BRIEF COMMUNICATIONS

POPULATION STRUCTURE IN ARABIDOPSIS LYRATA: EVIDENCE FOR DIVERGENT SELECTION ON TRICHOME PRODUCTION

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Abstract.—Leaf trichomes may serve several biological functions including protection against herbivores, drought, and UV radiation; and their adaptive value can be expected to vary among environments. The perennial, self-incompatible herb Arabidopsis lyrata is polymorphic for trichome production, and occurs in a glabrous and a trichome-producing form. Controlled crosses indicate that the polymorphism is governed by a single gene, with trichome production being dominant. We examined the hypothesis that trichome production is subject to divergent selection (i.e., directional selection favoring different phenotypes in different populations) by comparing patterns of variation at the locus coding for glabrousness and at eight putatively neutral isozyme loci in Swedish populations of A. lyrata. The genetic diversity (H) and allele number at isozyme loci tended to increase with population size and decreased with latitude of origin, whereas genetic diversity at the locus coding for glabrousness did not vary with population size and increased with latitude of origin. The degree of genetic differentiation at the glabrousness locus was much higher than that at isozyme loci. Genetic identity at isozyme loci was negatively related to geographic distance, suggesting isolation by distance. In contrast, there was no significant correlation between genetic identity at the glabrousness locus and at isozyme loci. The results are consistent with the hypothesis that divergent selection contributes to population differentiation in trichome production in A. lyrata.

Key words.—Arabidopsis, divergent selection, FST, herbivory, local adaptation, neutral markers, trichomes.

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The study of variation in adaptive traits with a simple inheritance can provide valuable insights into processes governing the genetic structure of natural populations, and has long had a prominent place in evolutionary biology (Futuyma 1998; Barrett 2002). This is largely because the maintenance and evolutionary dynamics of variation at loci governing these traits can be modeled relatively simply (e.g., Wright 1978; Sinervo et al. 2000; Turelli et al. 2001). Although traditionally such traits have been considered rare in nature, recent studies suggest that simple inheritance of adaptive traits may not be uncommon (Johanson et al. 2000; Bradshaw and Schemske 2003; Majerus and Mundy 2003).

The importance of selection for population differentiation in a given character can be assessed by comparing the observed patterns of differentiation to those expected under the assumption of selective neutrality (Kimura 1983). To test for selective neutrality, population divergence in the focal trait can be compared to that observed at putatively neutral marker loci. If population differentiation is due to genetic drift, the between-population divergence estimated from neutral markers and that estimated for the trait of interest should be of similar magnitude. The magnitude of population differentiation at neutral loci is predicted to be lower than that for a trait subject to divergent selection (i.e., directional selection favoring different phenotypes in different populations), but higher than that observed for characters subject to unifying selection (stabilizing selection for a uniform phenotype). The comparison is straightforward if the character of interest is governed by a single Mendelian locus, because then the FST statistic (Wright 1978) can be used to quantify population differentiation both at this locus and at the neutral marker loci.

Leaf trichomes (hairs) may serve several biological functions, and trichome production has been shown to be a variable character with simple inheritance in several species. Leaf trichomes may offer protection against herbivores, drought, and UV radiation (e.g., Ågren and Schemske 1993; Skalska et al. 1994; Espigares and Peco 1995), and their adaptive value can be expected to vary among environments. Many plant species are polymorphic for trichome production, and occur in trichome-producing and glabrous forms. Genetic analyses indicate that the inheritance of glabrousness may often be simple (one gene, with a recessive allele coding for glabrousness; e.g., Westerbergh and Saura 1992; Sharma and Waines 1994; Kärkkäinen and Ågren 2002). In several species, the frequency of glabrous and trichome-producing morphs has been reported to vary geographically or between habitats (e.g., Westerbergh and Saura 1992; Barnes and Han 1993).

We examined patterns of variation in trichome production and isozyme markers in Swedish populations of the perennial, self-incompatible herb Arabidopsis lyrata, which is polymorphic for trichome production. Trichomes of A. lyrata are unicellular, nonglandular hairs that develop on leaves, sepals, and stems of the plant. The frequency of the glabrous morph varies considerably among natural populations of A. lyrata, and the results of controlled crosses indicate that the polymorphism is governed by a single gene, with trichome production being dominant to glabrousness (Kärkkäinen and Ågren 2002). To assess the relative importance of genetic drift and selection in causing population differentiation in trichome production, we compared patterns of variation at isozyme loci and at the locus causing glabrousness throughout the Swedish range of A. lyrata. In particular, we asked...
whether population differentiation was higher at the glabrousness locus than at isozyme loci, and whether there was any evidence of isolation by distance at these loci.

