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Phenotypic plasticity in *Saxifraga osloensis*: comparisons among populations

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SUMMARY

In a laboratory experiment the variation in plasticity of traits and trait mean values among populations of *Saxifraga osloensis* was examined. *S. osloensis* is a winter annual plant of allopolyploid origin, endemic to Scandinavia. Five populations from different parts of the species distribution range were grown in three treatments, differing in temperature and water availability. Most traits were plastic in response to the treatments. The pattern of plasticity varied among the populations, as well as the mean values of the traits. There was some correspondence in differentiation between the trait mean values and the plasticity of the traits. The pattern of differentiation was consistent with geographical distances between the populations. Correlation coefficients between traits were estimated for all populations. The start of flowering was correlated to the initial growth rate. The production of capsules and the number of seeds per capsule were not dependent on any of the other measured traits. There were no indications of buffering of reproductive traits by plasticity in other traits. The results are discussed in relation to local weather conditions at the population sites, but no consistent conclusions about environmental adaptation can be drawn.

Key-words: phenotypic plasticity, polyploidy, population differentiation, *Saxifraga osloensis*, Scandinavia.

INTRODUCTION

Phenotypic plasticity is a common feature of all species, and is of utmost evolutionary importance in plants due to their sedentary life-style (Bradshaw 1965). As phenotypic plasticity gives rise to a non-heritable variation, it may reduce the coupling between genotype and phenotype, and hence the impact of selection (Levin 1988). It has been discussed whether phenotypic plasticity and genetic variation can replace each other as means to cope with a spatially and temporally heterogeneous environment (Schlichting 1986; Sultan 1987). Implicitly, one then assumes that reduced selection decreases the amount of genetic variation. There is, however, no simple correlation between selection and amounts of genetic variation (e.g. Stearns 1992). Furthermore, the objectives for finding a relationship are unclear, as genetic variability is a characteristic of the population, while plasticity is a characteristic of the individual (Schlichting 1986). There are few studies that have found a relationship between plasticity and genetic variation (Jain 1979), and others, e.g. Scheiner & Goodnight (1984), have found no relationship.

Levin (1988) suggested that plastic variation and genetic variation instead might be positively correlated, both responding to selection for increased variation in a heterogeneous environment. Much of the environmental variation is too fine-scale and to unpredictable to be tracked genetically, and instead plasticity can be expected to be the means of adaptation (Sultan 1987).

Phenotypic plasticity is not always adaptive (Bradshaw 1965; Schlichting 1986). Traits highly correlated to fitness would, in some circumstances, be buffered from fluctuations in the environment instead, to ensure reproduction under severe conditions (Marshall *et al.* 1986; Taylor & Aarssen 1988). Stability in reproductive traits does not exclude plasticity, as the mechanism to achieve stability in reproductive traits can be plasticity in physiological traits (Bradshaw 1965).

This paper presents the results of a laboratory experiment on phenotypic variation within and among five populations of *Saxifraga osloensis* Knaben. The main questions are: (i) In what degree are the populations plastic in growth and reproductive traits? (ii) How much are the populations differentiated from each other in trait mean values and in the plasticity of these traits? An additional question is to what extent the differentiation is consistent with geographical distances between the populations. The study is one part of a project concerning various aspects of the population biology and evolution of allopolyploid *S. osloensis*. The species is one of few endemic plants in Scandinavia. Polyploid species have often been assumed to be more plastic than their diploid relatives, even though few studies have confirmed that connection (Thompson & Lumaret 1992). Nilsson (1995a) found no allozyme variation within populations of *S. osloensis*, and only small amounts of variation among populations. This suggests that phenotypic plasticity may be the only way for this species to cope with a variable environment. Weather has a marked influence on the population dynamics of *S. osloensis* (Nilsson 1995b), and is thus probably a strong selective force.

To design an experiment which aims to compare variation on several hierarchical levels is a difficult task, in that the number of replicates multiplies for each additional level. This usually leads to a decreased number of replicates on each hierarchical level as the number of hierarchical levels increases. In this study the inclusion of the species level (several populations) led to a reduced number of replicates on the population and individual levels. As a consequence, the implications of this study are on the level of species and population rather than on the level of individual.

