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DENSITY DEPENDENCE AND POPULATION DIFFERENTIATION OF GENETIC ARCHITECTURE IN *IMPATIENS CAPENSIS* IN NATURAL ENVIRONMENTS

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Abstract.—We identified environment-dependent constraints on the evolution of plasticity to density under natural conditions in two natural populations of *Impatiens capensis*. We also examined the expression of population divergence in genetic variance-covariance matrices in these natural environments. Inbred lines, originally collected from a sunny site with high seedling densities and a woodland site with low seedling densities, were planted in both original sites at natural high densities and at low density. Morphological and life-history characters were measured. More genetic variation for plastic responses to density was expressed in the sun site than in the woodland site, so the evolutionary potential of plasticity was greater in the sun site. Strong genetic correlations between the same character expressed at different densities and correlations among different characters could constrain the evolution of plasticity in both sites. Genetically based trade-offs in meristem allocation to vegetative growth and reproduction were apparent only in the high-resource environment with no overhead canopy and no intraspecific competition. Therefore, genetic constraints on the evolution of plasticity depended on the site and density in which plants were grown, and correlated responses to selection on plastic characters are also expected to differ between sites and densities. Population differentiation in genetic variance-covariance matrices was detected, but matrix structural differences, as opposed to proportional differences, were detected between populations only in the sun site at natural high density. Thus, population divergence in genetic architecture can occur rapidly and on a fine spatial scale, but the expression of such divergence may depend on the environment.

Key words.—Environment-dependent genetic parameters, environmental heterogeneity, genetic constraints, phenotypic plasticity, reciprocal transplant, trade-offs.

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Phenotypic plasticity is thought to be an important and ubiquitous adaptation to variable environments (Bradshaw 1965; Schlichting 1986; van Tienderen 1991; Schlichting and Pigliucci 1998). Consequently, recent studies have investigated its adaptive value (e.g., Bonser and Aarssen 1994; Schmitt et al. 1995; Dudley and Schmitt 1996; DeWitt 1998; Fox et al. 1997; Donohue et al. 2000). However, the adaptive evolution of plasticity may be constrained by genetic architecture (Via and Lande 1985; Schlichting 1986; Via 1987; Scheiner 1993; Sultan 1995). Such genetic constraints include lack of genetic variation for plasticity, strong genetic correlations between the expression of a character in different environments (Via and Lande 1985; Fry 1992; Scheiner 1993; Windig 1997), and strong genetic correlations among different characters within environments (Lande and Arnold 1983; Arnold 1992). Correlations among characters within and across environments can strongly influence evolutionary trajectories by determining the pattern of correlated responses to selection (Lande and Arnold 1983) and thereby constrain or facilitate responses to selection on correlated characters (Wagner 1988). Because phenotypic plasticity often involves concurrent responses of several characters to environmental variation, the evolution of suites of plastic characters depends on the genetic relationships among those characters (Schlichting 1986; Schlichting and Levin 1986; Schlichting and Pigliucci 1998; Donohue and Schmitt 1999).

If the pattern of genetic variation in plasticity differs among traits, the expression of genetic constraints may depend on the environment (e.g., Hillesheim and Stearns 1992; Scheiner and Istock 1992; Partridge and Fowler 1993; van Tienderen and van Hinsberg 1996; van Hinsberg 1998; Donohue and Schmitt 1999). Such environment dependence has been observed for both heritability (e.g., Mazer and Schick 1991; Kawecki 1995; Hoffman and Schiffer 1998) and genetic correlations (e.g., Mazer and Schick 1991; Pigliucci et al. 1995; Bennington and McGraw 1996; van Tienderen and van Hinsberg 1996; Donohue and Schmitt 1999). The expression of genetic variation in plasticity (genotype-by-environment interaction) may also differ among natural environments. For example, genetic variation in plastic responses of plants to density of neighbors involves genetic variation in response to both the reduced ratio of red : far red wavelengths (R:FR) and the decreased light availability characteristic of dense stands (Smith 1982; Ballaré et al. 1987, 1990; Smith et al. 1990; Donohue and Schmitt 1999). Beneath a forest foliage canopy, however, irradiance and R:FR are low even at low neighbor density (Morgan and Smith 1979), so the light environment may not differ much with density. Thus, genetic variation in light-mediated plasticity to density is more likely to be expressed in open habitats than in forest understories. Such environmental differences in genetic architecture may produce differences among natural environments in the potential for direct and correlated responses of plastic characters to selection. If we are interested in measuring genetic constraints to evolution by natural selection, it is therefore important to measure genetic parameters under the field environments in which selection actually occurs (Platenkamp 1991; Bennington and McGraw 1996).

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It is also important to determine the extent to which genetic architecture differs among natural populations with different histories of selection. How strongly genetic architecture imposes constraints on evolutionary change depends on how constant that architecture remains over time (Cheverud 1984; Turelli 1988; Arnold 1992; Phillips and Arnold 1999). If genetic variances and covariances among characters evolve slowly, then standard quantitative genetic techniques may be used to model evolutionary change over short periods of time (Lande 1979; Arnold 1992; Phillips and Arnold 1999). If they do not remain constant, then the dynamics of their evolution must be incorporated into predictive models. Impermanence of the genetic variance-covariance matrix (**G**-matrix) can have important consequences for evolutionary divergence of populations and higher taxa (e.g., Cheverud 1984, 1988; Turelli 1988; Roff 1996; Steppan 1997b). An important test for constancy or evolution of genetic architecture is to compare **G**-matrices or genetic correlations between natural populations or higher taxa (e.g., Lofsvold 1986, 1988; Billington et al. 1988; Wilkinson et al. 1990; Shaw 1991; Platenkamp and Shaw 1992; Brodie 1993; Shaw et al. 1995; Paulsen 1996; Podolsky et al. 1997; Arnold and Phillips 1999; Roff and Mousseau 1999; Roff et al. 1999). Because genetic architecture can vary with the environment, the expression of differences between populations in their genetic architecture may also depend on the environment. If genetic architecture does evolve, and particularly if divergence in genetic architecture is caused by responses to particular selective environments (Lofsvold 1988; Roff 1996; Roff and Mousseau 1999), then differentiation in genetic architecture may be more likely to be expressed in the particular selective environments in which the populations evolved rather than in an environment that did not impose selection and promote subsequent divergence. Thus, the ability to detect divergence in **G**-matrices may depend on the environment in which the **G**-matrix is measured, especially if the changes in genetic relationships were due to selection rather than drift. It is therefore important to investigate such divergence in genetic architecture under natural conditions when possible.

Here we investigate environment-specific genetic constraints on the evolution of plastic responses to density and test for population differences in genetic architecture under field conditions in the annual plant *Impatiens capensis* Meerb. (Balsaminaceae). Density varies widely within and among natural *I. capensis* populations (M. S. Heschel, unpubl. data), and plastic responses to density have important fitness consequences in this species (Dudley and Schmitt 1996; Donohue et al. 2000). Moreover, we have observed adaptive differentiation in plasticity between natural populations on a microgeographic scale. Genotypes originating in woodland populations are less plastic to density (K. Donohue, E. Hammond-Pyle, D. Messiqua, M. S. Heschel, and J. Schmitt, unpubl. ms.), foliage shade (Dudley and Schmitt 1995), and irradiance levels (Schmitt 1993) than genotypes from a nearby open site. Direct measurement of selection on plastic traits in these populations demonstrated that the observed population differentiation is adaptive (Donohue et al. 2000). It is therefore possible to compare the genetic architecture of plasticity to density in natural populations that have experienced different histories of natural selection.