MATERIAL AND METHODS

Population Structure: Trichome Production and Isozyme Analysis

*Arabidopsis lyrata* ssp. *petraea* (Brassicaceae; syn. *Arabis petraea* L., syn. *Cardaminopsis petraea* [L.] Hiit.) is closely related to *A. thaliana* L. (Price et al. 1994; Kärkkäinen et al. 1999) and has a disjunct distribution in Europe. In Sweden, it occurs in an area along the coast of the Gulf of Bothnia (Hultén 1971). In this study we assume that glabrousness has the same genetic basis in all Swedish populations of *A. lyrata*. Simple inheritance of glabrousness was well supported by the results of a Mendelian crossing experiment, which included two Swedish populations of *A. lyrata* located about 25 km apart (P6 and P9; Kärkkäinen and Ågren 2002). Since the distance between the northernmost and southernmost population in Sweden is less than 100 km (Fig. 1), and population differentiation in neutral markers within the area is rather modest (see Results in this study; Jonsell et al. 1995), similar inheritance of glabrousness in all populations seems very likely.

In 1999, the frequency of glabrous plants was scored in 20 populations of *A. lyrata* throughout the distribution area in Sweden (Table 1, Fig. 1). In each population, 200 randomly selected plants were carefully checked and classified as glabrous (no trichomes on leaves or stems) or trichome-producing (in populations P5 and P11, which included fewer than 200 plants, all plants were checked). Population size

![Figure 1](image_url)
was estimated to the nearest 50 plants (populations ≤ 500 plants) or 100 plants (populations > 500 plants) by counting all individuals in all but the largest populations. In the largest populations (>2000 plants), population size was estimated to the nearest 1000 plants by multiplying the total area by the mean density of plants in transects laid out across the population. Twelve of the 20 study populations were sampled for variation at isozyme loci (Table 1, Fig. 1). In 1996, seeds were collected from at least 30 randomly selected maternal plants in each of the 12 populations, and 2–3 seeds per maternal plant were sown in a greenhouse. Seed germinability was high (>90%) and seedling mortality low (<10%). After two months, young leaves were collected for isozyme analysis from one randomly selected individual per maternal plant. Six enzyme systems were analyzed by starch gel electrophoresis: leucine aminopeptidase (LAP; E.C.3.4.11.1), acid phosphatase (ACP; E.C.3.1.3.2), malic enzyme (ME; E.C.1.1.1.40), glutamate-oxaloacetate transaminase (GOT; E.C.2.6.1.1), glucos- eosphosphate isomerase (GPI; E.C.5.3.1.9), and phosphoglucosecomutase (PGM; E.C.2.7.5.1). LAP, ACP, ME, and GOT were analyzed on a Tris-borate-EDTA buffer system; GPI and PGM on a discontinuous system KA3. The details of isozyme extraction, electrophoretic techniques, and genetic interpretation of isozymes have been described in van Treuren et al. (1997).

The plants sampled for isozyme analysis in the greenhouse were scored for trichome production to ascertain that the frequency of glabrous plants in this sample reflected the morph composition observed in the source population. With the exception of population P4, the frequency of the glabrous morph observed in the greenhouse was not significantly different from that observed in the field (Table 1). The difference recorded for population P4 was most likely caused by uneven distribution of morphs in the field and a sampling effect. The frequency of glabrous plants among those sampled for seeds in population P4 (0.13, N = 31) was very similar to the frequency observed among the offspring raised in the greenhouse (0.16, N = 31), but markedly lower than that observed in the field survey (0.54, N = 200; Table 1).

**Genetic Diversity, Hierarchical Genetic Structure and Genetic Divergence**

To characterize within-population diversity, we determined the average number of alleles and Nei’s (1978) unbiased estimate of average expected heterozygosity. To infer recent changes in population size, we studied the distribution of allele frequencies (Nei et al. 1975) using the BOTTLENECK software by Cornuet and Luikart (1996; mode-shift indicator, which discriminates bottlenecked populations from stable populations with L-shaped distribution of alleles).

