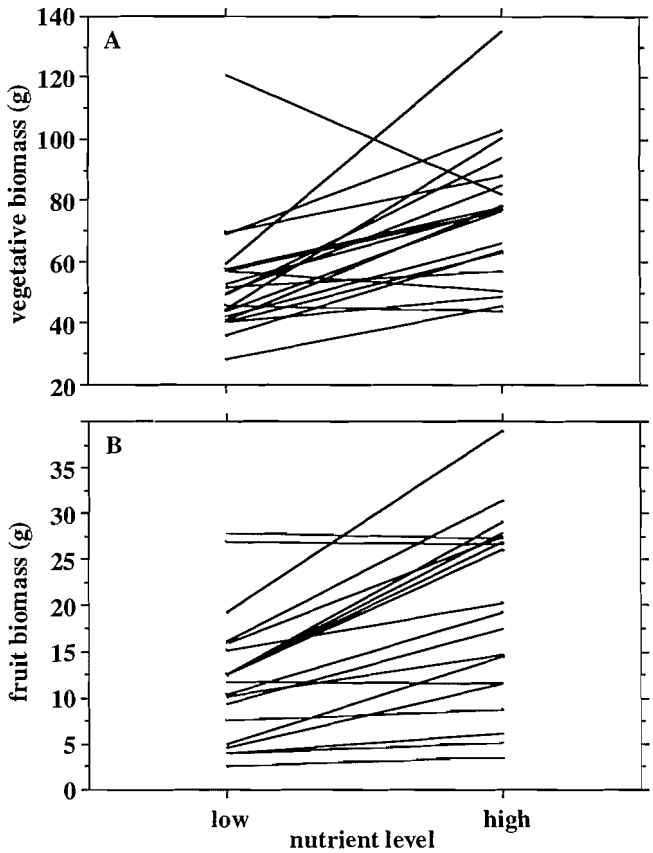
Univariate two-way analyses of variance were used to examine the effects of genotype and fertilizer on plant leaf number, nitrogen content, coefficient of dispersion, and mean aphid densities (on a per-leaf basis), calculated from either all leaves or the 20 most densely infested leaves on each plant. Pearson correlation coefficients were calculated to assess the relationships between aphid densities and plant performance (as indicated by total fruit biomass and total plant biomass) and between aphid densities and other plant characteristics (leaf number, total biomass, and nitrogen concentration). All biomass data were log transformed and counts were square-root transformed prior to analyses.

Results

Plant responses

Nutrient treatment significantly enhanced both total biomass and total fruit biomass (Wilks' $\lambda = 0.245$, $s = 2$, $m = 8$, $n = 18$, $p = 0.0001$; Table 1). There was significant variation among genotypes in both measures of plant performance (Wilks' $\lambda = 0.055$, $s = 1$, $m = 0$, $n = 8$, $p = 0.0001$). Genotypic responses did not depend on the nutrient level,

Fig. 1. Norms of reaction to two levels of nutrients in 20 genotypes of *Polygonum pensylvanicum* grown in an experimental garden. (A) Total vegetative biomass. (B) Total fruit biomass.



as shown by the lack of significant genotype–environment (G × E) interaction term (Wilks' $\lambda = 0.471$, $s = 2$, $m = 8$, $n = 18$, $p = 0.58$). Lack of qualitative crossovers in genotypic ranks between nutrient levels (Fig. 1) was confirmed in separate bootstrap tests for total vegetative biomass ($p = 0.15$) and total fruit biomass ($p = 0.52$).

Mean leaf number was marginally higher in the low- than in the high-nutrient treatment ($F_{(1, 19)} = 3.274$, $p = 0.086$), with a significant effect of variation among genotypes ($F_{(19, 40)} = 1.848$, $p = 0.05$). Mean number of fruits varied significantly between nutrient levels ($F_{(1, 19)} = 36.358$, $p = 0.0001$) and among genotypes ($F_{(19, 40)} = 11.721$, $p = 0.0001$). Leaf concentrations of nitrogen correlated weakly with plant size (as estimated by leaf number; $r = 0.273$, $p = 0.014$), but were not affected by either genotypic identity ($F_{(19, 40)} = 0.970$, $p = 0.51$) or nutrient addition ($F_{(1, 19)} = 0.155$, $p = 0.70$), with genotypic means ranging from 2.95 to 3.66% of nitrogen (Table 1). As in the case of vegetative and fruit biomass, the G × E interaction term was not significant either for leaf number ($F_{(19, 40)} = 0.756$, $p = 0.74$) or fruit number ($F_{(19, 40)} = 1.195$, $p = 0.31$) or for nitrogen concentration ($F_{(19, 40)} = 0.978$, $p = 0.5$).

