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Genetic basis of trichome production in *Arabidopsis lyrata*

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Leaf trichomes may protect plants against herbivorous insects, and may increase tolerance to drought and UV-radiation. The perennial herb *Arabidopsis lyrata* (Brassicaceae) is polymorphic for trichome production and occurs in a glabrous and trichome-producing form. In addition, there is quantitative variation in trichome density among trichome-producing plants. To examine the genetic basis of glabrousness, we conducted controlled crosses with plants originating from two natural populations in Sweden (one polymorphic for trichome-production, and one consisting of glabrous plants only). In addition, we estimated the heritability of trichome number from parent-offspring regressions for plants originating from the polymorphic population. Crosses between glabrous plants resulted in glabrous offspring only, whereas crosses between glabrous and trichome-producing plants, and crosses between trichome-producing individuals, resulted in either all trichome-producing offspring or both phenotypes. In segregating crosses between trichome-producing plants, the ratio of glabrous:trichome-producing offspring did not deviate significantly from 1:3, while in segregating crosses between glabrous and trichome-producing individuals the ratio did in most cases not deviate from 1:1. Within- and between-population crosses gave similar results. The heritability of trichome number estimated from regression of offspring on mid-parent was high ($h^2 \pm$ SE, 0.65 ± 0.15). The results suggest that glabrousness is inherited in a simple Mendelian fashion, with the allele coding for trichome production being dominant over that for glabrousness. They further indicate that glabrousness is due to a mutation at the same locus in both populations.

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The genetic basis of adaptive traits determines how they can be moulded by selection, but is still poorly known. Many adaptive characters vary continuously and have within a quantitative-genetic framework been assumed to be influenced by a large number of genes, each with a small effect. However, recent studies have suggested that adaptive traits can be controlled by few genes with large effects (SCHEMSKE and BRADSHAW 1999; JOHANSON et al. 2000; FRARY et al. 2000; WEBER et al. 1999). On the other hand, some traits that have been thought to have a simple monogenic inheritance have been found to be much more complex than earlier was believed (SCRIVER and WATERS 1999). Additional studies of the genetic basis of adaptive characters are therefore clearly needed.

Trichomes are uni- or multicellular hairs that develop on the leaves, sepals, and stems of plants, and may serve several functions. They may protect plants against UV-radiation and drought (EHLERINGER 1984; SKALTSA et al. 1994; ESPIGARES and PECO 1995), and also against damage caused by herbivores (LEVIN 1973; ÅGREN and SCHEMSKE 1993; VALVERE et al. 2001) and pathogens (HAGLEY et al. 1980). The production of trichomes may thus be beneficial for several reasons, but can also be associated with a cost: In environments where trichomes do not confer an advantage, glabrous plants may be able to allocate more resources to growth and reproduction (ÅGREN and SCHEMSKE 1993; BERGELSON 1994; MAURICIO and RAUSHER 1997; MAURICIO 1998).

Genetic variation in leaf trichome number has been detected in several members of the Brassicaceae, including *Arabidopsis thaliana* (MAURICIO and RAUSHER 1997), *Brassica rapa* (ÅGREN and SCHEMSKE 1994), and *Sinapis arvensis* (ROY et al. 1999). Mutations affecting trichome formation have been identified in *A. thaliana* and many of them have also been cloned and sequenced (MARKS 1997). Trichome density may further be influenced by environmental conditions (AGRAWAL 1999; ROY et al. 1999).

The outcrossing perennial herb *Arabidopsis lyrata* is polymorphic for trichome production and occurs in a glabrous (G) and a trichome-producing form (T). In addition, there is considerable variation in trichome density among trichome producing *A. lyrata*. To investigate the inheritance of glabrousness and whether the genetic basis of glabrousness in *A. lyrata* is consistent across populations in Sweden, we conducted crosses between glabrous and trichome-producing plants originating from two natural populations separated by about 32 km (one polymorphic for trichome-production, and one consisting of glabrous plants only). We documented the segregation of glabrousness in the resulting offspring. We further estimated the heritability of trichome number from parent-offspring regressions for plants originating from the polymorphic population.