Wright’s F-statistics (Wright 1978) were used to compare the degree of genetic subdivision in isozyme markers and in trichome production. In a two-level analysis, the magnitude of between-population differentiation at isozyme loci and at the locus coding for glabrousness was compared. For isozyme loci, single-locus F-statistics were calculated using FSTAT by Goudet (1999), and for glabrousness using a Bayesian approach suggested by Holsinger et al. (2002). Differentiation between northern, central, and southern populations was studied by conducting a three-level hierarchical analysis of genetic variance using the GDA software of Lewis and Zaykin (1999) for isozyme data, and TFPGA of Miller (1997) for the glabrous locus. Populations P1–P7 represented the

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**Table 1.** Location (N, northern; C, central; S, southern area), estimated size (number of established vegetative and flowering plants), and morph composition (proportion of glabrous plants) of the studied Arabidopsis lyrata populations. The proportion of glabrous plants was estimated in the field (200 plants scored per population except in P5 and P11, in which all plants were scored) and among plants raised in the greenhouse for the isozyme study (N = 21–46, median 30 plants per population). Expected heterozygosity in the locus causing glabrousness (Hₑ(glabrous) estimated from the field data), mean expected heterozygosity in isozyme loci (Hₑ), the percent observed heterozygosity in isozyme loci (Hₑ), and average number of alleles per isozyme locus (A) are given (N = 8 isozyme loci).

<table>
<thead>
<tr>
<th>Population</th>
<th>Location</th>
<th>Size</th>
<th>Field</th>
<th>Greenhouse</th>
<th>Hₑ(glabrous)</th>
<th>Hₑ</th>
<th>Hₑ</th>
<th>A</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1</td>
<td>N</td>
<td>350</td>
<td>0.96</td>
<td>0.81</td>
<td>0.04</td>
<td>0.35</td>
<td>0.33</td>
<td>2.00</td>
</tr>
<tr>
<td>P2</td>
<td>N</td>
<td>800</td>
<td>0.38</td>
<td>—</td>
<td>0.48</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>P3</td>
<td>N</td>
<td>3000</td>
<td>1.00</td>
<td>—</td>
<td>0.00</td>
<td>0.39</td>
<td>0.36</td>
<td>2.25</td>
</tr>
<tr>
<td>P4</td>
<td>N</td>
<td>1200</td>
<td>0.54</td>
<td>0.16</td>
<td>0.40</td>
<td>0.45</td>
<td>0.40</td>
<td>2.25</td>
</tr>
<tr>
<td>P5</td>
<td>N</td>
<td>100</td>
<td>0.99</td>
<td>1.00</td>
<td>0.00</td>
<td>0.24</td>
<td>0.21</td>
<td>2.13</td>
</tr>
<tr>
<td>P6</td>
<td>N</td>
<td>1400</td>
<td>0.63</td>
<td>0.33</td>
<td>0.34</td>
<td>0.30</td>
<td>0.33</td>
<td>2.00</td>
</tr>
<tr>
<td>P7</td>
<td>N</td>
<td>1500</td>
<td>0.35</td>
<td>—</td>
<td>0.49</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>P8</td>
<td>C</td>
<td>4000</td>
<td>1.00</td>
<td>—</td>
<td>0.00</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>P9</td>
<td>C</td>
<td>3000</td>
<td>1.00</td>
<td>1.00</td>
<td>0.00</td>
<td>0.43</td>
<td>0.43</td>
<td>2.63</td>
</tr>
<tr>
<td>P10</td>
<td>C</td>
<td>500</td>
<td>1.00</td>
<td>1.00</td>
<td>0.00</td>
<td>0.37</td>
<td>0.34</td>
<td>2.63</td>
</tr>
<tr>
<td>P11</td>
<td>C</td>
<td>150</td>
<td>1.00</td>
<td>1.00</td>
<td>0.00</td>
<td>0.39</td>
<td>0.36</td>
<td>2.25</td>
</tr>
<tr>
<td>P12</td>
<td>C</td>
<td>400</td>
<td>1.00</td>
<td>—</td>
<td>0.00</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>P13</td>
<td>C</td>
<td>15000</td>
<td>1.00</td>
<td>0.99</td>
<td>0.00</td>
<td>0.43</td>
<td>0.43</td>
<td>2.75</td>
</tr>
<tr>
<td>P14</td>
<td>C</td>
<td>200</td>
<td>1.00</td>
<td>—</td>
<td>0.00</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>P15</td>
<td>S</td>
<td>300</td>
<td>1.00</td>
<td>0.91</td>
<td>0.05</td>
<td>0.43</td>
<td>0.40</td>
<td>2.75</td>
</tr>
<tr>
<td>P16</td>
<td>S</td>
<td>500</td>
<td>0.99</td>
<td>0.92</td>
<td>0.01</td>
<td>0.42</td>
<td>0.36</td>
<td>2.75</td>
</tr>
<tr>
<td>P17</td>
<td>S</td>
<td>3000</td>
<td>1.00</td>
<td>1.00</td>
<td>0.00</td>
<td>0.50</td>
<td>0.46</td>
<td>2.75</td>
</tr>
<tr>
<td>P18</td>
<td>S</td>
<td>2000</td>
<td>0.99</td>
<td>—</td>
<td>0.00</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>P19</td>
<td>S</td>
<td>600</td>
<td>0.95</td>
<td>0.85</td>
<td>0.06</td>
<td>0.40</td>
<td>0.39</td>
<td>2.63</td>
</tr>
<tr>
<td>P20</td>
<td>S</td>
<td>400</td>
<td>0.96</td>
<td>—</td>
<td>0.04</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