To identify constraints on the evolution of plasticity under natural conditions and to examine population differences in genetic architecture, we applied a quantitative genetics design to a reciprocal transplant experiment coupled with a density manipulation using two natural populations of *I. capensis*. Specifically, we asked (1) Does the expression of genetic variation for plastic responses to density differ between open and woodland sites? (2) Do genetic correlations across natural density environments constrain the evolution of plasticity? (3) How does the genetic architecture of shade avoidance characters vary with density and canopy environment in the field? and (4) Have the populations diverged in their genetic variance-covariance matrices, and does the expression of such divergence depend on the environment?

Methods

Experimental Design

Seeds were originally collected from two sites at Brown University's Haffenreffer Reserve in Bristol, Rhode Island (Dudley and Schmitt 1995; Donohue and Schmitt 1999). Inbred lines (henceforth "genotypes") were maintained through single-seed descent of self-pollinated seeds for six generations. The sun population occurs in an open area near a seep, and seedlings grow in densities up to 3000 per m^2. The woodland population grows beneath an oak-hickory canopy, and maximum seedling densities are 450 per m^2. The two source populations are separated by less than 1 km, and land-use history suggests that both are probably less than 100 years old.

Seeds collected from 18 genotypes from the sun population and 17 genotypes from the woodland population were weighed, stratified in distilled water in 96-well microtiter trays at 4°C for 4 months, and planted in plug trays in late April 1997. The plug trays were kept in a cold frame for 2 weeks, until the majority of the seedlings had emerged. The emergence date of each seedling was recorded. Up to three seedlings from each line were then transplanted into randomized positions in each of three low density blocks and three natural density blocks in both the woodland and sun sites, giving a total of 1115 seedlings in a split-plot design. In both sites, seedlings in the low density blocks were planted in a 7×16 array, 15 cm apart, giving a density of 53 seedlings/m^2. Natural high density treatments approximated the natural high densities in the two sites. Seedlings were therefore planted in 12×14 arrays, 5 cm apart (450 seedlings/m^2) in the woodland site and 3 cm apart (1305 seedlings/m^2) in the sun site. Additional details of the planting design are given by Donohue et al. (2000).

The comparison of low and natural density treatments within each site reveals the effect of density particular to each site. Note that the density treatments differ between the sites in two ways. First, natural density is much higher in the sun than in the woodland site. Second, the presence of the overhead canopy in the woodland site may reduce differences in the light environment between natural- and low-density treatments; low-density plants experience shading and reduced R:FR due to the canopy in the woodland site but not in the sun site. The experimental treatment that most closely resembles the natural environment experienced by the sun pop-

ulation is the sun site, natural, high-density treatment. The treatment that most closely resembles the natural environment of the woodland population is the woodland site, low-density treatment.

Two weeks after the seedlings were planted into the treatments, the following traits were measured: length of the first and second internodes; total height; the number of nodes; the number of branches (''primary branches''), axillary flowers (''primary flowers''), and quiescent buds at each node on the main stem; and length of the largest leaf. The second internode had not fully elongated in many plants at this point, so the length of the first internode was the best indicator of elongation in response to the various treatments. In addition, after 7 weeks, stem anthocyanin content was scored on a qualitative scale from zero to four, with zero representing no visible anthocyanins present in the internodes. Twice a week, plants were censused for the presence of cleistogamous or chasmogamous flowers, and the date of first flowering was estimated from these censuses. Potential outcrossing rate is a function of chasmogamous flower production and was estimated as the total number of chasmogamous flowers divided by the total number of flowers.

Statistical Analyses

A mixed-model multivariate analysis of variance tested for genetic variation for the characters (genotype main effects) and their plasticity to density (genotype-by-density interaction). Differences between populations are discussed elsewhere (Donohue et al., unpubl. ms.). First, a full model was run, with both site and density (with block nested within site and density) included in the model. However, because of highly significant three-way interactions between site, density, and genotype (results not presented, but indicated in the tables), each site was analyzed separately to determine the effect of density and its interactions with genotype. Genotype, a random effect, was nested within population. Block, also a random effect, was nested within density. Germination date was used as a covariate in all analyses. Interactions between genotype and block and interactions between population and block were pooled with the error term. Main effects of density were tested over the interaction between density and genotype and the block effect (nested in density). Main effects of population were tested over the genotype effect. Individual ANCOVAs were conducted on each variable using the same model structure as that used in the MANOVA. ANCOVAs were also performed separately for each population. For two characters, anthocyanin content and potential outcrossing, variance was very low in all treatments except the sun site, low-density treatment and nearly zero in the woodland site, natural-density treatment. Consequently, these traits were excluded from the genetic analyses discussed below. In addition, potential outcrossing rate could not be analyzed by ANCOVA because most plants did not produce chasmogamous flowers in most treatments. This trait was therefore compared across treatments, pooled over genotypes, using t-tests based on unequal variances.

All genetic parameters estimated in this study are broad-sense parameters because inbred lines were used. They therefore include contributions of nonadditive genetic effects and may include some maternal effects despite being grown in a common environment for several generations. Broad-sense genetic parameters, however, are informative in highly selfing species such as *I. capensis* because response to natural selection occurs largely by sorting among lineages.

Genetic correlations across density environments (Via and Lande 1985) were calculated from variance and covariance partitioning using restricted maximum likelihood (SAS, Proc Mixed; Fry 1999). Correlations were estimated separately for each population because genetic constraints within populations are of interest.

Genetic correlations among characters were estimated for plants grown in each of the four experimental treatments for each trait pair separately. Correlations were based on variance component estimation through linear models, and significance levels were estimated through permutation tests using the program Freestat (Mitchell-Olds 1989). Genetic variance-covariance matrices were also estimated with maximum likelihood, using the program Quercus (Shaw 1989), which estimates all elements of the matrix jointly. The REML estimates did not differ appreciably from those obtained using Freestat. The variance-covariance matrices estimated with REML are not presented here, but are available from K. Donohue upon request. Genetic correlations were also estimated from genotypic mean values (Via 1984; Geber 1990; Campbell 1997), but the estimates did not differ qualitatively from estimates based on variance components and are therefore not reported. Genetic variance-covariance matrices and genetic correlations were estimated from the sample pooled across populations. The pooled sample comprised deviations from the population mean values to prevent correlations from being distorted by differences between population mean phenotypic values. The correlation matrices based on deviations from the population means were very similar to those based on actual values.