MATERIAL AND METHODS

The species

Arabidopsis lyrata (L.) O'Kane and Al-Shehbaz ssp. *petraea* (Brassicaceae, syn. *Arabis petraea* L., and *Cardaminopsis petraea* (L.) Hiit.) is a perennial, self-incompatible herb, closely related to *A. thaliana* L. (PRICE et al. 1994; KOCH et al. 1999; SAVOLAINEN et al. 2000). Four geographically separated subspecies have been identified in *A. lyrata*: *A. lyrata* ssp. *petraea* in Europe, *A. lyrata* ssp. *lyrata* in North America, and *A. lyrata* ssp. *kamchatica* and ssp. *kawasakiana* in eastern Asia (O'KANE and AL-SHEHBAZ 1997).

Arabidopsis lyrata has a disjunct distribution in Europe. It is a common species in Iceland and in the Faroes, and is found in the north-western parts of the British Isles, in southern Germany and in the Alps (JALAS and SUOMINEN 1994). In Scandinavia, *A. lyrata* occurs only in western Norway and in a limited area along the coast of eastern Sweden (HULTÉN 1971).

The 5–20 cm long inflorescence is produced from a leaf rosette. The rosette leaves are typically 3–10 cm long and 0.5–1.0 cm wide. *Arabidopsis lyrata* may produce trichomes on leaves and stems. Leaf trichomes form up to five branches, whereas those on the stems are predominantly unbranched. Among trichome-producing plants, there is considerable variation in the density of leaf trichomes, from plants producing only a few trichomes on the leaf margin to those with leaves densely covered by trichomes (JONSELL et al. 1995).

Genetic basis of glabrousness

To examine the genetic basis of glabrousness, we conducted controlled crosses using plants produced from seeds collected in two *A. lyrata* populations in eastern Sweden. One population was polymorphic for trichome production and located at Storstensudden (63° 12′ N, 18° 48′ E; proportion of glabrous plants about 30 %), while the other population consisted of glabrous plants only and was located at Norrfällsviken (62° 35′ N, 18° 32′ E; proportion of glabrous plants > 98 %). Seeds were collected from glabrous (G) and trichome-producing (T) plants and sown in a greenhouse in the autumn 1997. The following spring, the phenotype of flowering individuals was scored as glabrous (no trichomes observed) or trichome-producing. Plants were randomly assigned as maternal and paternal parents for the crosses. We crossed the two morphs in all combinations (G × G, G × T, T × G, and T × T), and conducted crosses both within and between the two populations. The crosses were repeated with different maternal and paternal plants.

The segregation of glabrousness was examined among the offspring from 43 crosses (38 within-population crosses and 5 between-population crosses). Seeds were sown in a greenhouse in early spring 2000 and the phenotypes of the seedlings (altogether 822 individuals) were scored three months after sowing. Twenty to seventy individuals were scored from each of 18 crosses, while 8–10 individuals were scored from each of the remaining 24 crosses. Crosses were classified as segregating when the offspring included both glabrous and trichome-producing plants, and non-segregating when all offspring were of the same phenotype in terms of trichome production.