1 Statistically significant difference in frequency of the glabrous morph between greenhouse-grown plants and source population; G = 8.38, P = 0.04.
northern area, P8–P14 the central, and P15–P20 the southern area (Table 1; Fig. 1). Genetic differentiation at the glabrous locus was estimated based on morph frequencies observed both in the field and among plants screened for isozyme variation in the greenhouse.

Both differences in allele number and dominance may influence comparisons of \( F_{ST} \)-values obtained for different loci. Loci with high numbers of alleles may give lower estimates of population differentiation than loci with less variation (Hedrick 1999). However, in the present study, the number of alleles at the glabrousness locus (two) was similar to the number of alleles observed at isozyme loci (maximum five alleles, mean number of alleles = 2.45; see below). Simulations indicate that the expected value of \( F_{ST} \) should be insensitive to differences in allele number of this magnitude (Kalinowski 2002). The dominance of the trichome-coding allele complicates estimation of population differentiation compared to codominant isozyme loci. Estimation of allele frequencies from dominant loci is usually based on the assumption that genotypes are in Hardy-Weinberg proportions within populations (e.g. Lynch and Milligan 1994). We used both a new Bayesian approach, in which the assumption of Hardy-Weinberg equilibrium within populations is relaxed (Holsinger et al. 2002), and a more traditional method (Lynch and Milligan 1994; Miller 1997) to estimate \( F_{ST} \) for the locus causing glabrousness (two-level hierarchical analysis of variance). The two methods gave very similar results, and only results based on the Bayesian approach are presented below.

Genetic identities between populations with respect to isozyme loci and the locus coding for glabrousness were estimated using the method of Nei (1978). The correlation between genetic and geographical distances was examined with Mantel’s test (Manly 1985) using the program TFPGA of Miller (1997). Matrices were log-transformed prior to analyses.

**RESULTS**

The frequency of the glabrous morph varied from 0.35 to 1.00 in the 20 study populations (Table 1). Most polymorphic populations were found in the northern area, whereas large populations in the central area lacked the trichome-producing morph (Fig. 1).

Isozyme polymorphisms indicated a high degree of genetic variability within populations: the genetic diversity \( (H_e) \) varied between 0.24 and 0.50 (Table 1; for sample sizes and allele frequencies see Appendix published online only at http://dx.doi.org/10.1554/04-138.1.s1). By comparison, genetic diversity at the glabrousness locus varied between 0.00 and 0.49 (Table 1).

Genetic diversity at the locus coding for glabrousness \( (H_e) \) increased with latitude of origin \((r = 0.654, N = 20, \text{two-tailed } P = 0.02)\), but was not correlated with population size \((r = 0.432, \text{two-tailed } P = 0.875)\). In contrast, both genetic diversity \( (H_e) \) and allele number at isozyme loci decreased with latitude of origin \((r = -0.617, \text{two-tailed } P = 0.033, \text{and } r = -0.893, \text{two-tailed } P < 0.001, \text{respectively; } N = 12)\), and tended to be positively related to population size \((r = 0.508, \text{one-tailed } P = 0.046, \text{and } r = 0.406, \text{one-tailed } P = 0.095)\), respectively.

