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Effects of genotype, habitat, and seasonal variation on iridoid glycoside content of *Plantago lanceolata* (Plantaginaceae) and the implications for insect herbivores

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Summary. We investigated the effects of genotype, habitat, and seasonal variation on production of the iridoid glycosides, aucubin and catalpol, in leaves of the common weed *Plantago lanceolata*. Two genotypes, one each from a lawn and an adjacent abandoned hayfield population, were clonally replicated in the greenhouse, and then planted back into the two habitats. One quarter of the plants from each treatment were harvested on each of four dates, at approximately two-week intervals. Over the course of the growing season, and in both habitats, we found a significant increase in the concentration of both aucubin and catalpol in *P. lanceolata* leaves. The genotypes differed in their response to environmental variation, both in time and between sites, as indicated by significant genotype × date and genotype × site interactions. Early in the season, habitat (lawn or field) had a greater effect on iridoid glycoside concentration than did plant genotype, but later in the season, plant genotype was more influential in determining the iridoid glycoside concentration. Thus, the relative palatability of *Plantago* genotypes to specialist and generalist herbivores may vary in time and space.

Key words: Seasonal variation – Iridoid glycosides – Herbivory – *Plantago* – Genotype × environment interactions

Spatial and temporal variation in the concentration of plant allelochemicals has been shown to exist in a variety of plant species (e.g., Mabry 1970; Mooney and Chu 1974; Lincoln and Langenheim 1979, 1981; McKey 1979; Nelson et al. 1981; Krischik and Denno 1983; Janzen and Waterman 1984; Johnson et al. 1984; Rodman and Louda 1984; Lindroth et al. 1987; Mauffette and Oechel 1989; Waterman and Mole 1989). One such source of variation is the phenological change that occurs as a plant develops over the course of a growing season (Berenbaum 1981; Hatcher 1990). Moreover, defense production may differ among plant genotypes (Simms and Rausher 1989; Bowers and Stamp 1992; Fajer et al. 1992) and may also be influenced by environmental variation among sites (Maddox and Cappucino 1986; Mihaliak and Lincoln 1989; Strauss 1991).

For insect herbivores encountering these plants as potential hosts, changes in plant chemistry associated with plant phenology or environment may have a profound influence on their choice of, and performance on, various host plants (Kearsley and Whitham 1989). If plant genotypes differ in their responses to environmental variation in time or space, then the potential for response to selection exerted by herbivores may also be variable. However, relatively little is known about genetic variation in plastic responses of defensive chemistry to environment.

Plantago lanceolata (Plantaginaceae) is a common, introduced weed which produces two iridoid glycosides, aucubin and catalpol, known to influence feeding by both specialist and generalist insect herbivores (Bowers 1983, 1984; Bowers and Puttick 1988). In order to further our understanding of the phenological changes in plant allelochemistry to which herbivores are exposed, and to assess the relative influence of genotype versus environment in determining iridoid glycoside content of leaves, we asked three questions: 1) Are there phenological changes in iridoid glycoside content of *Plantago lanceolata* leaves? 2) Are there differences between sites in iridoid glycoside production? 3) Do genotypes differ in iridoid production or in plastic response of iridoid production to temporal and spatial environmental heterogeneity?

Materials and methods

Plantago lanceolata plants were collected from two contrasting habitats at Brown University's Haffenraffer Reserve (Bristol Co., R.I.): a lawn population and an abandoned hayfield population, and vegetatively propagated in the Brown University greenhouse.

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Light availability varied significantly between these two sites: plants in the field site received, on average, five percent of available sunlight above the canopy, whereas those in the lawn received 89 percent of available sunlight (Schmitt et al. 1992). In early May 1988, two genotypes, one each from lawn (="L15") and field (="F20"), were clonally replicated using the method of Wu and Antonovics (1975). Plants were grown in the greenhouse until June 28, 1988, when they were planted back into the two habitats at Haffenraffer Reserve in the following arrangement. Twenty-two plants (11 replicates of each of the two genotypes) were randomly planted at 0.5 m spacing in a 4 × 6 array within each block; there were two blocks in the lawn and two in the field, for a total of 88 plants. In addition, eight plants (4 of each genotype) were harvested on June 28 to estimate plant status at the time of field planting.