Aphid responses and effects

Mean per-leaf densities of aphids did not differ between the nutrient treatments (2.8 versus 2.3 individuals per leaf, at high and low nitrogen fertilization levels, respectively; $F_{(1, 19)} = 1.965$, $p = 0.18$). However, there was significant variation among genotypes in the intensity of aphid infestation (i.e., mean per-leaf densities, averaged over both nutrient treatments; $F_{(19, 40)} = 1.997$, $p = 0.03$). The degree to which aphid distribution was clumped on leaves, quantified by the coefficient of dispersion (CD), was not affected by genotypic identity ($F_{(19, 40)} = 1.385$, $p = 0.189$) or genotype–nutrient interaction ($F_{(19, 40)} = 0.602$, $p = 0.88$). Aphids were marginally more clumped on high-nutrient (CD = 12.2) than on low-nutrient (CD = 9.5) plants ($F_{(1, 19)} = 3.740$, $p = 0.07$).

Table 1. Plant performance and aphid infestation of *Polygonum pensylvanicum* genotypes grown under two nutrient levels.

	Nutrient level	
	Low	High
Total vegetative biomass (g)	52.8 (3.98)	75.7 (3.87)
Leaf number	175.0 (7.65)	157.8 (6.53)
Total fruit biomass (g)	12.0 (1.27)	19.8 (1.65)
Total fruit number	3119 (296)	4689 (354)
Nitrogen concentration (%)	3.34 (0.045)	3.36 (0.040)
Aphid number (mean per leaf)	2.3 (0.29)	2.8 (0.33)
Coefficient of dispersion	9.5 (0.88)	12.2 (1.52)

Note: Values are given as means (SE).

Mean number of aphids per leaf (per plant) was positively correlated with total fruit biomass ($r = 0.232$, $n = 80$, $p = 0.038$), and marginally correlated with total fruit number ($r = 0.194$, $p = 0.086$,), but not with vegetative biomass ($r = 0.157$, $p = 0.165$). Mean number of aphids per leaf per plant was negatively correlated with percent leaf nitrogen ($r = -0.280$, $p = 0.012$). This relationship holds if the effect of plant size is removed through partial correlation analysis ($r = -0.320$, $p < 0.05$).

To eliminate variation among plants in the number of leaves infested and to avoid confounding effects of total leaf number on plant attractiveness to aphids, similar analyses were performed on the data set limited to the 20 most densely infested leaves from each plant. While the genotypic differences became nonsignificant ($F_{(19, 40)} = 1.473$, $p = 0.15$), plants from the high nutrient treatment had 50% higher mean aphid densities (15.2 aphids per leaf) than unfertilized plants (10.4 aphids per leaf; $F_{(1, 19)} = 9.718$, $p = 0.006$). There was no significant interaction of plant genotype and plant nutrient environment in the case of the mean number of aphids per leaf per plant, either calculated from all leaves ($F_{(19, 40)} = 0.826$, $p = 0.67$) or from the 20 most densely infested leaves ($F_{(19, 40)} = 0.601$, $p = 0.88$).

Discussion

Annual plants, especially early-successional, sun-adapted species such as *Polygonum pensylvanicum* (Zangerl and Bazzaz 1983), have the ability to exploit resource enhancements owing to disturbance, e.g., soil nutrient pulses (Parrish and Bazzaz 1982), and are characterized by wide species-level response breadths (Bazzaz 1996; Jasieński et al. 1997). In fact, as argued by Sultan and Bazzaz (1993), plasticity is expected in the case of plant responses to variation in soil

nutrients, since it entails no physiological costs and edaphic variation is expressed at small spatial scales. For example, Lee et al. (1986) found that response to a gradient of nutrient fertilization was very broad, with declining productivity at very low and very high levels of soil nutrients, especially for reproductive characters. Responses of six genotypes of *P. pensylvanicum* to gradients of light and temperature were similar and plastic (Zangerl and Bazzaz 1983). Lack of significant genotype–environment interaction terms may signify that under the experimental nutrient levels genotypes maintained similar relative rates of growth and reproduction, leaf nitrogen concentrations, and levels of susceptibility to aphids, regardless of nutrient environment. Therefore, it appears unlikely that naturally occurring levels of heterogeneity in soil nutrients similar to those used in this experiment will lead to microevolutionary changes in natural populations of *P. pensylvanicum*. In a comprehensive study of plasticity in *P. persicaria*, a related species, Sultan and Bazzaz (1993) also did not find significant genotype–nutrient interactions in most studied plant characteristics.