MATERIALS AND METHODS

Study species

Saxifraga osloensis is an allopolyploid species with *S. tridactylites* and *S. adscendens* as the parental species (Knaben 1954; Nilsson 1995a). The fact that *S. osloensis* is endemic for Scandinavia indicates that the speciation occurred in connection with the recolonization of Scandinavia by plants after the last glaciation. *S. osloensis* grows on limestone rocks covered with a very thin soil layer. Most of the individuals show a winter-annual life cycle, i.e. seed germination occurs in late summer and early autumn, and flowering and capsule production occur in spring. However, a low proportion of plants emerge in spring (Nilsson 1995). These plants have a much shorter life-span, as they perform the whole 'above-ground' life-cycle during spring. The seeds are primarily dispersed by

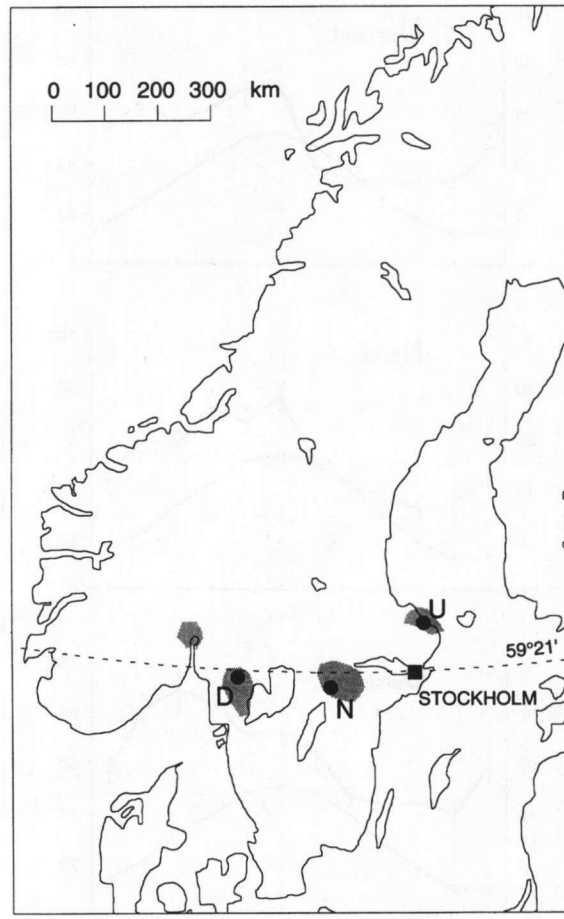


Fig. 1. Map of Scandinavia showing the sites of the populations of *Saxifraga osloensis*. D denotes Dalsland, N Närke and U Uppland (all provinces of Sweden). Three populations from Uppland were included in the study, U1–U3. One population each was included from Dalsland, D, and Närke, N. The shaded areas show the geographical distribution of the species.

gravity, but rain water can be a secondary dispersal agent. Self-fertilization occurs easily when flowers are bagged in the glasshouse. In an experiment, anthers were found to shed their pollen when the corolla was still closed (unpublished results), which suggests that self-fertilization is the common mode of breeding.

Description of populations

Seeds were collected in spring 1990 at five localities in Sweden, here called populations D, N, U1, U2 and U3 (D denotes Province of Dalsland, N Province of Närke, and U Province of Uppland) (Fig. 1). The populations were chosen in order to cover a large part of the species geographical range in Sweden. The D, N and U areas are separated from each other by distances of hundreds of km. The U populations are situated *c.* 10 km from each other. Mean monthly values for temperature and precipitation within the three areas (D, N and U) are given in Fig. 2.