Plants were censused approximately every other week throughout the growing season, when the number of leaves and reproductive stalks on each plant were counted (July 7, 19, August 1, 17, and 31). At this time, plants were also searched for signs of herbivory. One quarter of the plants, chosen at random from each block, were harvested on each of four harvest dates, approximately one week after each census (July 26, August 10 and 23, and September 5, 1988). Because plants were being harvested, the number of plants censused declined from 88 on July 7 to 28 plants on August 31. The actual number of plants harvested per date was 22, 22, 21 and 20, respectively, due to a very low rate of mortality. The lawn population was mowed four times during the growing season (July 12, 27, August 9, and 23).

At harvest, individual plants were clipped at the base, approximately 2 cm from the ground, and placed into a labelled brown paper bag. Bags containing *P. lanceolata* leaves were dried at 50° C to a constant weight. Leaves from each individual plant to be analyzed for iridoid glycosides were ground to a fine powder in a mortar and pestle and redried at 50° C. A 100 mg aliquot was taken for extraction and quantification of iridoid glycosides (aucubin and catalpol) by gas chromatography (Gardner and Stermitz 1988).

To understand the relative contribution of new and mature leaves of these genotypes to the iridoid glycoside content of the entire plant, we separated five individuals of each of the two genotypes into new and mature leaves. These plants were growing in pots in the greenhouse, and were of approximately the same size as the plants that were planted into the field and lawn sites. They were harvested for analysis in March, and were never transplanted into the field or lawn. Because *P. lanceolata* leaves grow in a rosette, we were easily able to determine which leaves were new and which were mature. We designated the newest eight leaves as "new" and the rest of the leaves as "mature". We analyzed these new and mature leaves separately for iridoid glycosides using the procedure described above.

Climatological data were obtained from monthly summaries of the National Climatic Data Center for the closest station, T.F. Green Airport, Warwick, Rhode Island. Statistical analyses were performed using the GLM procedure of SAS, using the arcsine transformed iridoid glycoside concentrations.

Results

The summer of 1988 was relatively dry, with the exception of substantial precipitation during the end of July (Fig. 1). Mean daily temperatures fluctuated between 14 and 31° C during the course of the experiment, but did not fall below 22° C from July 6 to August 21 (Fig. 1). During this period, censuses showed that the mean number of leaves increased for plants of both genotypes in the lawn population, but stayed relatively constant for plants of both genotypes in the field site (Fig. 2 top). Plants of both genotypes in both sites had few flowers at the beginning of the growing season, and the number of flowers

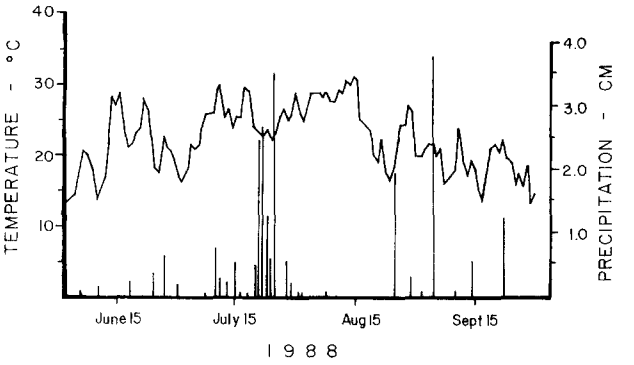

Fig. 1. Fluctuation in temperature (°C, continuous line) and precipitation (cm, vertical lines) over the course of the 1988 growing season. Data are from the National Climatic Data Center for the station closest to the field site at Haffenraffer, in Warwick, Rhode Island