To determine whether **G**-matrices differed with the environment, matrices were compared across the sun and woodland sites at both densities, and they were compared across low and natural density in each site. For these matrix comparisons, not all characters could be included in the analysis because of high correlations among characters that rendered the matrices nonpositive definite. Consequently, flowering date, which was highly correlated with number of primary flowers, was not included, and the length of the second internode was also excluded. Three methods of comparison were used. First, restricted maximum-likelihood analysis, using program cprf1.p in Quercus (Shaw 1987; Shaw et al. 1995), estimated likelihood values for the unconstrained model and for the model in which the matrices were constrained to be equal across the two treatments. Twice the difference in the log likelihood values is distributed as chi-square. Degrees of freedom are the number of parameters estimated in the unconstrained model minus the number estimated in the constrained model (null hypothesis). If the two likelihood values differed significantly, then the two matrices were considered to be significantly different from each other. When many characters are included in the analysis, the degrees of freedom are high, and the power of the test to detect differences is consequently low. Comparisons between **G**-matrices were also made using Flury's hierarchical common

principal components (CPC) analysis (Flury 1988; Steppan 1997a; Phillips and Arnold 1999). CPC analysis tests whether the matrices are equivalent (i.e., share both eigenvectors and eigenvalues). If matrices are not equivalent, the analysis determines whether matrices are proportional. Proportional matrices are identical except that each element is multiplied by a single constant (the eigenvalues differ by a proportional constant). If the matrices are not proportional, they can differ either in eigenvalues or in eigenvectors (principal components). The analysis then tests whether matrices have CPCs or eigenvector structure. We used the jump-up procedure of hypothesis testing, which tests each hypothesis (equivalence, proportionality, and CPCs) against the hypothesis of unrelated structure (Phillips and Arnold 1999). We used CPCrand, a randomization test developed by P. Phillips (Phillips 1998) to compare quantitative genetic matrices. This method of comparison has not been thoroughly tested for genetic data, however. Some of the matrices were nonpositive definite and had to be bent to conduct the comparisons, making significance levels suspect. When matrices are bent, eigenvalues are adjusted just enough to eliminate the negative eigenvalues. Consequently, results of CPCrand were verified by comparing the variance-covariance matrices based on genotypic means, which are constrained to be positive definite. Although estimates based on genotypic means are biased (Via 1984; Roff 1997; Lynch and Walsh 1998), the use of genotypic means eliminates problems of negative variance components and permits well-characterized parametric analyses. These comparisons of matrices based on genotypic mean values were performed using parametric CPC analysis (CPC program, developed by P. Phillips, 1998). It should be noted that all these methods of matrix comparisons were intended to compare matrices from genetically independent populations, not matrices from the same population replicated in different environments. However, there is no current methodology available for this sort of matrix comparison, so these methods were applied with this caveat (Promislow et al. 1996).

To test for differences between populations in genetic architecture, **G**-matrices and genetic correlations were calculated separately for each population. The **G**-matrices were compared between the two populations for each experimental treatment using REML (Shaw 1987; Shaw et al. 1995) and using Flury's hierarchical CPC analysis. Both randomization tests (CPCrand) and parametric tests (CPC Program) were performed. Genetic correlations were calculated using Freestat and were compared to estimates obtained through maximum likelihood and genotypic mean correlations. Because all methods provided similar estimates, only estimates calculated through Freestat are reported. For these comparisons between populations, flowering date and length of the second internode were excluded from analysis, as before. For some comparisons using REML, not all meristem characters could be included in the same analysis, so separate analyses using different meristem characters were performed.

Results

Patterns of Plasticity and Genetic Variation

In the sun site, plants grown at natural high density had longer first internodes, greater height, fewer flowers and branches, more quiescent buds, and less anthocyanin, and they flowered earlier than plants grown at low density (Fig. 1; Tables 1, 2). No character varied significantly with density in the woodland site, although the direction of the effect of density on character expression was often similar to that in the sun site (Fig. 1; Tables 1, 2), and the effect of density was significant in the MANOVA (Fig. 1, Table 1).

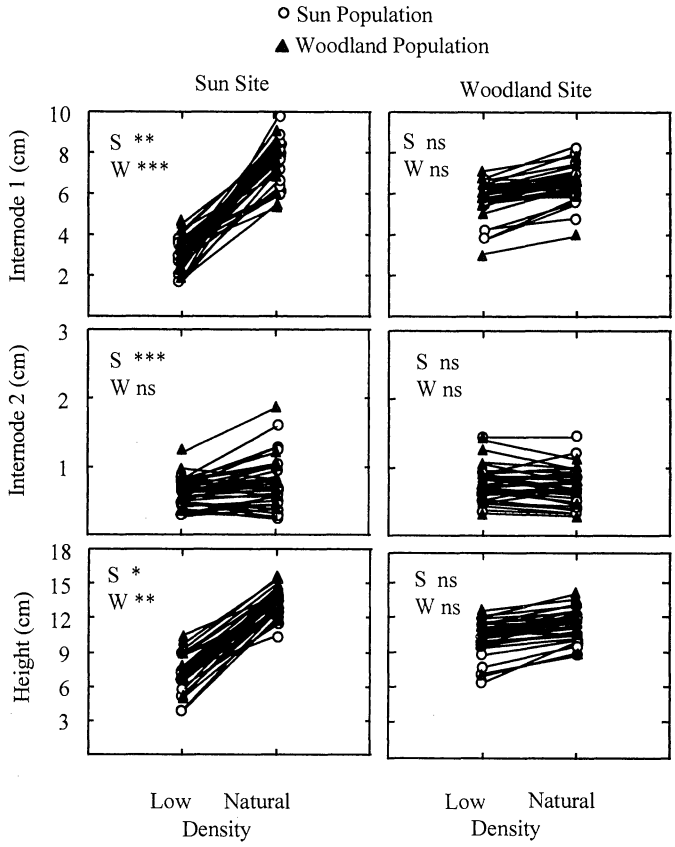

FIG. 1. Reaction norms of genotypes from sun and woodland populations in response to natural densities in sun and woodland sites. Mean phenotypes are shown for each genotype in the four experimental treatments. Asterisks indicate significant genotype-by-density interaction for the sun population (S) and woodland population (W). $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; ns, nonsignificant.

For both populations in the sun site, potential outcrossing rate was higher at low density than at natural high density (Fig. 1), but only significantly so for the woodland population (sun population $t = 1.84$, $P = 0.07$; woodland population $t = 4.70$, $P < 0.0001$). Potential outcrossing rate was significantly lower in the woodland site than in the sun site at both densities for both populations (sun population at low density $t = 8.23$, $P < 0.0001$; natural high density $t = 2.03$, $P = 0.046$; woodland population at low density $t = 6.63$, $P < 0.0001$; natural high density $t = 2.16$, $P = 0.033$). In the woodland site, less than 2% of the flowering plants produced chasmogamous flowers at low density, and no plants produced chasmogamous flowers at natural high density. Consequently, potential outcrossing rate did not differ significantly with density in the woodland site for either population. Significant genetic variation was detected for potential outcrossing rate in both populations in the sun site, low density