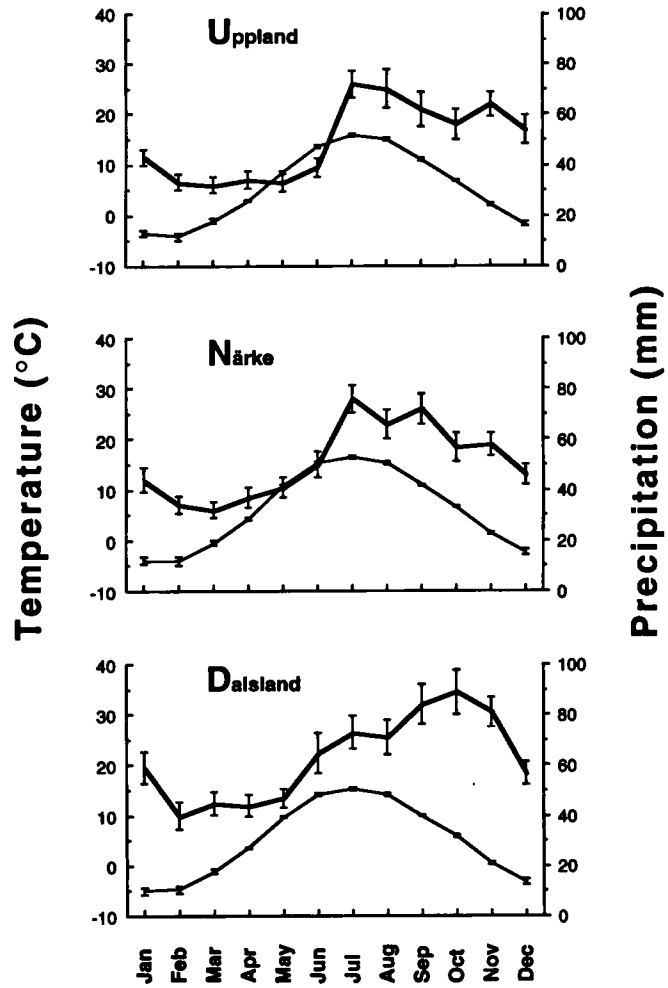


Fig. 2. Mean monthly values and standard error of means for temperature (°C) and precipitation (mm) at three meteorological stations (Uppland: Singö, Närke: Örebro, Dalsland: Blomskog). Temperature curves are denoted by thin lines, and precipitation curves by thick lines. A temperature curve close to or above the precipitation curve indicates drought. The statistics concern the years 1961–90. The values were obtained from the Swedish Meteorological and Hydrological Institute.

Experimental design

At each locality, 50 plants were chosen for seed collection. The chosen plants were evenly distributed within the populations. The seeds were kept separate for each plant to enable comparison between the performance of genotypes in different treatments. Sibs are the nearest equivalent to genotype in a non-clonal species. As self-fertilization occurs in *S. osloensis*, the sibs will often be full-sibs. The lack of allozyme variation within the populations (Nilsson 1995a), suggests that all individuals within a population are closely related. The seeds were germinated on filter paper in Petri dishes in a growth cabinet at 25°C day temperature (12 h) and 5°C night temperature (12 h). Thirty 'genotypes' from each population were used in the subsequent experiment. As the treatments were separated in time, the germination procedure was repeated for each

treatment. When possible the same genotypes were represented once in each treatment (this was the case for 18 genotypes from population D, 23 from N, 21 from U1, 18 from U2, and 23 from U3). Full representation failed because of low germinability in some cases (probably because the seeds were not fully developed when collected in field).

Each seedling was planted in a pot made of a plastic bottle with a diameter of 5 cm, and a height of 6 cm. In each pot, 5·0 g horticultural clay pellets were placed at bottom, and on top 68·0 g of a soil mixture containing 47% volume garden soil, 47% sand and 6% lime, giving a pH of *c.* 7·3. The initial weight, including the weight of the pot, was 82 g. Without any water added this represents rather dry conditions, even if the garden soil in the mixture contained small amounts of moisture. During the planting period the plants were watered twice a week, each time up to a total weight of 100 g per pot. During the 2 weeks following planting the temperature was kept to 21°C day temperature (12 h) and 8°C night temperature (12 h). The pots were watered up to a total weight of 95 g per pot twice a week. These conditions were assumed to represent a low-stress environment for the plants. The experiment was differentiated into three treatments in the third week after planting. Because all seeds did not germinate simultaneously, the planting period was extended over 1–2 weeks.

Variation in two factors, temperature and moisture, gave three treatments. The treatments were chosen in order to roughly correspond to naturally occurring conditions.

Treatment I: warm, moist conditions. Temperature was kept to 8°C at night (12 h) and to 21°C during the day (12 h). The pots were watered twice a week up to 95 g total weight per pot.

Treatment II: warm, dry conditions. Temperature as in treatment I; watering once a week up to 90 g total weight per pot.

Treatment III: cold, moist conditions. Temperature was kept to 15°C during the day and 4°C at night; watering twice a week up to 95 g total weight per pot. Because of lower temperature the pots did not dry up as much as in treatment I, despite the same watering conditions.

The populations were segregated in the growth cabinet, but rotated during the experiment to avoid problems with different conditions in different parts of the growth cabinet. The treatments were performed in the same growth cabinet, but due to limited space they had to be separated in time. Each treatment was run for 7 months.

The light conditions were the same in all treatments. The day length was gradually increased through the experiment to initiate flowering. During the planting period and the following 2 weeks, the lengths of day and night were 12 h each. From week 3 until week 11 day length was gradually increased from 14 to 18·5 hours. This increase in day length is consistent with the natural change from the end of April to the end of June at the latitude of Stockholm (59°21′N; see Fig. 1). The first flower was bagged to prevent cross-fertilization, thereby making it possible to compare seed set under the same conditions. Iron solution was supplied to the pots after 2 months, and horticultural fertilizer after 3 months.