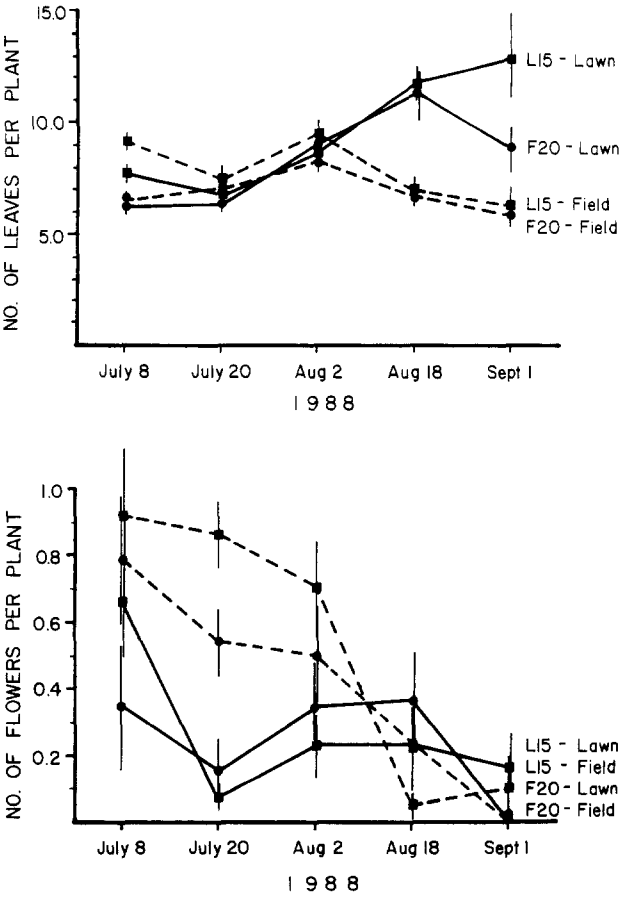

Fig. 2. Development of *P. lanceolata* plants of two genotypes (L15 and F20), planted in two environments (lawn = solid line, field = broken line), censused over the growing season. Means with standard errors are shown. Top – number of leaves per plant; Bottom – number of flowers per plant

declined on plants at both sites and for both genotypes over the summer (Fig. 2 bottom). This was likely due to shading in the field population and mowing in the lawn population. Herbivore damage was minor in both populations.

Three-way ANOVA revealed significant main effects of date, site, and genotype on aucubin, catalpol, and total

Table 1. Results of 3-way ANOVAs of iridoid glycoside content of *Plantago lanceolata*. NS = Not significant

Source of variation	Aucubin		Catalpol		Total iridoids		Proportion catapol	
	F	*P*	F	*P*	F	*P*	F	*P*
genotype	24.20	<0.0001	13.33	<0.001	21.74	<0.0001	0.25	NS
date	46.14	<0.0001	34.27	<0.0001	43.98	<0.0001	14.68	<0.0001
site	28.00	<0.0001	9.02	<0.005	20.84	<0.0001	1.16	NS
block (site)	0.55	NS	0.32	NS	0.29	NS	0.30	NS
geno × site	7.39	<0.01	1.58	NS	4.44	<0.05	2.07	NS
geno × date	7.50	<0.001	4.83	<0.005	6.93	<0.001	1.02	NS
site × date	0.45	NS	6.92	<0.0005	1.35	NS	9.67	<0.0001
geno × site × date	2.61	NS	0.89	NS	1.95	NS	0.27	NS