Based on the results of the crosses (see below), we postulated a simple Mendelian model for the inheritance of glabrousness (a one gene, two-allele model in which the allele coding for trichome-production is dominant over the allele coding for glabrousness). The fit of the model was evaluated by testing the following predictions: First, if the glabrous phenotype (G) is a recessive homozygote, crosses between glabrous individuals (G × G) should produce only glabrous offspring. Second, crosses between trichome-producing individuals (T × T) should produce either only trichome-producing offspring if at least one parent is homozygous for trichome-production or, if both parents are heterozygous with respect to the gene coding for trichome production, progenies with a 1:3 ratio of glabrous to trichome-producing individuals. Third, the offspring from crosses between glabrous and trichome-producing individuals should segregate in a 1:1 ratio of glabrous to trichome-producing plants if the trichome-producing parent is a heterozygote, and all offspring should be trichome-producing if the trichome-producing parent is homozygous for the dominant allele. Finally, if segregation ratios do not differ between reciprocal crosses (G × T vs T × G), trichome production is likely to be governed by nuclear genes rather than by cytoplasmic factors. Crosses between populations (G × G and G × T) were conducted to assess whether the genetic basis of glabrousness was similar in the populations.

For segregating crosses, deviations from expected ratios of glabrous to trichome-producing plants were examined with G-tests. This was done separately for each cross with a large number of offspring ($N = 20$–70), and for data pooled over each cross type (T × T, G × T, T × G). For crosses with large numbers of offspring, the data on phenotypes of maternal and paternal grandmothers (determined in the field when

Table 1. *Summary of the results of 42 controlled crosses between glabrous (G) and trichome-producing (T) Arabidopsis lyrata ssp. petraea. The plants used in the crosses originated from two natural populations in eastern Sweden (Norrfällsviken (N) and Storstensudden (SU)). In segregating crosses, both glabrous and trichome-producing plants were observed among the offspring*

Type of cross ♀ × ♂	Origin of parental plants ♀ × ♂	Number of crosses		Offspring phenotype in non-segregating crosses	Total number of offspring
		Segregating	Non-segregating		
G × G	N × N	0	9[1]	G	208
	SU × SU	0	3	G	32
	N × SU	0	1[2]	G	42
T × T	SU × SU	4	8[3]	T	250
G × T	SU × SU	5	2	T	81
	N × SU	3	0		93
T × G	SU × SU	6	1	T	62
	SU × N	1	0		34

[1] One of the 208 offspring studied had produced two trichomes.

[2] One of the 42 offspring had two trichomes

[3] In one cross, one out of 60 offspring was glabrous.

sampling seeds) were used to infer the genotypes of the parental plants used in the cross.

Phenotypic and genetic variation in trichome number

To document the frequency distribution of trichome number per leaf, we grew in the greenhouse two plants from each of 50 maternal families collected in the polymorphic Storstensudden population. Three months after planting, we counted the number of trichomes on the adaxial (upper) surface of one randomly selected leaf from each plant under a dissecting microscope. The length and width of the sampled leaf were measured to the nearest mm, and leaf area was estimated as the product of these two measures.

The heritability of trichome number in the Storstensudden population was estimated based on parent-offspring regressions. Trichome number per leaf was determined as above for both parents and offspring in the 28 controlled crosses that resulted in at least some trichome-producing plants (Table 1 and 2). The mean number of trichomes on the upper leaf surface in the offspring was regressed on (a) the maternal parent, (b) the paternal parent, and (c) the mid-parent value (Falconer and Mackay 1996). To achieve normality, trichome number per leaf was log-transformed (log(trichome number + 1)) prior to analyses.

RESULTS

Genetic basis of glabrousness: controlled crosses

All crosses between glabrous individuals (within and between populations) produced glabrous offspring only (Table 1). Four crosses between trichome-producing plants produced both glabrous and trichome-producing offspring, while eight such crosses produced trichome-producing offspring only (Table 1). Crosses between the two morphs produced either only trichome-producing individuals, or progenies with both glabrous and trichome-producing plants (Table 1).

In segregating crosses between trichome-producing plants, the observed ratio of glabrous vs. trichome-producing offspring did not statistically deviate from the expected 1:3 ratio in Cross 1 (N = 62), or in the data pooled from four crosses (N = 86; Table 2). The mothers of both plants used in Cross 1 were glabrous, thus the latter were inferred to be heterozygous at the locus causing glabrousness (Table 2).