Measurements

The diameter of the rosettes was measured regularly on four occasions during the first 2 months. The observation days were not exactly the same in all treatments; an effect of

the separation of treatments in time. Interpolations between the measured values gave standardized values for size on day 35 and day 55 after planting. The day when the first flower appeared was noted. When the first flower was developed to a ripe capsule it was collected, and its seeds were counted. The number of capsules was counted 1 month after the appearance of the first flower, and then the plants were harvested for determination of the dry weight. One single plant (in population N, treatment III) did not survive day 14 after planting, when the differentiation into treatments started, and was not included in the analyses.

Statistical analyses

The amounts of plasticity were estimated by coefficients of variance (CV). The use of CVs is advocated by, e.g. Schlichting (1986). The advantage, in comparison with variance components of the ANOVA, is that the CVs are standardized and thus can be compared between traits. CV_{within} (treatments) was calculated as the mean of CVs within each treatment. CV_{among} (treatments) was calculated as the CV of the mean values of each treatment.

Whether a plant flowers or not is a qualitative trait, and means and standard deviations make no sense in such a case. Yet, to be able to discuss the plasticity of this trait, I have used the proportions of reproductive plants in each population in each treatment as mean values of the probability to start flowering (called reproductive probability). These values were then used to calculated the CV_{among} in the same way as described above. Differences in proportions of reproductive plants among treatments and populations were tested by a log-linear model.

For quantitative traits, the effects of treatment, population, and the interaction treatment by population were estimated by a two-way ANOVA. Differences between groups were tested by the Tukey–Kramer test. The interaction term in an ANOVA cannot be estimated if any cell in the matrix (of factors) is empty. As population U2 did not flower at all in treatment II, all values of traits related to reproduction are missing. In this case, the interaction term was estimated by first excluding population U2, and then instead treatment II. If incongruences appeared in probability values between the models, the value presented was chosen in a conservative manner. Pearson correlation analyses were used for detection of relationships between traits.

To better fit the normal distribution curve, the trait 'number of capsules per plant' was log transformed, and the trait 'number of seeds per capsule' was square root transformed. All statistical computations were performed in the statistical module of SYSTAT (ver. 5.2 for Macintosh, Evanston IL, Systat Inc., 1992). The tables and the figures of this article present some selected descriptive statistics, and the outcome of the statistical tests. Summary statistics and the mean square- and *F*-values of the ANOVAs are given in Appendix.

RESULTS

Pattern of plasticity

The pattern of plasticity in each trait and each population is shown in Fig. 3. The diagrams enable comparison of the amount of plasticity and the pattern of plasticity among populations for each trait separately. It is also possible to make comparisons between traits, but only in pattern since the scale on the *y*-axes are not the same. For

comparisons of amount of plasticity the given coefficients of variation among populations (CV_{among}) are more appropriate. The amount of variation within populations are both given by the error-bars in the diagrams and by the coefficients of variation within populations (CV_{within}). The model column shows whether there are any significant effects of treatments over all populations, i.e. plasticity, and whether there is any significant interaction term (treatment by population), i.e. differences in plastic response between populations.

All traits, except 'seeds per capsule', were plastic in response to the treatments, as shown by the significant differences among treatments. The trait 'size at day 55' showed large amounts of plasticity in all populations. In some of the traits ('size at day 35', 'plant weight' and 'capsule production') the treatment effect was only expressed between two of the treatments. The variation within treatments (CV_{within}) was in many cases larger than the variation among treatments (CV_{among}), which weakens the estimate of amounts of plasticity. In 'size at day 35' and 'capsule production' the variation within treatments was in all populations larger than the variation among treatments. The trait 'seeds per capsule' had generally higher coefficients of variation within than among treatments.

There were large differences in reproductive probability among the treatments, especially in the U populations. Noteworthy are the extremely low values in treatment III. In population U2 there were no reproductive plants at all in that treatment. The low reproductive probabilities in the U populations were mainly an effect of a high proportion of plants remaining vegetative (Table 1). In population D and N, high mortality risks decreased the reproductive probability.