While total vegetative biomass and fruit biomass production were significantly enhanced by the nutrient addition (43 and 65%, respectively), nitrogen concentration in leaves did not change significantly. Such a result is expected, if there is a negative relationship between plant size and nitrogen concentration in tissues, caused either by dilution of nitrogen through starch accumulation (e.g., Kuehny et al. 1991) or by higher nitrogen use efficiency (e.g., Hilbert et al. 1991). Coleman et al. (1993) demonstrated that a reduction in concentration of nitrogen in plants grown at two CO_2 levels may be an artifact, resulting from size dependence. In contrast, we did not find a negative correlation between plant size and nitrogen concentration: plants with more leaves were actually more likely to have higher leaf nitrogen content. Lack of a significant effect of the fertilization treatment on nitrogen concentration in the leaf tissue might have been due to mean leaf number being marginally lower at the high nutrient level, or due to responses expressed in leaf area (not recorded in this study) and nitrogen content per leaf, rather than in nitrogen concentration.

Genetic variation among host plants in the susceptibility to aphid colonization and infestation is especially well documented for crop species, with more cases of crop resistance to aphids known than for any other insect (Painter 1958). It has been shown that host plant genotypes for noncultivated species vary in resistance to insect herbivores, including aphids (Service 1984*b*; Maddox and Cappuccino 1986; Weis and Abrahamson 1986; Fritz 1990; Whitham 1989; Moran and Whitham 1990). Our data, however, demonstrated very little variation among host plants for numbers of *C. hippophaes* based on genotypic identity and no variation due to genotype–environment interaction. Low levels of intergenotypic differences in aphid infestation may be owing to past strong selection pressure related to aphid herbivory, although this appears unlikely because the host plant population originated in Illinois, while the aphids are a local Massachusetts population. Also, an environmentally induced variation in plant phenotype owing to environmental heterogeneity in the garden might have reduced expression of genetically based differences. For example, it is known that the growth and reproduction of aphids differed depending on *Solidago* host genotype, but expression of this difference depends on water availability (Maddox and Cappuccino 1986).

Aphid numbers have been shown to increase with nitrogen application to plants (van Emden 1966; van Emden and Bashford 1969), in agreement with our result in the case of the 20 most densely infested leaves, although decreases in aphid density have also been frequently reported (van Emden et al. 1969). A marginally significant difference between nutrient treatments in the pattern of spatial intraplant distribution of aphids, as shown by the dispersion index, indicates that nitrogen addition may indirectly modify aphid behavior, through some effects on plant form, and potentially, leaf demography (see Hartnett and Bazzaz 1984).

However, aphid numbers were negatively correlated with percent leaf nitrogen, suggesting that the relationship between nutrients and aphid numbers (as measured by the 20 most densely infested leaves per plant) is due to factors other than levels of tissue nitrogen. It is unlikely that aphids are capable of modifying %N in plant tissues by preferentially removing nitrogen from the phloem. Hawkins et al. (1986) reported lower percent nitrogen in infested, compared with uninfested, cowpea and pea seedlings, which could correspond to the result obtained in this study. There was no difference in percent nitrogen between infested and control alfalfa plants (e.g., Summers and Coviello 1984). Host plants resistant to aphids have been found to have sap containing lower nitrogen concentrations than susceptible individuals (van Emden and Bashford 1969; Whitham 1978). Aphids may also cause higher nitrogen content in attacked compared with unattacked leaves, by affecting plant metabolism and leaf chemistry (Mattson 1980; Capinera 1981; Raven 1983). The negative correlation observed in this study is not easy to explain in light of the great efficiency of aphids in finding nitrogen-rich resources. Aphids might have responded negatively to another character correlated with high levels of leaf nitrogen; young, nitrogen-rich leaves of many ephemeral species also have relatively high concentrations of secondary compounds (e.g., alkaloids) that can repel herbivores (Mattson 1980; Krischik and Denno 1983).

There is no evidence in our data that aphid infestation had a negative impact on plant fitness. Total vegetative biomass or fruit production, good proxies of fitness in annual plants, either were not related to aphid number or showed a weak positive relationship. This contrasts with much available data, which have demonstrated negative effects of aphids on the fitness of their host plants. For example, aphids reduced sycamore (*Acer pseudoplatanus* L.) stem wood production and sapling growth (Dixon 1971); in field beans (*Vicia faba* L.), all measures of reproductive output were reduced by a prolonged, heavy aphid infestation (Banks and Macaulay 1967). Likewise, an impact of aphids on the host plants might have been detectable in our study if aphid population levels had been experimentally elevated. However, aphid population sizes resulted from a naturally occurring infestation and, consequently, the reported results represent realistic levels of infestation likely to be experienced by the plants under field conditions.

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