Both within- (SU × SU) and between-population crosses (N × SU or SU × N) between glabrous and trichome-producing individuals resulted in segregating progenies. The ratio of glabrous to trichome-producing plants did not deviate from the expected 1:1 ratio in the two T × G crosses with large number of offspring (one within-population and one between-population cross), or in the pooled analysis of six segregating T × G crosses (40 glabrous vs 48 trichome-producing individuals, G = 0.73, NS). However, two of four segregating G × T crosses produced G:T ratios that deviated significantly from the expected 1:1 ratio (both were between-population crosses; Table 2). The number of glabrous individuals was lower than expected among the offspring of G × T Cross 1, and higher than expected among the offspring of G × T Cross 2. In the other two segregating G × T crosses analysed separately (one within- and one between-population cross), and in the pooled analysis of G × T crosses, the ratio of glabrous to trichome-producing plants did not deviate from the

Table 2. *Comparison of observed and expected ratios of glabrous (G) to trichome-producing offspring (T) in segregating crosses with $N > 20$, and in data pooled for segregating crosses of each type. The plants used in the crosses originated from two populations of Arabidopsis lyrata ssp. petraea in eastern Sweden (Norrfällsviken (N) and Storstensudden (SU)). The fit of observed ratios to those expected under a single-locus two-allele model with the allele coding for trichome production being dominant over the allele coding for glabrousness was examined with G-tests ($df = 1$). For crosses represented by 20 or more offspring, the phenotypes of the maternal and paternal grandmothers, and the inferred genotypes of parental plants are given*

Cross type ♀×♂	Origin ♀×♂	Offspring phenotypes		Expected ratio of G:T in the offspring	G-test	Phenotypes of grandmothers		Genotypes of parental plants [1]
		G	T			♀	♂	♀×♂
T×T:								
Cross 1	SU×SU	22	40	1:3	3.34 NS	G	G	tT×tT
Pooled data, 4 crosses		29	57	1:3	3.25 NS			
G×T:								
Cross 1	N×SU	8	22	1:1	6.68 **	G	G	tt×tT
Cross 2	N×SU	31	10	1:1	11.15 ***	G	T	tt×Tt or tt×tT
Cross 3	N×SU	7	15	1:1	2.91 NS	G	T	tt×Tt or tt×tT
Cross 4	SU×SU	21	25	1:1	0.34 NS	G	T	tt×Tt or tt×tT
Pooled data, 8 crosses		86	88	1:1	0.02 NS			
T×G:								
Cross 1	SU×N	15	19	1:1	0.46 NS	G	G	tT×tt
Cross 2	SU×SU	9	11	1:1	0.20 NS	G	G	tT×tt
Pooled data, 6 crosses		40	48	1:1	0.73 NS			

[1] The allele received from the maternal plant is presented before the allele received from the paternal plant.

expected 1:1 ratio (eight crosses, 86 glabrous vs 88 trichome-producing individuals, $G = 0.02$, NS; Table 2). Under the postulated model of inheritance of glabrousness, the trichome-producing parent in segregating crosses should be heterozygous at the locus causing glabrousness. The observation that the trichome-producing parent had a glabrous mother in three of the segregating crosses is consistent with this view (Table 2: G × T Cross 1; T × G Cross 1 and T × G Cross 2).

Phenotypic and genetic variation in trichome number

The plants established from seeds collected in the Storstensudden population and grown in the greenhouse exhibited considerable variation in trichome number per leaf (mean = 18.9, SD = 32.5, $N = 96$; Fig. 1). The distribution of trichome number deviated significantly from the normal distribution (Kolmogorov-Smirnov test of normality 0.302, $df = 96$; $p < 0.001$), with high values of skewness (2.10, SE = 0.25) and kurtosis (3.42, SE = 0.49). This was true also if glabrous individuals were excluded from the analysis (Kolmogorov-Smirnov 0.296, $df = 60$, $p < 0.001$; skewness 1.46, SE = 0.31, kurtosis 0.87, SE = 0.61). Variation in trichome density (trichome number per unit leaf area) was a function of variation in total number of trichomes produced, rather than of variation in leaf size: trichome number per unit leaf area was strongly correlated with trichome number per leaf ($r = 0.946$, $N = 406$, $p < 0.001$), but was not correlated with leaf area ($r = -0.07$, $N = 406$, NS).