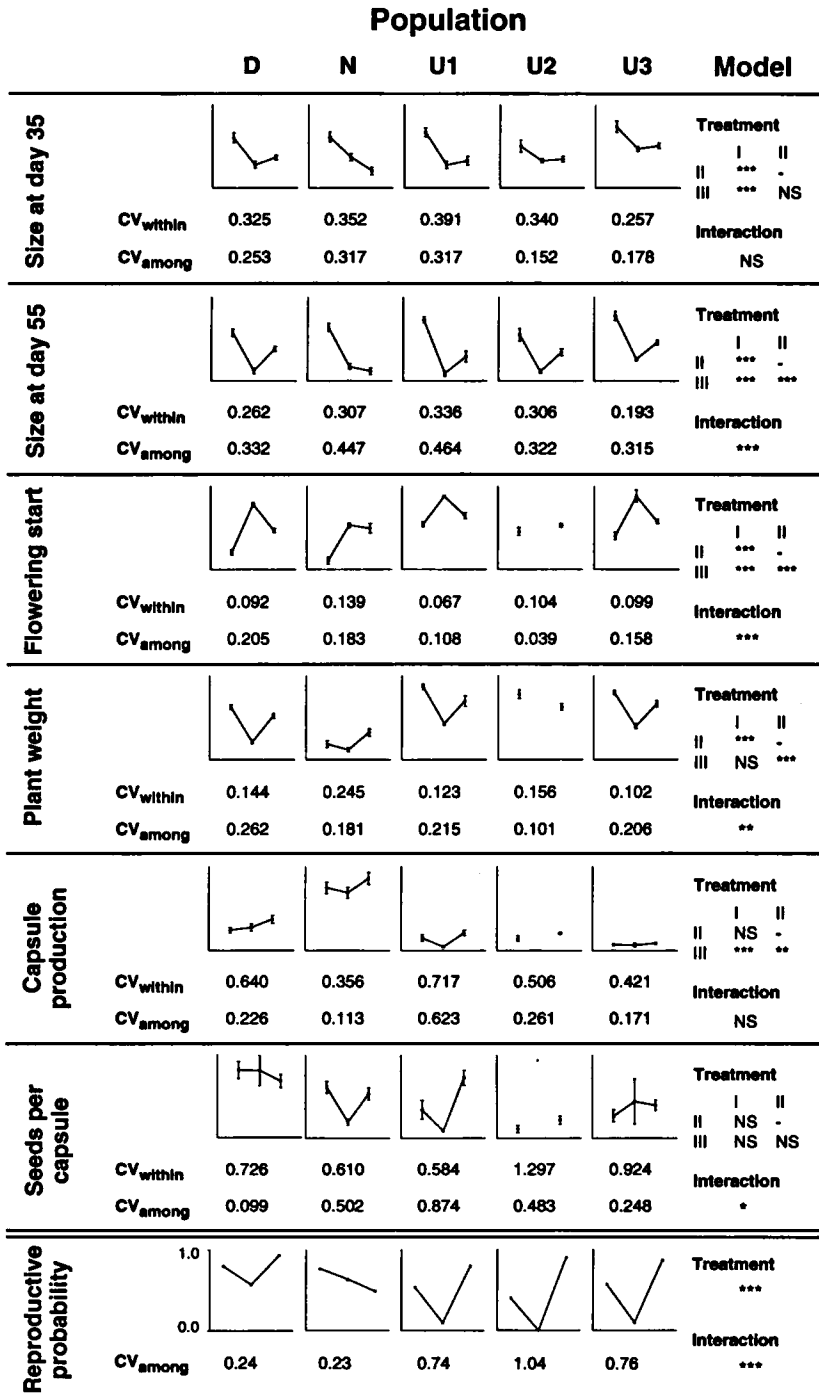
There were several significant correlations between the traits (Table 2). Correlations with the reproductive traits are of particular interest as they represent different measures of fitness. Size, at both day 35 and day 55, was significantly correlated to flowering start in all populations except U2. Larger plants flowered earlier than smaller plants. In population D, start of flowering and final plant weight were also significantly correlated. There were no correlations to the reproductive traits 'capsule production' and 'seeds per capsule' in any of the populations.

Differences in trait means among populations

There were genetic differences in trait mean values among the populations (Table 3). Most remarkable is the differentiation of population D and N from the U populations, in almost all measured traits. The plants of population D and N were much lighter and produced more capsules. Hence, their reproductive allocation was higher. Most outstanding was population N with the lowest weight and the highest capsule production. The U populations were to a low degree differentiated from each other. An exception is the significantly higher growth rate during the first 55 days of population U3 compared to all other populations.