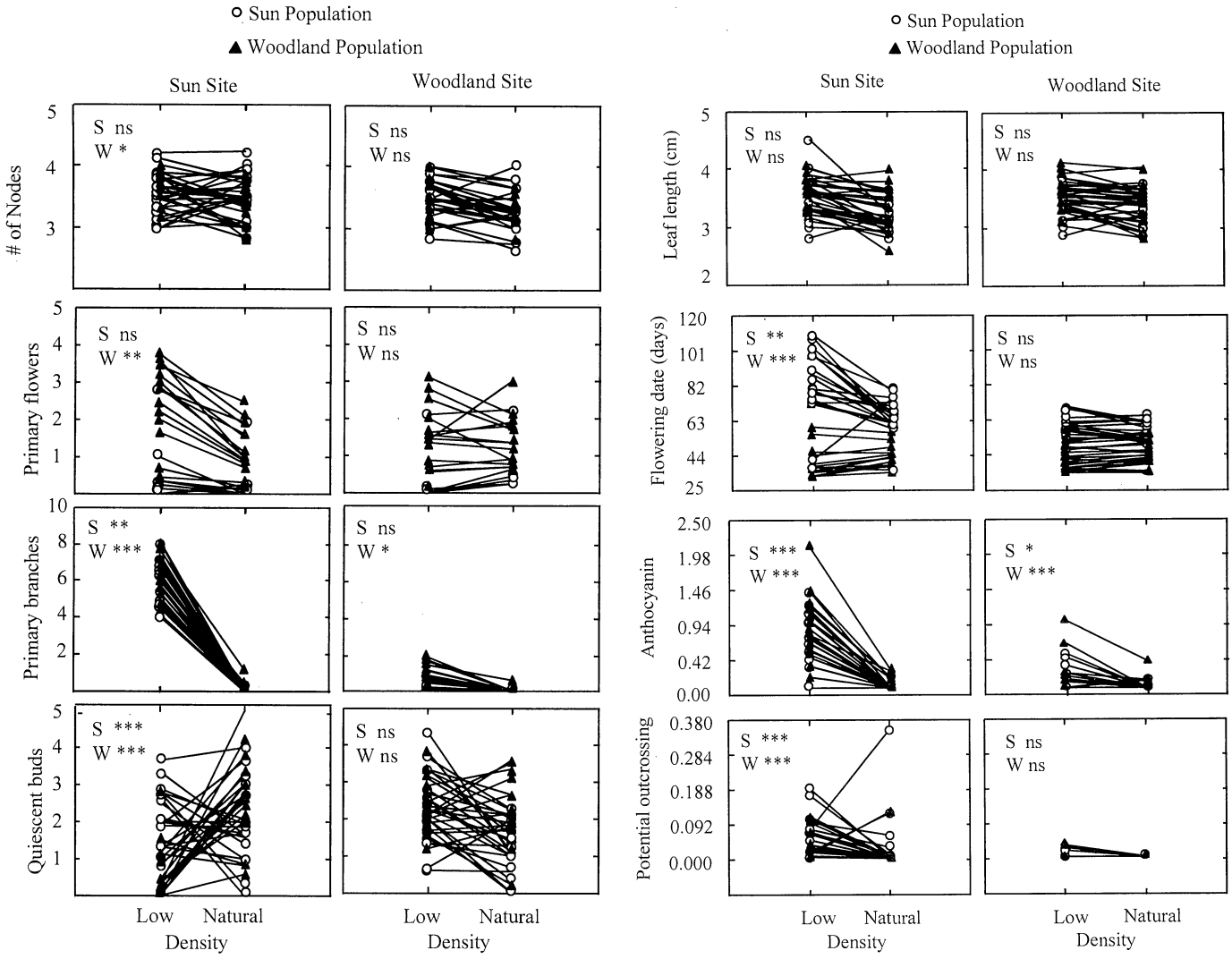

FIG. 1. Continued.

treatment (sun population: $F = 4.01$, $P < 0.0001$; woodland population: $F = 5.81$, $P < 0.0001$).

More genetic variation for plasticity was expressed in the sun site than in the woodland site for many characters, as indicated by the significant genotype-by-density interactions (Table 2). Genetic variation for plastic responses to density was found within populations for all characters, except leaf length for plants grown in the sun site. However, plants grown in the woodland site displayed significant genetic variation for responses to natural density only for flowering date,

TABLE 1. MANOVA to test for population differentiation and genetic variation for plasticity to density in sun and woodland sites. Characters included in the analysis were lengths of first and second internodes; height; number of nodes; number of primary flowers, branches and buds; leaf length; and flowering date. *F*-values are based on Wilk's λ. ndf, numerator degrees of freedom; ddf, denominator degrees of freedom. Degrees of freedom were given by SAS MANOVA option in Proc GLM when error terms were specified as described in the Methods.

	Sun site		Woodland site	
Source	ndf/ddf	*F*	ndf/ddf	*F*
Germination day	10/413	23.18***	10/420	29.30***
Block	40/1568	10.73***	40/1594	11.86***
Density	10/23	267.87***	10/24	47.47***
Population	10/24	2.66*	10/24	4.60**
Family	330/248	1.91***	330/258	3.66***
Population × density	10/23	2.38*	10/24	2.14†
Family × density	320/3978	2.00***	330/4056	1.15*

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 2. *F*-ratios from analysis of covariance to determine population differentiation and genetic variation in the sun site (left) and woodland site (right). Effects of block and germination date are not shown. Flowers and branches refer to the number of primary flowers and branches, respectively; bud refers to the number of quiescent buds on the main stem. Significant interactions with site in the full model that included site and density are indicated by superscripts: [a] density × site; [b] population × site; [c] family × site; [d] density × population × site; [e] density × family × site.

	Sun site					Woodland site				
Trait	Density	Population	Family	Density × Pop.	Density × Family	Density	Population	Family	Density × Pop.	Density × Family
Internode 1[ae]	50.10**	0.05	1.18	5.13*	2.57***	3.42	0.36	7.73***	2.63	0.59
Internode 2	1.88	2.39	1.93*	0.00	2.08***	0.12	1.11	5.30***	0.00	0.97
Height[a]	30.24**	3.91†	2.83**	2.88†	2.14***	3.22	4.77*	6.64***	0.59	0.90
No. of nodes	0.18	0.52	1.37	0.17	1.59*	1.57	0.01	2.51**	0.01	0.88
Flowers[abde]	29.76***	18.66***	10.40***	22.06***	1.90**	0.00	18.79***	10.08***	0.62	1.29
Branches[ae]	210.84***	1.34	0.82	0.56	2.85***	2.16	18.47***	1.24	18.68***	1.47*
Buds[abe]	6.84*	6.54*	0.39	11.57**	3.61***	1.24	8.10**	1.31	5.17*	1.32
Leaf length[c]	4.84†	0.15	1.34	0.47	1.27	0.26	0.13	4.86***	0.75	0.69
Flowering date[abcde]	15.52***	31.71	5.33***	15.66***	3.28***	0.19	30.61***	10.78***	4.50*	1.61*
Anthocyanin[ae]	96.73***	1.09	1.57†	1.07	3.60***	4.22†	0.47	2.15*	0.07	2.89***

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

branch production, and anthocyanin content. Significantly more genetic variation for plasticity was expressed in the sun site for length of the first internode, number of primary flowers, number of primary branches, number of quiescent buds, flowering date, and anthocyanin content, as shown by significant three-way interactions between site, density, and genotype.