Among-population differentiation was markedly stronger at the locus coding for glabrousness than at isozyme loci. A two-level analysis of variance at the glabrousness locus based on the field data yielded an estimate of \( F_{ST} = 0.45 \) (SD = 0.09; Table 2). The corresponding analysis based on the greenhouse-grown plants originating from 12 populations gave almost identical results (Table 2). By comparison, the among-population variation at eight isozyme loci was significantly lower (95% confidence intervals do not overlap), mean \( F_{ST} = 0.13 \) (SD = 0.02; Table 2).

In a hierarchical three-level analysis of variance, genetic differentiation both among areas and among populations within areas was higher for the locus coding for glabrousness than for isozyme loci (Table 2).

There was no correlation between genetic identity at the glabrous locus and geographic distance \((r = -0.102, Z = 1303, P = 0.07, N = 20 \text{ populations})\), or between genetic identity at the glabrousness locus and isozyme loci \((r = 0.260, Z = 27, P = 0.170, N = 12)\). However, genetic identity at isozyme loci was negatively correlated with geographic distance \((r = -0.29, Z = 2340, P = 0.02, N = 12)\), as would be expected with isolation by distance.

**Table 2.** Hierarchical analysis of allele frequencies at the glabrous locus and at eight isozyme loci within Arabidopsis lyrata populations in Sweden. The means of population estimates of expected heterozygosities \((H_e)\) and among-population differentiation \((F_{ST})\) in the two-level hierarchical analysis of genetic variance are given. In the three-level hierarchical analysis, \( F_{ST} \) (Area) describes differentiation between southern, central, and northern areas of distribution in Sweden, and \( F_{ST} \) (Pop) the differentiation among populations within areas.

<table>
<thead>
<tr>
<th>Locus</th>
<th>(H_e)</th>
<th>(F_{ST})</th>
<th>SD</th>
<th>(F_{ST}) (Area)</th>
<th>(F_{ST}) (Pop)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glabrous1</td>
<td>0.120</td>
<td>0.446</td>
<td>0.087</td>
<td>0.190</td>
<td>0.317</td>
</tr>
<tr>
<td>Glabrous2</td>
<td>0.124</td>
<td>0.450</td>
<td>0.105</td>
<td>0.168</td>
<td>0.395</td>
</tr>
<tr>
<td>Isozyme loci:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>0.392</td>
<td>0.133</td>
<td>0.020</td>
<td>0.036</td>
<td>0.141</td>
</tr>
<tr>
<td>GPI2</td>
<td>0.165</td>
<td>0.199</td>
<td>0.064</td>
<td>0.059</td>
<td>0.189</td>
</tr>
<tr>
<td>ME</td>
<td>0.258</td>
<td>0.102</td>
<td>0.057</td>
<td>-0.002</td>
<td>0.098</td>
</tr>
<tr>
<td>ACP</td>
<td>0.492</td>
<td>0.172</td>
<td>0.070</td>
<td>0.088</td>
<td>0.190</td>
</tr>
<tr>
<td>GOT1</td>
<td>0.114</td>
<td>0.223</td>
<td>0.086</td>
<td>-0.030</td>
<td>0.207</td>
</tr>
<tr>
<td>GOT2</td>
<td>0.483</td>
<td>0.155</td>
<td>0.046</td>
<td>0.040</td>
<td>0.167</td>
</tr>
<tr>
<td>LAP</td>
<td>0.533</td>
<td>0.171</td>
<td>0.047</td>
<td>0.026</td>
<td>0.180</td>
</tr>
<tr>
<td>PGM2</td>
<td>0.618</td>
<td>0.079</td>
<td>0.033</td>
<td>0.029</td>
<td>0.086</td>
</tr>
<tr>
<td>PGM3</td>
<td>0.473</td>
<td>0.057</td>
<td>0.026</td>
<td>0.016</td>
<td>0.059</td>
</tr>
</tbody>
</table>

1 A total of 20 populations analyzed; frequency of glabrous morph scored in the field.

2 A total of 12 populations (same as in isozyme analysis) analyzed; frequency of glabrous morph scored among greenhouse-grown plants.
DISCUSSION

The patterns of variation in the gene controlling trichome production differed significantly from those of isozyme loci and were consistent with the hypothesis that trichome production is subject to divergent selection in the perennial, outcrossing herb *Arabidopsis lyrata*. The magnitude of among-population differentiation was markedly higher at the locus coding for glabrousness than at isozyme loci. The largest populations in the central part of the distribution area were highly variable with respect to isozyme loci, but monomorphic with respect to the locus coding for glabrousness. A significant negative correlation between geographic distance and genetic distance in isozyme loci suggested isolation by distance, whereas genetic distance based on the glabrousness locus did not significantly correlate with those of isozyme loci or with geographic distance.