Differences in plastic response among populations

The plastic response diagrams in Fig. 3 show that population N more than the other populations deviated from the general pattern of plasticity. This deviation explains to a great extent the significant interaction terms in 'size at day 55', 'start of flowering', 'plant weight', and 'reproductive probability'. For all plants from population N, treatment II was not the overall worst treatment. The start of flowering was almost


Population
D
N
U1
U2
U3
Model
Size at day 35
CV within 0.325 0.352 0.391 0.340 0.257
CV among 0.253 0.317 0.317 0.152 0.178
Treatment
I II
II *** -
III *** NS
Interaction
NS
Size at day 55
CV within 0.262 0.307 0.336 0.306 0.193
CV among 0.332 0.447 0.464 0.322 0.315
Treatment
I II
II *** -
III *** ***
Interaction
***
Flowering start
CV within 0.092 0.139 0.067 0.104 0.099
CV among 0.205 0.183 0.108 0.039 0.158
Treatment
I II
II *** -
III *** ***
Interaction
***
Plant weight
CV within 0.144 0.245 0.123 0.156 0.102
CV among 0.262 0.181 0.215 0.101 0.206
Treatment
I II
II *** -
III NS ***
Interaction
**
Capsule production
CV within 0.640 0.356 0.717 0.506 0.421
CV among 0.226 0.113 0.623 0.261 0.171
Treatment
I II
II NS -
III *** **
Interaction
NS
Seeds per capsule
CV within 0.726 0.610 0.584 1.297 0.924
CV among 0.099 0.502 0.874 0.483 0.248
Treatment
I II
II NS -
III NS NS
Interaction
*
Reproductive probability
1.0
0.0
CV among 0.24 0.23 0.74 1.04 0.76
Treatment
***
Interaction
***

the same in treatments II and III. In comparison with the other populations the flowering start in treatment II was much earlier in population N than in the other populations. As treatment II represented the warmest and driest conditions, population N seems to be the relatively best adapted to these conditions. In treatment II, the plant size of population N was notably smaller than of the other populations. The final plant weight of population N in all treatments was less than that of the other populations.

DISCUSSION

All investigated traits, except the number of seeds per capsule, were plastic across the treatments. The number of seeds showed high amounts of variation within treatments, which can explain the lack of significant variation among treatments. The large within-treatment variation in several traits makes the interpretation of amounts of plasticity problematic. Large variation within treatments weakens the estimate of variation among treatments, as the actual value of the mean becomes more uncertain. However, the ANOVA model takes variation on all levels into consideration when estimating effects. The coefficients of variation must only be used for comparisons when there is a significant treatment effect in the ANOVA. As the genotypes were not replicated, we could not determine whether the within-treatment variation only had a genetic component, or if there was an added component of noise.

Clearly, there were differences in amounts and patterns of plasticity among the populations. The variation in plasticity among populations of *S. osloensis* agrees with studies of other species (e.g. Taylor & Aarssen 1988; Schlichting & Levin 1990). The differentiation in trait means among the populations of *S. osloensis* is consistent with geographical distances (see Fig. 1). The three populations from Uppland (U1–U3) are slightly differentiated from each other, while the Uppland populations together, the population from Närke (N), and the population from Dalsland (D) are considerably differentiated from each other. The process of differentiation can have started at the earliest 10 000 years BP, when the ice retreated from Scandinavia. This gives maximally 10 000 generations. I have discussed elsewhere (Nilsson 1995) the possibility that *S. osloensis* has a persistent seedbank, which would decrease the number of generations. However, the number of generations should be enough for substantial evolutionary change. Life-history traits, such as those measured in this study, can be assumed to be selected in slightly different directions at different sites, due mainly to variation in climate. Alternatively, founder effects in connection with colonization of the different sites, or later genetic drift due to population bottle-necks, may have caused the differentiation.

My results show some correspondence in differentiation between the trait means and the plasticity of the traits. Population N was the most differentiated in mean values from

Fig. 3. Pattern of plasticity in each trait and each population. Plastic responses are visualized in the diagrams. Mean values for treatments I, II and III in order from left to right in each diagram. The error bars are the standard errors of means. The scale of the *y*-axes is adjusted in order to use the whole range of the *y*-axis. In each trait the scale is the same for all populations. CV_{within} and CV_{among} are the coefficients of variation within and among treatments. The model column shows significances of the effects of treatment and interaction (treatment × population). The following significance levels were used: ***$P<0{\cdot}001$, **$P<0{\cdot}01$, *$P<0{\cdot}05$, NS, $P>0{\cdot}05$.