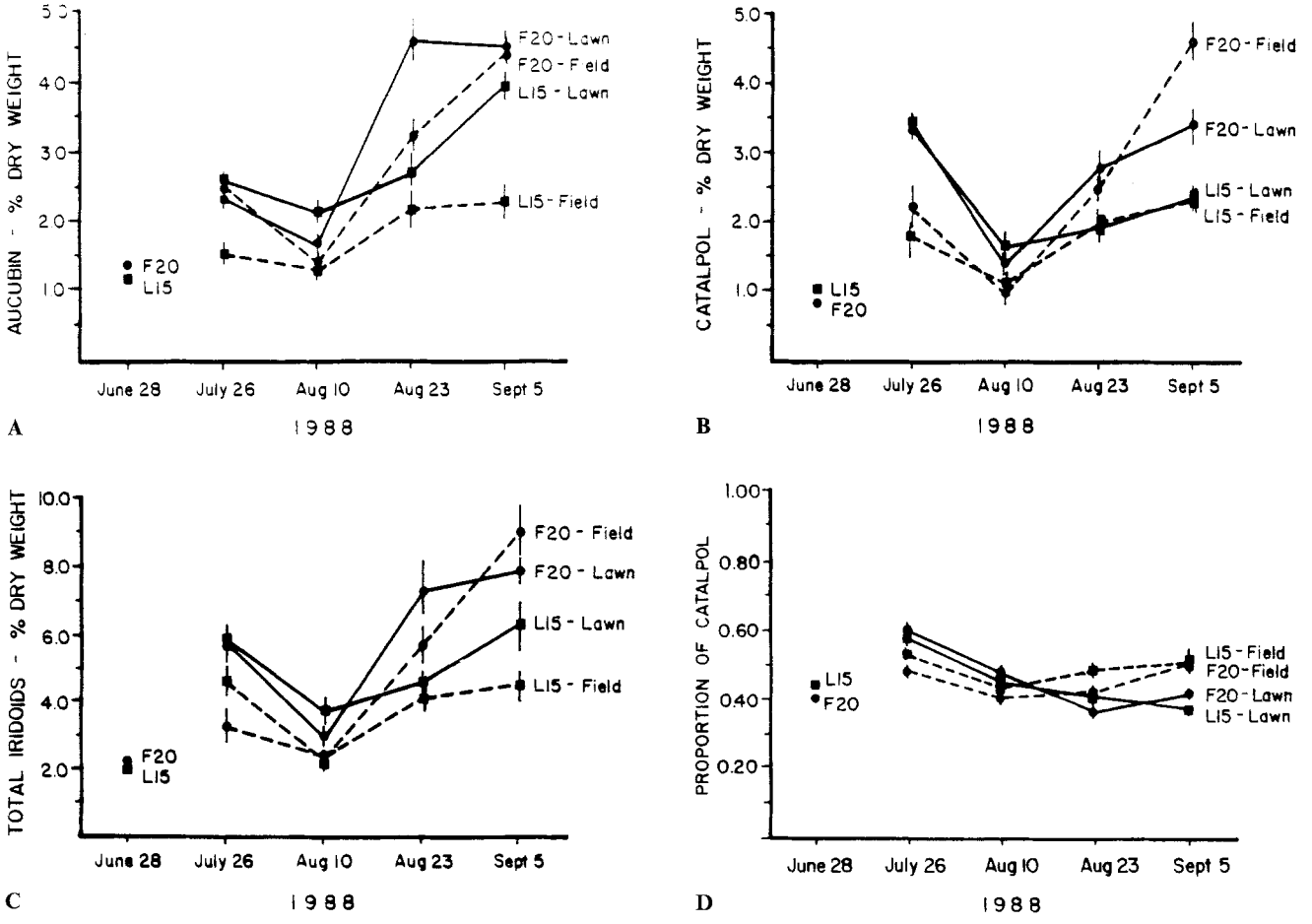

Fig. 3A–D. Iridoid glycoside content of *P. lanceolata* plants of two genotypes (L15 and F20), planted in two habitats (lawn = solid line, field = broken line), harvested over the growing season. The points for L15 and F20 on June 28 are the means for plants analyzed at the time of planting. Means with standard errors are shown. **A.** Aucubin concentration. **B.** Catalpol concentration. **C.** Total iridoid glycoside concentration. **D.** Proportion of the total iridoid glycoside concentration that is catalpol

iridoid concentrations in *P. lanceolata* leaves (Table 1). Relative proportion of catalpol also differed significantly over dates but showed no overall genotype or site effects (Table 1). Plants in different blocks did not differ significantly in iridoid glycoside content (Table 1). Overall mean iridoid concentration was higher in genotype F20 and for both F20 and L15 in the lawn site. However, there were also significant genotype × date interactions for aucubin, catalpol, and total iridoid concentration, indicating that genotypes differed in phenology of iridoid production, and significant genotype × site interactions for aucubin and total iridoid concentration, indicating genetic variation in overall plastic response to site (Table 1). Catalpol concentration and relative proportion of catalpol displayed significant site × date effects, suggesting that phenology of catalpol production differed between sites (Table 1).