The estimates of the heritability of trichome number per leaf obtained from regressions of offspring on maternal, paternal and midparent values were all high ($h^2 \pm$ SE, 1.17 ± 0.25, 1.03 ± 0.53, and 0.65 ± 0.15, respectively, $N = 28$, Fig. 2).

In crosses between glabrous and trichome-producing plants most offspring produced fewer leaf trichomes than the trichome-producing parent (Fig. 3).

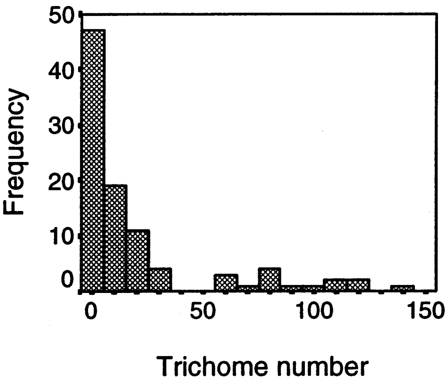

Fig. 1. Phenotypic variation in trichome number on the upper side of the leaf in *Arabidopsis lyrata* ssp. *petraea.* Plants were raised in the greenhouse from seeds collected in the Storstensudden population, and were scored for trichome number three months after planting ($N = 100$).

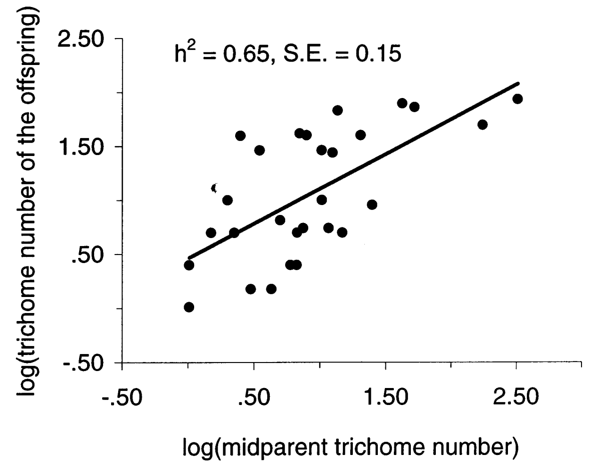

Fig. 2. Mean number of leaf trichomes in the offspring as a function of mean number of leaf trichomes of the parental plants (mid-parent value) in 28 crosses conducted with plants originating from the Storstensudden population. Both the parental plants and the offspring were raised in the greenhouse and scored for trichome number on the upper leaf surface three months after planting. Trichome number was log-transformed prior to analysis. The heritability estimate (± SE) is indicated in the figure.

In contrast, in crosses between trichome-producing individuals, a large proportion of the offspring produced more leaf trichomes than either parent (Fig. 4).

DISCUSSION

Genetic basis of glabrousness

The results of the present study indicate that glabrousness has a simple Mendelian inheritance in *Arabidopsis lyrata* ssp. *petraea*, and that glabrousness is determined by allelic variation at the same locus in the two populations studied. Moreover, they indicate that there is considerable genetic variation in the number of trichomes formed by trichome-producing plants. The fact that crosses between glabrous plants did not produce any trichome-producing offspring, while crosses between trichome-producing plants resulted in either all trichome-producing plants or segregating progenies suggests that glabrousness is a recessive character to trichome-production. Moreover, the ratio of glabrous:trichome-producing plants in the segregating progenies did not statistically deviate from the expected 1:3 ratio. As expected under a one-locus, two-allele model, some between-morph crosses produced only trichome-producing offspring. The ratio of glabrous to trichome-producing plants did not statistically deviate from the expected 1:1 ratio in four of the six crosses between glabrous and trichome-producing plants, or in the pooled analysis of such crosses.