Table 1. Mortality before reproductive stage, and the proportion of plants that remained in vegetative stage during the experiment

	D		N		U1	
Treatment	Mortality	Proportion vegetative	Mortality	Proportion vegetative	Mortality	Proportion vegetative
I	0·20	0·00	0·23	0·00	0·07	0·40
II	0·27	0·17	0·33	0·03	0·17	0·73
III	0·03	0·03	0·31	0·21	0·10	0·10

	U2		U3	
Treatment	Mortality	Proportion vegetative	Mortality	Proportion vegetative
I	0·17	0·43	0·13	0·30
II	0·07	0·93	0·07	0·83
III	0·07	0·03	0·03	0·10

the other populations, and population N was also the most different in plastic response. Population N was much better adapted to treatment II than the other populations. Treatment II represents warm and dry conditions. All the investigated populations experience drought under natural conditions in spring, when the precipitation is generally low and the temperature rises (Fig. 2). For plants growing on rocks, the availability of water in one day is highly correlated to the same day's precipitation and temperature. The drought is most profound in the provinces of Närke and Uppland. Although the mean temperature is slightly higher in Närke than in Uppland during spring, both populations can be expected to be adapted to very similar environments. This makes it difficult to explain the differences in trait means and plasticity between the N and U populations. The province of Dalsland is in comparison the wettest area. The reproductive probability as well as the capsule production of population D are highest in treatment III, representing cold and moist conditions. However, the U populations have also the highest values in these traits in treatment III, although the natural conditions in Uppland are considerably dryer than in Dalsland. The variation among populations in amounts of plasticity cannot be explained by the weather, since the variation in temperature and precipitation is of the same magnitude in all provinces (see the error bars in Fig. 2).

Stability, especially in reproductive output, may be the most adaptive option in many cases (Marshall *et al.* 1986; Taylor & Aarssen 1988). Sultan & Bazzaz (1993) found constancy in functional traits across a nutrient gradient. In my study, population N was the least plastic in capsule production, although it had the overall highest mean values in that trait. Population N was also the least variable in reproductive probability, but here the other populations had higher values in treatment III. Plasticity in some traits can be a way to buffer reproductive traits (Marshall *et al.* 1986). This does not seem to

Table 2. Pearson pairwise correlations between traits within the populations. The correlations were estimated across the three treatments. Asterisks denote Bonferroni corrected significance levels

	Size at day 35	Size at day 55	Start of flowering	Plant weight	Capsule production
D					
Size at day 55	0·865***				
Start of flowering	−0·420**	−0·724***			
Plant weight	0·322	0·622***	−0·668***		
Capsule production	−0·079	−0·015	−0·120	−0·031	
Seeds per capsule	0·317	0·324	−0·152	0·044	0·234
N					
Size at day 55	0·884***				
Start of flowering	−0·777***	−0·935***			
Plant weight	−0·521**	−0·393	0·356		
Capsule production	0·232	0·189	−0·226	0·245	
Seeds per capsule	0·019	0·274	−0·385	0·049	0·100
U1					
Size at day 55	0·908***				
Start of flowering	−0·607***	−0·692***			
Plant weight	0·474	0·639**	−0·079		
Capsule production	0·035	0·186	−0·374	0·657	
Seeds per capsule	−0·178	−0·180	−0·077	0·097	0·415
U2					
Size at day 55	0·904***				
Start of flowering	−0·442	−0·528*			
Plant weight	0·294	0·360	0·180		
Capsule production	−0·327	−0·395	−0·157	0·070	
Seeds per capsule	−0·180	−0·196	−0·294	−0·420	0·185
U3					
Size at day 55	0·869***				
Start of flowering	−0·502**	−0·661***			
Plant weight	0·468*	0·443	−0·167		
Capsule production	−0·054	−0·173	−0·134	−0·117	
Seeds per capsule	0·009	−0·081	−0·190	−0·303	−0·062

***$P<0·001$, **$P<0·01$, *$P<0·05$.

be the case in population N, however, since the amounts of plasticity in the other traits were on average the same in population N as in the other populations.

How much of the plasticity in *S. osloensis* is a consequence of the polyploid state? No answer can be given here, since the diploid progenitors were not examined. Nilsson (1995) argued that the extended germination period in *S. osloensis* could be an effect of polyploidy. Whether polyploid species actually are more plastic is a much discussed question (Thompson & Lumaret 1992). Macdonald *et al.* (1988) found larger amounts of plasticity in diploids than in polyploids in the *Stellaria longipes* complex. Garbutt & Bazzaz (1983) reported very similar amounts of plasticity in diploid and polyploid populations of *Phlox drummondii*. The inclusion of the diploid parental species of

Table 3. Significant differences between populations in the measured traits. 'Growth' is used collectively for 'size at day 35' and 'size at day 55', as the differences were the same at both occasions. Differences were tested by the Tukey–Kramer test, as part of the estimation of a two-way ANOVA with the factors treatment and population

	D	N	U1	U2
N	Weight*** Capsules***			
U1	Flowering*** Weight*** Capsules***	Flowering*** Weight*** Capsules***		
U2	Flowering** Weight* Capsules** Seeds***	Flowering*** Weight*** Capsules*** Seeds***	Flowering* Seeds**	
U3	Growth*** Flowering** Weight** Capsules*** Seeds**	Growth*** Flowering*** Weight*** Capsules***	Growth***	Growth*** Capsules***

***$P<0.001$, **$P<0.01$, *$P<0.05$.

S. osloensis in a similar experiment to the one presented here would clarify the role of polyploidy in the evolution of phenotypic plasticity.