Leaf iridoid glycoside content increased in both genotypes and habitats over the course of the growing season (Fig. 3A–C). Total iridoid glycoside concentra-

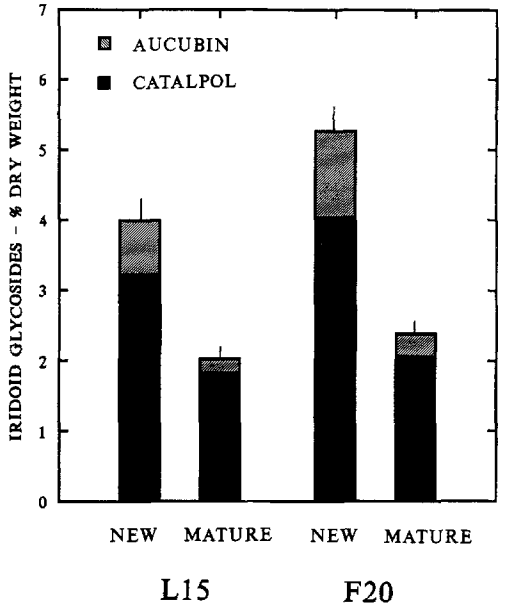

Fig. 4. Iridoid glycoside content of mature and new leaves of *P. lanceolata* plants of two genotypes (L15 and F20). $N=5$ for each genotype. Means are shown. The standard error bars indicate the standard error for the total iridoid glycoside concentration

tions increased from about 2% dry weight for both L15 and F20 at the beginning of the experiment, to a high of over 9% for genotype F20 grown in the field (Fig. 3C). However, the increase was not strictly monotonic; plants harvested on August 10 had lower concentrations of both aucubin and catalpol than did those on the other three harvest dates (Figs. 3A, B). Relative catalpol proportion declined over the season in the lawn site, but not in the field site (Fig 3D).

Because we observed significant genotype × date and site × date interactions, we performed separate 2-way ANOVAs to examine the effects of genotype and site within each sampling date (Table 2). Earlier in the growing season (sampling dates July 26 and August 10), aucubin, catalpol, and total iridoid glycoside content were significantly higher in the lawn site than in the field, but no genotype differences were detected (Fig. 3; Table 2). In contrast, later in the season (sampling dates August 23 and September 5) genotype F20 displayed significantly higher iridoid concentrations than genotype L15, but main effects of site disappeared for catalpol and total iridoid concentration. Relative catalpol content did not differ among genotypes at any date. At the first harvest the proportion of catalpol was significantly greater in the lawn site, whereas by the final harvest it was significantly higher in the field (Table 2; Fig. 3D).

New leaves of *P. lanceolata* had about twice as much iridoid glycoside as mature leaves (Fig. 4). Aucubin, catalpol, and total iridoid glycoside content were significantly higher in new leaves (Table 3). Individuals of genotype F20 had significantly higher concentrations of aucubin, catalpol and total iridoid glycosides than did those of genotype L15 (Table 3). The proportion of catalpol was significantly higher in genotype F20, and in new leaves (Fig. 4, Table 3)

Discussion

Seasonal variation, between-site environmental differences, and genotype all influenced iridoid glycoside pro-

Table 2. Results of 2-way ANOVAs at each sampling date, of iridoid glycoside content of *Plantago lanceolata*. NS = Not significant