The comparison of population differentiation at isozyme loci and in trichome production rests on the assumptions that glabrousness has a common genetic basis in the populations studied (see Materials and Methods), and that variation at isozyme loci is selectively neutral. The magnitude of population differentiation was similar across isozyme loci, suggesting that in this study the patterns of variation at the isozyme loci examined are mainly affected by migration and genetic drift. Strong selection acting on any of these loci should cause variation among individual-locus $F_{ST}$ estimates (e.g., Lewontin and Krakauer 1975).

The absence of the dominant allele for trichome production from many populations does not appear to be a function of recent population bottlenecks. Instead, the isozyme data suggest that the northern populations, including those polymorphic for trichome production, may have been more strongly affected by founder events and genetic drift than the monomorphic, glabrous southern populations. The overall level of genetic variability at isozyme loci was high, which is consistent with previous studies of neutral markers in Swedish *A. lyrata* populations (Jonsell et al. 1995; van Treuren et al. 1997). However, in isozyme loci, levels of genetic diversity (mean $H_e$) and allele number were slightly reduced in the northern compared to the southern populations. In addition, allele frequency distributions deviated from the expectations of stable populations in three of four northern populations, but in only two of eight central and southern populations.

As expected, genetic diversity at isozyme loci was positively related to population size, whereas no such relationship was observed for genetic diversity at the glabrous locus.

*Arabidopsis lyrata* is polymorphic for trichome production also in other parts of Europe, and in North America (Jonsell et al. 1995; Fernald 1950), and population differentiation at the locus coding for glabrousness may be stronger than that at isozyme loci also on a larger spatial scale than considered in the present study. Jonsell et al. (1995, fig. 3) presented data on trichome production of greenhouse-grown plants originating from across northern Europe. By assuming that glabrousness has a common genetic basis across the geographic range examined, we obtained an estimate of population differentiation ($F_{ST}$) at the locus coding for glabrousness that was considerably higher than that calculated by Jonsell et al. (1995) on the basis of variation at isozyme loci (0.61 vs. 0.35).

The most likely explanation for the high degree of among-population differentiation in trichome production is divergent selection (i.e., selection favoring different phenotypes in different populations). For selection to cause divergence in the frequency of the glabrous morph, populations should be long-lived, and selection should be rather consistent in direction. The modest degree of population differentiation at isozyme loci and the correlation between geographic and genetic distances at these loci suggest that Swedish populations of *A. lyrata* have been relatively stable. Thus, a higher degree of differentiation in trichome production than at neutral marker loci may reflect long-term consistent differences in the adaptive value of trichome production among populations of *A. lyrata*.

Trichomes may protect the plant against, for example, herbivory and drought, but production of trichomes may be costly (e.g., Ågren and Schemske 1993; Mauricio 1998). In this situation, the relative fitness of glabrous and trichome-producing plants in a given population should depend on the balance between benefits and costs (Simms and Rausher 1987). The results from field surveys are consistent with the hypotheses that trichome production contributes to resistance against insect herbivores in *Arabidopsis lyrata*, and that polymorphic populations are more heavily affected by insect herbivory. In a three-year study, glabrous plants experienced higher levels of damage from insect herbivores than trichome-producing plants in polymorphic populations, and glabrous plants in polymorphic populations were more heavily damaged than glabrous plants in monomorphic populations in two of three years (G. Løe and J. Ågren, unpubl. data).

We are presently quantifying selection on trichome-production in natural and experimental *A. lyrata* populations experiencing different levels of herbivory. Because *A. lyrata* is a potentially long-lived perennial herb, and damage levels are temporally variable, long-term studies are needed to acquire meaningful estimates of the mode and consistency of selection on trichome production in the field.

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