The two populations sometimes differed in the amounts of genetic variation for plasticity to density (Fig. 1). In the sun site, significant genetic variation for plasticity in the length of the second internode was found only in the sun population, and significant variation for plasticity in the number of nodes and number of primary flowers was found only in the woodland population. In the woodland site, significant genetic variation for plasticity in branch production was found only in the woodland population.

Correlations across Environments

When plants were grown in the sun site, significant positive genetic correlations across density were found for length of the second internode, height (nearly significant for sun population), number of nodes (sun population only), number of primary flowers, leaf length, and flowering date (Table 3).

TABLE 3. Genetic correlations across densities. See Table 2 for explanation of character names. NE, nonestimable. Tests for significant difference from zero: † $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	Sun site		Woodland site	
	Sun pop	Woods pop	Sun pop	Woods pop
Internode 1	0.22[a]	0.36[a]	1.00***	1.00***
Internode 2	0.91***	1.00***	1.00***	1.00***
Height	1.00†	0.84*	1.00***	1.00***
No. of nodes	0.92**	0.58	1.00***	1.00†
Flowers	1.00***	1.00***	1.00***	1.00***
Branches	NE	0.44[a]	NE	1.00
Buds	−0.95*	−0.40[a]	1.00†	NE
Leaf length	0.87*	1.00**	1.00***	1.00***
Flowering date	0.79**	1.00***	0.95***	0.98***

[a] Significantly different from 1 if positive or −1 if negative.

Correlations were significantly less than one for the length of the first internode and branch production (woodland population only), indicating weaker constraints on the further evolution of plasticity in these characters in the sun site. Negative correlations across density were found in the sun site for bud production, suggesting specialization of allocation in different density environments, although these correlations were significant only within the sun population. This correlation was significantly greater than −1 in the woodland population. When plants were grown in the woodland site, significant genetic correlations across density were observed for all characters except node (nearly significant in woodland population), branch, and bud (nearly significant) production (Table 3). Correlations across density environments tended to be stronger for plants grown in the woodland site. In contrast with the sun site, a positive correlation across density environments was found for bud production in the sun population when grown in the woodland site, although this correlation was not significant (Table 3). Such strong correlations across density environments reflect constraints on the evolution of plasticity to density, with the constraint being somewhat stronger in the woodland site.

Environment-Dependent Correlations among Characters

Genetic relationships among characters depended on the site in which plants were growing (Tables 4, 5, 6). For plants grown at low density, all methods of matrix comparison detected significant differences in covariance relationships between sun and woodland sites (Table 4). A significant deviation from proportionality was detected between sites at low density. Eigenvector structure differed significantly between matrices based on parametric analysis and tended to differ ($P < 0.1$) based on randomization tests. Thus, the principal component structure was influenced by environmental differences between sites, independent of density. In particular, the genetic architecture of meristem allocation traits was strongly site dependent (Tables 5, 6, below diagonals). In the sun site, the number of dormant buds was negatively correlated with elongation traits and primary flower production, and a trade-off was observed between meristem allocation to

TABLE 4. Comparisons of *G*-matrices between experimental treatments. Probabilities given in the REML analysis indicate significant deviation from the hypothesis of equality of the matrices based on χ^2 with 28 df. No. CPCs refers to the number of principal components shared between matrices, with five principal components being the maximum. Likelihood ratios were estimated with randomization tests using CPCrand (Phillips 1998). Bending coefficients used in CPCrand are as follows: sun, low versus woods, low = 0.1480; sun, natural versus woods, natural = 0.1034; sun, low versus sun, natural = 0.412; woods, low versus woods, natural = 0.1480. χ^2 values were estimated from parametric techniques based on genotypic means using CPC (Phillips 1998).

Hypothesis	Comparisons across site				Comparisons across density			
	Sun, low vs. woods, low		Sun, natural vs. woods, natural		Sun, low vs. sun, natural		Woods, low vs. woods, natural	
REML log likelihood (unconstrained, constrained)	−1371.20, −1402.22***		−900.39, −918.79		−1422.66, −1468.12***		−850.01, −877.22**	
CPC analysis	Random. likelihood	Parametric χ^2	Random. likelihood	Parametric χ^2	Random. likelihood	Parametric χ^2	Random. likelihood	Parametric χ^2
Equality	219.57***	87.77***	215.42***	35.33	328.03***	171.69***	218.13***	85.33***
Proportionality	206.24***	83.84***	209.03***	32.65	321.41***	168.76***	214.16***	84.47***
CPC	57.45†	32.65*	71.67*	26.40	123.82**	42.17**	52.56	38.90**
No. CPCs	0	0	2	5	1	0	5	2

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

branches and allocation to flowers. In contrast, in the woodland site, the number of dormant buds was positively correlated with elongation traits and node number and uncorrelated with allocation to flowers, whereas branch and flower production were positively correlated. REML and parametric CPC detected no significant differences in covariance relationships across sites at natural density (Tables 4, 5, 6, above diagonals), but CPC randomization tests detected significant differences between matrices, including differences in their principal components. No meristem allocation trade-offs were observed in natural-density treatments in either site.

Density influenced the genetic relationships among characters in the sun site, as indicated by all methods of analysis (Tables 4, 5). According to both CPC analyses, these matrices differed in their principal components. Characters of elongation (lengths of first and second internodes and height) and size characters (number of nodes and leaf length) were positively correlated at both low and natural density in the sun site (Table 5). At low density, increased internode length was associated with earlier flowering, increased primary flower production, and decreased bud dormancy, indicating that those genotypes that elongated also allocated meristems to reproductive structures early in the season. At natural density, increased elongation was somewhat more weakly associated with early flowering date and primary flower production, and it was associated with increased branch production (weakly) and bud dormancy. At high density, therefore, genotypes that elongated the most tended to keep their meristems dormant or even allocate some meristems to branches. Thus, longer internodes at low density may indicate faster growth rates, which accelerate reproduction, but at natural density may indicate successful competitive outcome, which may permit greater vegetative growth and meristem reserves.

At low density in the sun site, genotypes with more nodes flowered early, produced more flowers and branches, but tended to maintain fewer dormant buds (Table 5). Consequently, larger genotypes at low density committed their meristems to reproduction and vegetative growth rather than keeping meristems dormant. At natural density, genotypes with more nodes also tended to have more branches, but number of nodes was positively correlated with number of dormant buds and uncorrelated with flower number. In this treatment, larger genotypes did not commit their meristems to reproductive structures early in the season. The fastest growing genotypes at natural density, therefore, were not necessarily the first to flower, and flowering date was not significantly correlated with number of nodes in this treatment.

At both densities in the sun site, early flowering genotypes allocated more meristems to primary flowers early in the season (Table 5). Trade-offs among meristem allocation traits were observed at low density, but meristem traits were positively correlated at natural density. At low density, high allocation to flowers was at the expense of branches and dormant buds, and a nonsignificant but negative genetic correlation was observed between branches and buds. Early flowering genotypes therefore produced fewer branches and dormant buds. At natural density, in contrast, genotypes with many primary flowers also produced many branches and

TABLE 5. Genetic correlations among characters for plants grown in the sun site. Correlations using plants grown in low density are shown below the diagonal, and correlations using plants grown at natural density are shown above the diagonal. 1° Fl, the number of primary flowers; 1° Br, number of primary branches; Buds, number of quiescent buds on main stem; FD, flower date. Boldface indicates significance after sequential Bonferroni adjustments.