Harvest Date	Source of variation	Aucubin		Catalpol		Total iridoids		Proportion catalpol	
		F	*P*	F	*P*	F	*P*	F	*P*
July 26	genotype	2.41	NS	0.47	NS	1.22	NS	1.01	NS
	site	3.32	NS	16.14	<0.001	10.26	<0.005	18.56	<0.001
	geno × site	5.08	<0.05	0.55	NS	2.05	NS	3.32	NS
August 10	genotype	1.21	NS	0.33	NS	0.95	NS	0.12	NS
	site	8.45	<0.01	7.93	<0.02	9.71	<0.01	1.10	NS
	geno × site	2.25	NS	0.22	NS	1.01	NS	0.37	NS
August 23	genotype	23.13	<0.0005	5.20	<0.05	15.26	<0.005	3.69	NS
	site	9.64	<0.01	0.14	NS	3.69	NS	6.33	0.02
	geno × site	0.91	NS	0.29	NS	0.72	NS	0.00	NS
Sept. 5	genotype	14.39	<0.002	35.59	<0.0001	31.42	<0.0001	0.60	NS
	site	7.77	<0.02	3.36	NS	0.93	NS	12.15	<0.005
	geno × site	5.98	<0.05	4.06	NS	7.57	<0.02	0.81	NS

Table 3. Results of two-way ANOVA to compare the iridoid glycoside concentration of new and mature leaves of *Plantago lanceolata* genotypes F20 and LI5. NS = Not Significant

Source of Variation	Aucubin		Catalpol		Total iridoids		Proportion catalpol	
	F	*P*	F	*P*	F	*P*	F	*P*
Genotype (G)	4.475	0.05	12.336	0.003	8.046	0.012	5.489	0.032
Leaf Age (LA)	49.250	<0.001	96.461	<0.001	76.053	<0.001	35.062	<0.001
G × LA	0.888	NS	1.050	NS	1.484	NS	0.259	NS

duction in *P. lanceolata*. The two plant genotypes differed in their plastic response to environmental variation both in time and in space. As a consequence, the relative palatability of *P. lanceolata* genotypes to generalist and specialist insect herbivores may vary through the season and across sites (Bowers and Puttick 1988, 1989). Furthermore, the potential response of *P. lanceolata* to herbivore-mediated selection may be similarly variable.

Evidence from other plant species suggests that environmental variation, such as drought, can strongly influence the production of secondary metabolites (Briske and Camp 1982; Gershenzon 1984; Mattson and Haack 1987; Waterman and Mole 1989). In *Plantago,* temporal and spatial environmental variation may influence the iridoid content of leaves in several ways. First, seasonal and between-site variation in temperature, water, light or nutrient availability may influence the rate of synthesis and degradation of iridoid compounds in a leaf of a given age. Second, environmental variation may affect the age structure of leaves within a plant. New leaves have approximately twice the iridoid glycoside content of old leaves (Fig. 4; Bowers and Stamp 1992). Quantification of iridoid glycoside concentration in individual leaves of *P. lanceolata* showed that amounts ranged from undetectable in the oldest leaves to as high as 20% dry weight in the newest leaves (Klockars and Bowers, unpublished data). Finally, environmental variation could affect reproductive allocation. *Plantago* inflorescences contain a higher proportion of catalpol and total iridoids than do leaves (Bowers, Schmitt, and Collinge, unpubl.), thus increased allocation to reproductive parts may alter iridoid glycoside content of leaves or entire plants.

Whatever the mechanism, mean iridoid glycoside content of *P. lanceolata* leaves generally increased about five-fold in both lawn and field populations over the course of the growing season. The exception to this general increase was for plants harvested on August 10, which had reduced levels of iridoid glycosides in their leaves relative to those harvested on the other three sampling dates. Seasonal changes in plant allelochemicals have been found in many plant species (e.g., Lindroth et al. 1986, 1987; Wagner et al. 1990; Kooi et al. 1991); however, most do not show an increase such as we found in plantain. For example, phenolic glycosides in *Populus* either decreased from May through September, or remained relatively constant, depending on whether there were high or low concentrations of these compounds (Lindroth et al. 1987). The alkaloid boschniakine in the leaves of *Penstemon digitalis* (Scrophulariaceae) declined steadily during the growing season (Lindroth et al. 1986). One possible reason for the difference between our results and those of previous studies is that *P. lanceolata* grows as a rosette, continuously producing leaves throughout the growing season, in contrast with most temperate woody plants, which produce most of their leaves at the beginning of the season (Lechowicz 1984).