Glabrousness may have a simple genetic basis also in other plant species. Data from segregating crosses indicate that glabrousness is controlled by one, autosomal recessive gene in *Silene dioica* (WESTERBERGH 1992), and *Silene latifolia* (DE VRIES 1900). Moreover, trichome morphology (glandular vs. non-glandular trichomes) can be inherited in a simple Mendelian fashion as was recently documented for *Datura wrightii* (VAN DAM et al. 1999).

Information on the genetic basis of trichome development suggests that glabrousness may have a simple genetic basis also in in *Arabidopsis thaliana*. Although there are many genes involved in trichome formation, only a few low in the developmental pathway (GLABROUS-1 and TTG) have been found to block trichome production completely (MARKS 1997).

GLABROUS-1 encodes a protein with sequence homology to a myb-related transcription factor (OPPENHEIMER et al. 1991). Plants homozygous for the gl1-1 allele are virtually devoid of trichomes, although trichomes are occasionally found at the margin of rosette and cauline leaves. Plants homozygous for the weaker allele gl1-2 have reduced trichome number with trichomes near the margin of leaves (ESCH et al. 1994). Mutation in the gene TTG1,

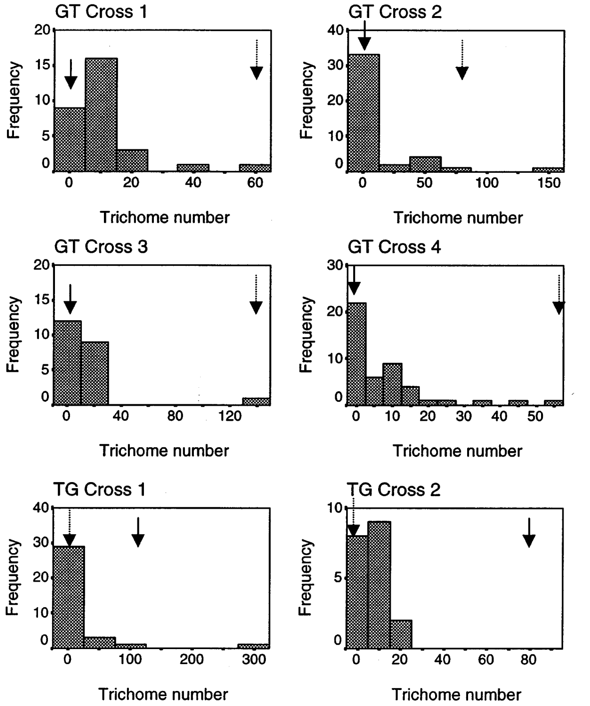

Fig. 3. Variation in trichome number on the upper leaf surface among offspring from controlled crosses between glabrous and trichome-producing plants (G × T, Crosses 1–4, and T × G Crosses 1–2 in Table 2). Trichome numbers of maternal (solid line arrow) and paternal parents (broken line arrow) are indicated.