	Int 1	Int 2	Height	No. nodes	1° Fl	1° Br	Buds	Leaf	FD
Int 1		**0.59*****	0.76*	**0.63*****	0.08	**0.30****	**0.52*****	**0.74*****	−0.14
Int 2	**0.70*****		**0.75*****	**0.87*****	**0.23*****	0.13†	**0.40*****	**0.66*****	−0.08
Height	**0.95*****	**0.65*****		**0.95*****	0.40**	0.21	0.61**	**0.60****	−0.75**
No. nodes	**0.45****	**0.78*****	**0.44****		0.06	0.19*	**0.39*****	**0.83*****	−0.02
1° Fl	**0.71*****	**0.54*****	**0.71*****	**0.34*****		**0.40*****	**0.26****	−0.08	−**0.94*****
1° Br	−0.14	0.17	−0.16†	0.47*	−**0.33*****		**0.61*****	**0.43*****	−**0.31*****
Buds	−0.38**	−0.26*	−**0.45*****	−0.29†	−**0.84*****	−0.22		**0.32****	−**0.37*****
Leaf	0.21	0.51*	0.28	**0.93****	−0.02	0.33	0.37		0.26**
FD	−**0.70*****	−**0.62*****	−**0.67*****	−**0.46*****	−**0.84*****	0.27**	**0.84*****	−0.19	

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

many buds, and an increase in all meristem allocation traits was associated with earlier flowering.

In the woodland site, density significantly altered the genetic relationships among characters, as indicated by all methods of matrix comparison (Table 4). Both CPC analyses detected a significant deviation from proportionality between matrices from plants grown in low and natural density. Randomization tests detected no differences in eigenvector structure, but the CPC analysis using genotypic means did. Overall, however, the correlations among characters of plants grown in the woodland site did not differ as dramatically between density treatments as correlations among characters of plants grown in the sun site (Table 6). Often, the genetic architecture of plants grown at low density in the woodland site (Table 6, below diagonal) more closely resembled that observed in plants grown at natural density in the sun site (Table 5, above diagonal) than the architecture observed at low density in the sun site (Table 5, below diagonal). Elongation and size characters were positively correlated at both densities in the woodland site. Numbers of nodes and dormant buds were positively correlated at low density, and plants with more nodes tended to allocate meristems to flowers and thereby flower earlier. Node production was unrelated to flower production and flowering date at natural density in the woodland site. Early flowering was associated with greater primary flower production at both densities. Early flowering genotypes had more branches at low density, and early flowering was associated with greater meristem dormancy at natural density. The trade-offs in meristem allocation observed at low density in the sun site were not detected in the woodland site; all meristem characters were either positively correlated or uncorrelated at both low and natural density.

Differences between Populations in Genetic Architecture

Differences in variance-covariance matrices between populations were detected only in some environments (Table 7). Bending coefficients were large in the randomization tests, so results of these tests should be interpreted with caution. No differences in **G**-matrices were detected between populations for plants in the sun site, low-density treatment (although **G**-matrices were nearly significantly different based on the randomization tests). Nor did population matrices differ strongly in the woodland site, natural-density treatment. Although randomization tests did detect significant differences between the populations in this treatment, only a deviation from proportionality was observed. Therefore, the principal components (eigenvectors) of the matrices were similar, but the eigenvalues of those principal components differed between populations. Comparison based on genotypic mean values detected no deviation from proportionality, however, suggesting that the magnitude of the covariances may have differed by a constant proportion between matrices. In general, correlations tended to be somewhat weaker in the woodland population in this environment (results not shown).

Significant differences in covariance relationships were detected between the two populations in the sun site, natural-density treatment with all methods of analysis (Table 7). A

TABLE 6. Genetic correlations among characters for plants grown in the woodland site. Correlations using plants grown in low density are shown below the diagonal, and correlations using plants grown at natural density are shown above the diagonal. See Table 5 for abbreviations of character names. Ψ, estimate exceeded 1 or −1 and was rounded off. Boldface indicates significance after sequential Bonferroni adjustments.

	Int 1	Int 2	Height	No. nodes	1° Fl	1° Br	Buds	Leaf	FD
Int 1		**0.75*****	0.64*	**0.91*****	0.19	−0.06	0.77*	0.42*	−0.22*
Int 2	**0.46*****		0.42**	**0.99*****	−0.04	−0.38*	**0.54*****	**0.39*****	0.04
Height	**0.85*****	0.39**		**0.63*****	0.43**	−0.20	0.42	0.17	−**0.40*****
No. nodes	**0.74*****	**1.00*****Ψ	**0.56*****		−0.04	−0.12	0.58**	0.45**	0.12
1° Fl	**0.32*****	**0.36*****	**0.47*****	0.24*		0.02	**0.77*****	−0.19*	−**0.91*****
1° Br	0.43†	0.35†	0.43†	0.22	**0.86*****		0.53	0.18	−0.00
Buds	**0.59****	**0.74*****	0.55**	**1.00*****Ψ	0.04	0.37		−0.02	−0.39**
Leaf	0.43†	0.54*	0.23	0.67*	−0.27*	−**1.00****Ψ	1.00**Ψ		**0.24*****
FD	−**0.47*****	−**0.27*****	−**0.52*****	−0.19*	−**0.80*****	−**0.78*****	0.04	0.08	

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 7. Comparisons of *G*-matrices between the sun and woodland populations. Probabilities given in the REML analysis indicate significant deviation from the hypothesis of equality of the matrices based on χ^2 with df specified in parentheses. See Table 4 for details. Bending coefficients used in CPCrand are as follows: sun low = 0.0611, sun natural = 0.4356, woods low = 0.3083, woods natural = 0.4512.

Treatment	Sun, low		Sun, natural[a]		Woods, low[b]		Woods, natural[c]	
REML log likelihood (unconstrained, constrained)	−676.80, −692.77 (df = 28)		−411.85, −425.28* (df = 15)		−92.54, −196.64*** (df = 21)		−420.20, −438.51* (df = 21)	
CPC analysis	Random. likelihood	Parametric χ^2	Random. likelihood	Parametric χ^2	Random. likelihood	Parametric χ^2	Random. likelihood	Parametric χ^2
Equality	112.02†	33.38	100.95**	87.53***	105.89*	105.71***	110.20**	22.10
Proportionality	104.58†	33.26	84.63**	80.33***	105.24*	101.94***	86.20**	20.48
CPC	53.03	26.48	5.88	42.18**	27.46	31.48†	7.54	15.37
No. CPCs	5	5	5	4	5	5	5	5

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

[a] Buds was not included in the REML analysis because inclusion caused the matrices to be nonpositive definite. Genetic variance and covariances with 1° Fl and 1° Br were estimated in separate analyses. Results given are for the matrix that contains 1° Fl. Significance level did not change when 1° Br was included instead.