The observed environmental lability of iridoid glycoside defenses in *P. lanceolata* has important implications for insect herbivores feeding on that plant species. First, as *P. lanceolata* leaves increase in iridoid glycoside content over the course of the growing season, they will become less palatable to generalist herbivores (Bowers and Puttick 1988, 1989), but more palatable to adapted specialists (Bowers and Puttick 1989). Such specialist insects may use iridoid glycosides as feeding or oviposition stimulants (Bowers 1983, 1984; Pereyra and Bowers 1989), and may prefer *P. lanceolata* plants later in the season. Moreover, the palatability and attractiveness of plants to herbivores may vary spatially in response to environmental heterogeneity. For example, in adjacent mowed and unmowed experimental plots containing identical arrays of cloned *P. lanceolata* genotypes, females of the specialist Baltimore checkerspot, *Euphydryas phaeton* (Nymphalidae) landed on plants in both treatments, but oviposited only on plants in the mowed treatment (Schmitt and Gamble, pers. obs).

Quantitative and qualitative variation in plant defensive chemistry due to environmental conditions has additional consequences for specialist insect herbivores that feed on *P. lanceolata* and sequester iridoid glycosides as a defense against their own predators. For example, *Euphydryas phaeton* (Bowers 1980; Bowers and Puttick 1986) and larvae of the buckeye, *Junonia coenia* (Nymphalidae) (Bowers and Collinge 1992), may contain higher levels of iridoid glycosides when they feed later in the growing season. The iridoid glycoside catalpol has been shown to be primarily responsible for unpalatability (Belofsky et al. 1989; Bowers 1992). Thus the differences between the lawn and the field populations in proportion catalpol (Fig. 3D) may affect the unpalatability of these specialist insects. *Euphydryas phaeton* has a univoltine life history, and late in the season only pre-diapause, early instar (I–III) larve are feeding. These larvae ingest relatively little plant material compared with later instars, so the phenomenon of higher leaf iridoid glycosides later in the season may be relatively unimportant. *Junonia coenia* however, may have several generations per year, and those larvae feeding later in the season may have much higher amounts of iridoid glycosides available in the hostplants, can sequester larger amounts of these compounds, and may thus be better defended against potential predators. The significant site differences detected in our study suggest that herbivore defensive chemistry may also vary among host plant sites as a result of spatial variation in iridoid production.

It seems likely that both specialist and generalist herbivores may select *Plantago* individuals on the basis of leaf iridoid content (Pereyra and Bowers 1988; Bowers and Puttick 1989), and that such differential herbivory may lead to fitness variation among plants (e.g., Berenbaum et al. 1986; Marquis 1983). However, for such herbivory to lead to an evolutionary response, it must discriminate among plant genotypes (e.g. Berenbaum et al. 1986; Simms and Rausher 1989; Marquis 1990). In our study, the two genotypes differed significantly both in phenology of iridoid production within sites and in plastic response of iridoid production to between-site environmental variation. Consequently, our ability to detect genotypic differences varied over the season. Early in the season, differences between sites were striking, but

differences among genotypes were largely undetectable. In contrast, later in the season, large differences between genotypes became apparent and site effects diminished in importance. These results illustrate an important consequence of genetic variation for phenology or environmental plasticity of defense production: genetic differences may be apparent to researchers and herbivores at particular times of year or in certain sites, but in other cases the same genotypes may not be distinguishable. As a result, the potential for insect herbivores to act as selective agents on plants may vary in space and time.

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