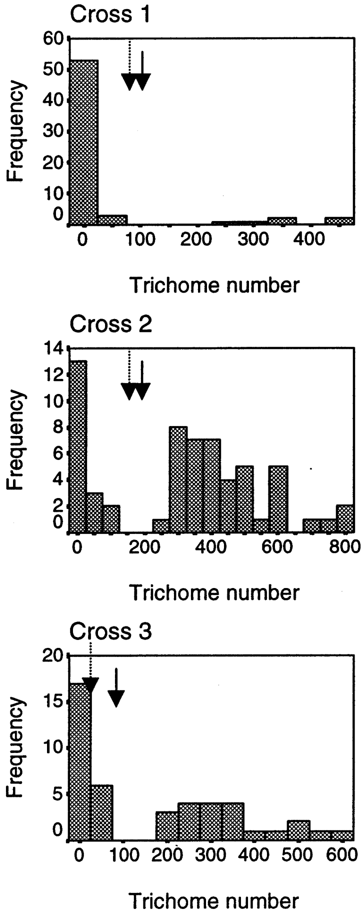

Fig. 4. Variation in trichome number on the upper leaf surface among offspring from controlled crosses between trichome-producing plants (T × T). In Cross 1, some of the offspring were glabrous, in the other two crosses all progeny were trichome-producing. Trichome numbers of maternal (solid line arrow) and paternal parents (broken line arrow) are indicated.

transparent testa glabra1, can also result in a complete loss of trichome formation on most areal surfaces (Koornneef 1981). The TTG1 gene encodes a WD40 repeat protein that may regulate signal transduction pathways governing leaf hair formation and anthocyanin biosyntesis (Walker et al. 1999). By now, several mutations that result in the loss or show reduction in trichome formation have been described for TTG1 (Walker et al. 1999).

The glabrous phenotype of *Arabidopsis lyrata* may be caused by one of the genes causing glabrousness in *Arabidopsis thaliana*. Based on sequence variation in rDNA, *A. lyrata* and *A. halleri* are the closest known outcrossing relatives of *A. thaliana* (O'Kane and Al-Shehbaz 1997; Koch et al. 1999). Thus, genes causing glabrousness in *A. thaliana* are good candidates for causing glabrousness also in *A. lyrata*. A recent study which included a glabrous plant from a Russian population (Hauser et al. 2001) and our own data on Swedish and Norwegian populations (Kärkkäinen, Kivimäki and Ågren, unpubl.) suggest that mutations either in the coding area or in the regulatory regions of GLABROUS-1 may cause glabrousness in *A. lyrata*.

Genetic basis of trichome number

Parent-offspring regressions indicated that the heritability of trichome number per leaf was high in the studied population. This suggests that this population may respond not only to selection on trichome formation per se, but also to selection on trichome density. The heritability estimate based on mid-parent values had a lower standard error ($h^2 = 0.65$, $SE = 0.15$) than the estimates based on maternal ($h^2 = 1.17$, $SE = 0.25$) and paternal values ($h^2 = 1.03$, $SE = 0.53$). The segregation of the recessive allele for glabrousness may have contributed to the high standard errors of the two latter estimates. The highest estimate was obtained when offspring trichome number was regressed on maternal value, as would be expected if maternal environmental effects contribute to variation in trichome number (Roach and Wulff 1987).

The skewed distribution of trichome number observed in the Storstensudden population can partly be attributed to the occurrence of glabrous plants. However, the distribution deviated from normality also when the completely glabrous individuals were excluded from the analysis. This is consistent with the hypothesis that there is one or several genes with major effect on trichome number in trichome-producing plants. In *Arabidopsis thaliana*, a QTL-analysis of trichome number of two ecotypes revealed a major QTL (Reduced trichome number, RTN) that explained 70 % of the variation in trichome number (Larkin et al. 1996). In a QTL-study on trichome density of cotton, one QTL with major phenotypic effect and a few with smaller effects were found (Wright et al. 1999). Thus, a few genes with major effect may influence variation in trichome number in several species.

Crosses between glabrous and trichome-producing plants yielded trichome-producing plants with a markedly lower trichome number than those produced in crosses between trichome-producing plants. This suggests that the mutation causing glabrousness may influence the density of leaf trichomes in heterozygous trichome-producing plants. To further clarify the genetic basis of trichome number in *Arabidopsis lyrata*, we are currently employing both complex segregation analysis (Lynch and Walsh 1998), and QTL- and candidate gene approaches.

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