[b] In the REML analysis, genetic variance and covariances with 1° Br were obtained in an analysis that did not include 1° Fl or Buds. Results given are for the matrix that contains 1° Fl and Buds. Significance level did not change when 1° Br was included instead.

[c] In the REML analysis, 1° Br was not included because inclusion caused the matrices to be nonpositive definite.

deviation from proportionality was observed with both the randomization tests and the parametric tests. Randomization tests detected no differences in eigenvectors, but significant differences between eigenvectors were detected when genotypic mean values were used. The two populations also differed significantly in variance-covariance relationships in the woodland site, low-density treatment based on all methods of comparison. A significant deviation from proportionality was detected. Randomization tests detected no significant differences in eigenvector structure, but analyses based on genotypic mean values detected nearly significant differences ($P < 0.1$).

The observed divergence in **G**-matrices can be partly or entirely attributed to deviations from proportionality for most cases. However, some evidence for differences in eigenvectors was observed in two treatments. The differences in covariance structure between populations in the sun site, natural-density treatment can be attributed to differences in relationships between size (specifically number of nodes and leaf size) and flowering characters (Table 8). Genotypes from the woodland population with many nodes produced more primary flowers and consequently flowered earlier, whereas genotypes with many nodes from the sun population tended to allocate fewer meristems to primary flower production and flower later. Likewise, genotypes with larger leaves had fewer primary flowers and therefore flowered later if they came from the sun population, but not if they came from the woodland population. Similar population differences were observed in the woodland site, low-density treatment (woodland plants: r[nodes, flowering date] = −0.49, $P < 0.001$; *r*[nodes, primary flowers] = 0.54, $P < 0.001$; *r*[leaf, flowering date] = −0.16, $P > 0.05$; sun plants: *r*[nodes, flowering date] = 0.00, $P > 0.05$; *r*[nodes, primary flowers] = 0.07, $P > 0.05$; *r*[leaf, flowering date] = 0.68, $P < 0.01$), although principal components did not differ significantly (Table 7).

DISCUSSION

In this study, the same array of genotypes expressed more genetic variation in plasticity to density in the sun site than in the woodland site. Moreover, across-density genetic correlations were slightly stronger in the woodland site than in the sun site. These site-specific genetic constraints suggest that plasticity to density may evolve more easily in the sun site than in the woodland site. The expression of genetic covariances between traits also differed between sites and varied dramatically with density. Consequently, the genetic potential for correlated responses to selection differed with environmental conditions. We also observed differences in the genetic covariance relationships of two populations with different histories of natural selection on a microgeographic scale. Thus, the genetic architecture of *I. capensis* is both environmentally labile and capable of rapid evolutionary change.

More genetic variation for plasticity to density was expressed in the sun site than in the woodland site, probably because the range of densities experienced in the woodland site was much lower than that in the sun site. Moreover, in the woodland site shade from the overhead tree canopy may have diminished the effect of density because plants in both

TABLE 8. Differences between populations in genetic correlations among characters for plants grown in the sun site, natural-density treatment. Correlations using plants from the sun population are shown below the diagonal, and correlations using plants from the woodland population are shown above the diagonal. See Table 5 for abbreviations of character names. Boldface indicates significance after sequential Bonferroni adjustments. NE, nonestimable; Ψ, estimate exceeded 1 or −1 and was rounded off.

	Int 1	Int 2	Height	No. nodes	1° Fl	1° Br	Buds	Leaf	FD
Int 1		**0.49****	0.79*	0.51**	0.21†	0.29*	**0.64*****	**0.66*****	−0.31**
Int 2	**0.74*****		0.49*	**0.82*****	**0.48*****	0.04	0.04	**0.52*****	**−0.28*****
Height	0.97	**1.00****		0.78**	0.30†	0.11	0.29	0.38†	−0.34*
No. nodes	**0.75*****	**0.91*****	**1.00**Ψ**		0.27*	0.24†	0.17	**0.69*****	−0.35**
1° Fl	−0.20*	−0.05	1.00*Ψ	−0.12†		**0.48*****	0.17	0.01	**−0.95*****
1° Br	NE	NE	NE	NE	NE		**0.64*****	**0.49*****	**−0.44*****
Buds	0.28	**0.85*****	1.00*Ψ	**0.64*****	**0.47*****	NE		0.30*	**0.36*****
Leaf	**0.86*****	**0.88*****	1.00*Ψ	**1.00***Ψ**	**−0.27*****	NE	0.37*		0.05
FD	NE	0.12	NE	0.26†	**−0.98*****	NE	−0.58*	**0.80*****	

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

treatments experienced reductions in total irradiance and R:FR that would affect only high-density plants in the sun site. Consequently, genetic variation for light-mediated responses to density may have been less apparent in the woodland site. Genetic correlations across densities also tended to be stronger in the woodland site, again reflecting the greater similarity in ecological conditions between density treatments in this site. Consequently, plasticity to density is expected to evolve more readily in the sun site than in the woodland site, even if the initial genetic composition of the two populations were identical. This result is consistent with the observation that the population that evolved in the sun site is, in fact, more plastic in selectively important life-history and shade-avoidance characters (Schmitt 1993; Dudley and Schmitt 1995; Donohue et al., unpubl. ms.).

The relative similarity between the density environments in the woodland site compared to the sun site was reflected in the nature of genetic correlations among characters. These correlations displayed much stronger density dependence in the sun site. Moreover, the genetic architecture expressed at low density in the woods resembled that expressed at high density in the sun site far more than that expressed at low density in the sun site. This result suggests that the overhead tree canopy in the woodland site altered the light environment in a manner similar to that of neighbor proximity under open canopy conditions. This interpretation is supported by the similarity in plastic responses to density and plastic responses to overhead canopy (Donohue et al., unpubl. ms.).

The genetic architecture of meristem allocation traits was especially labile. Genetically based trade-offs among meristem characters that were apparent at low density in the sun site were not expressed at high density. Nor were they expressed in the woodland site at either density. Even if characters are tightly developmentally linked, trade-offs will only be detectable if variation in resource allocation to those characters is greater than variation in resource acquisition (van Noordwijk and de Jong 1986; Charlesworth 1990; Houle 1991; Stearns et al. 1991). If genetic variation for resource acquisition is greater than genetic variation for resource allocation, then positive genetic correlations may be expressed (Charlesworth 1990; Stearns et al. 1991; Houle 1991). For example, fast-growing genotypes may have many meristems to allocate to branches, many flowers, and many buds in reserve, while slow-growing genotypes have fewer meristems available for producing any of these structures. The trade-offs observed at low density in the sun site suggest that greater genetic variation for meristem allocation (e.g., Geber 1990) was expressed under high light conditions. In contrast, the positive correlations observed at high density and beneath the overhead forest canopy suggest that greater genetic variation for resource acquisition was expressed under low resource conditions. Donohue and Schmitt (1999) hypothesized that such positive correlations might be more commonly expressed when competition for resources is exacerbated by asymmetric competition such that some individuals are suppressed beneath the canopy created by larger individuals (Stanton 1984; Weiner 1985, 1990; Schmitt et al. 1986; Scheiner 1989). The present study suggests, however, that genetic variation for resource acquisition may be substantial in shaded environments even when competition is not asymmetric, as in the low-density plots in the woodland site.

The relationship between plant size and the other characters in the sun site, low-density treatment also differed from that expressed in the other treatments. In this treatment, larger plants with more nodes and longer internodes displayed less meristem dormancy and greater meristem allocation to both flowers and branches, suggesting faster development. In the other treatments, larger plants with longer internodes produced flowers and branches but kept more meristems in reserve, suggesting a bet-hedging strategy that could permit plants to respond to improved future conditions by allocation to branches as opposed to flowers (Watson 1984). The number of nodes was positively associated with internode length in all treatments, suggesting either that internode length reflects plant size and developmental rate or that elongation enables faster development.

The observed environment-dependent genetic relationships among characters is expected to influence the evolution of these characters through correlated responses to selection (Lande and Arnold 1983). In the sun site, low-density treatment, for example, selection for later flowering would cause a correlated response for greater bud dormancy, because the two characters have a positive genetic correlation. In the other treatments, the correlation between flowering date and bud dormancy was negative. Therefore, even though selection on flowering date acts in the opposite direction in those treatments (Donohue et al. 2000), correlated responses to selection would still cause increased bud dormancy because the cor-

relation changed as well. Similar evidence of environmental differences in genetic architecture has been observed in other systems (Mazer and Schick 1991; Pigliucci et al. 1995; Bennington and McGraw 1996; van Tienderen and van Hinsberg 1996), suggesting that this phenomenon may be common in natural plant populations. Such environment-dependent genetic relationships among characters may play an important role in the evolution of suites of plastic traits (Schlichting and Levin 1986; van Tienderen 1990; van Tienderen and van Hinsberg 1996; Schlichting and Pigliucci 1998; Donohue and Schmitt 1999).

We observed population differentiation in genetic architecture. In general, we detected more deviations from proportionality (eigenvalues) than differences in principal components (eigenstructure), suggesting that the populations varied along the same allometric axis for many traits. Arnold and Phillips recently documented conservation of covariance structure but variability in eigenvalues in **G**-matrices of garter snake morphology (Arnold and Phillips 1999). They concluded that matrix structure was conserved over long periods of evolutionary time in their system, whereas eigenvalues can evolve rapidly. Several other studies have detected only deviations from proportionality among **G**-matrices or no changes at all (Platenkamp and Shaw 1992; Brodie 1993; Podolsky et al. 1997; Roff et al. 1999), although the ability to detect significant differences between **G**-matrices is notoriously difficult due to the low power of many statistical tests (Podolsky et al. 1997). Drift and mutations with similar pleiotropic effects can cause divergence in population means without changing genetic covariance relationships (Cheverud 1984; Roff 1996; Roff et al. 1999), but Arnold and Phillips point out that conserved patterns of multivariate selection also can conserve the structure of **G**-matrices (Arnold and Phillips 1999; Phillips and Arnold 1999). Although divergence in character means implies some changes in selection, the topography of the selection surface (or correlative selection) may have remained constant in some of the environments experienced by both populations (Brodie 1993; Podolsky et al. 1997; Arnold and Phillips 1999).

We did observe some differences between populations in the eigenstructure of their **G**-matrices based on parametric CPC analyses. Such differences were observed only in the sun site at natural high density, and a trend for such differences was observed in the woodland site at low density. These are the two most common selective environments in this system. In these two environments, larger genotypes flowered later if they came from the sun population, but they flowered earlier if they came from the woodland population. In other systems, such differences in character correlations have been proposed to be due to differences in the selective environments in which the populations evolve (Lofsvold 1988; Wilkinson et al. 1990; Roff 1996). In this system, a positive correlation between size and flowering date in the sun population could result from selection for delayed flowering of large individuals (Geber 1990; Schmitt 1995; Donohue et al. 2000) and selection for accelerated flowering of small, suppressed individuals beneath the vegetation canopy (Schmitt et al. 1986, 1987a,b). This prediction is consistent with the correlational selection observed in the sun site, which favored later flowering of large plants (Donohue et al. 2000). However, the observed correlational selection was likely to be due in part to environmentally induced covariance between large plants, late flowering, and high fitness (Rausher 1992), because a genotypic selection analysis revealed no significant correlational selection. The negative correlation between flowering date and size observed in the woodland population, however, does not correspond with the observed correlational selection, which favored early flowering of small individuals in the woodland site. The observed positive correlation therefore may reflect a constraint rather than a response to selection; because early flowering was strongly favored overall in the woodland site, faster growing plants may be able to flower earlier, whereas small plants may flower later simply because they need to attain a critical size to flower. Such a constraint, which results from all woodland plants flowering as early as possible, would lead to the positive correlation observed in the woodland population.

The observation that divergence in **G**-matrix structure may be environment dependent suggests that genetic correlations across environments, although strong, are not absolute; selection on characters in one environment does not necessarily result in a comparable magnitude of correlated selection on the same character expressed in a different environment. If selection alters genetic variance-covariance relationships, the resulting **G**-matrix may be expressed only in the environment in which it evolved when correlations across environments are not absolute. Consequently, divergence in **G**-matrices caused by divergent selection may be less likely to be detected in novel environments. Although several studies comparing **G**-matrices between populations within a species have detected little or no divergence in covariance structure (Platenkamp and Shaw 1992; Brodie 1993; Podolsky et al. 1997; Roff et al. 1999), few of these studies were conducted in the environments in which the populations evolved. If the characters measured are not strongly plastic, then the lack of pronounced divergence may be real, assuming adequate statistical power. However, for plastic characters with weak genetic correlations across environments, the environment in which divergence is measured is likely to be important, and divergence of **G**-matrices may be more common than has been observed experimentally. In fact, characters with weaker correlations across environments may be more likely to respond to variable selection and show divergence in covariance relationships; selection in one environment would not necessarily deplete genetic variation for the phenotype expressed in a different environment when across-environment correlations are weak. Thus, amounts of genotype-by-environment interaction may influence rates of divergence in **G**-matrices, although this possibility needs more exploration, both empirically and theoretically.

The results of this study emphasize the critical importance of measuring genetic parameters in natural environments. Expression of genetic variation and genetic constraints for plasticity to density differed substantially between nearby sunny and woodland sites of natural *I. capensis* populations. The structure of genetic covariances among traits also depended dramatically on the density of neighbors and the presence of an overhead canopy. This environment dependence of genetic parameters has important consequences for evolution by natural selection. Differences in expression of genetic con-

straints among natural sites may contribute to population divergence. Moreover, environment-specific trade-offs can alter correlated responses to selection in important life-history characters. This study also demonstrates that population divergence in genetic architecture can occur on a fine spatial scale, but that expression of this divergence may also depend on the environment. Not only is the genetic architecture of *I. capensis* strongly influenced by natural environmental variation, it has evolved rapidly in adaptively diverging natural populations. Environmental and evolutionary lability of the **G**-matrix has important implications for understanding the evolution of plasticity in natural plant populations.

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