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REFERENCES

Bradshaw, A.D. (1965): Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* **13:** 115–155.

Garbutt, K. & Bazzaz, F.A. (1983): Leaf demography, flower production and biomass of diploid and tetraploid populations of *Phlox drummondii* Hook. on a soil moisture gradient. *New Phytol.* **93:** 1129–1141.

Jain, S.K. (1979): Adaptive strategies: polymorphism, plasticity, and homeostasis. In: Solbrig, O.T., Jain, S., Johnson, G.B. & Raven, P.H. (eds) *Topics in Plant Population Biology*. 160–187. Columbia University Press, New York.

Knaben, G. (1954): *Saxifraga osloensis* n. sp., a tetraploid species of the Tridactylites section. *Nytt Mag. Bot.* **3:** 117–138.

Levin, D.A. (1988): Plasticity, canalization and evolutionary stasis in plants. In: Davy, A.J., Hutchings, M.J. & Watkinson, A.R. (eds) *Plant Population Ecology*. 35–45. Blackwell Scientific Publications, Oxford.

Macdonald, S.E., Chinnappa, C.C. & Reid, D.M. (1988): Evolution of phenotypic plasticity in the *Stellaria longipes* complex: comparisons among cytotypes and habitats. *Evolution* **42:** 1036–1046.

Marshall, D.L., Levin, D.A. & Fowler, N.L. (1986): Plasticity of yield components in response to stress in *Sesbania macrocarpa* and *Sesbania vesicaria* (Leguminosae). *Am. Nat.* **127:** 508–521.

Nilsson, T. (1995a): *Population biology, biogeography and evolution of* Saxifraga osloensis, *a polyploid plant endemic to Scandinavia.* Doctoral thesis, Stockholm University.

Nilsson, T. (1995b): Density-dependent processes and the importance of periodic germination in the

winter annual plant *Saxifraga osloensis*. *Ecography* **18**: 131–137.

Scheiner, S.M. & Goodnight, C.J. (1984): The comparison of phenotypic plasticity and genetic variation in populations of the grass *Danthonia spicata*. *Evolution* **38**: 845–855.

Schlichting, C.D. (1986): The evolution of phenotypic plasticity in plants. *Ann. Rev. Ecol. Syst.* **17**: 667–693.

Schlichting, C.D. & Levin, D.A. (1990): Phenotypic plasticity in *Phlox*. III. Variation among natural populations of *P. drummondii*. *J. Evol. Biol.* **3**: 411–428.

Stearns, S.C. (1992): *The Evolution of Life Histories*. Oxford University Press, Oxford.

Sultan, S.E. (1987): Evolutionary implications of phenotypic plasticity in plants. *Evolutionary Biology* **21**: 127–178.

Sultan, S.E. & Bazzaz, F.A. (1993): Phenotypic plasticity in *Polygonum persicaria*. III. The evolution of ecological breadth for nutrient environment. *Evolution* **47**: 1050–1071.

Taylor, D.R. & Aarssen, L.W. (1988): An interpretation of phenotypic plasticity in *Agropyron repens* (Graminae). *Am. J. Bot.* **75**: 401–413.

Thompson, J.D. & Lumaret, R. (1992): The evolutionary dynamics of polyploid plants: origins, establishment and persistence. *Trends Ecol. Evol.* **7**: 302–307.

APPENDIX

(a) Summary statistics of trait values in the different populations and treatments

		D			N			U1			U2			U3		
	Treatment	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD
Size at day 35 (mm)	I	24	17·0	5·8	23	17·2	6·0	28	18·4	5·5	28	15·0	7·8	27	19·8	7·1
	II	26	10·5	4·1	23	12·3	4·2	27	10·5	4·3	26	11·5	2·3	29	14·4	2·8
	III	28	12·2	2·9	14	9·1	3·3	29	11·5	5·4	29	11·9	3·6	27	15·1	3·3
Size at day 55 (mm)	I	24	27·4	6·5	23	29·3	7·1	28	31·9	5·5	26	26·5	11·3	26	33·4	7·8
	II	23	13·6	4·9	22	15·2	5·0	25	12·7	4·4	26	13·6	2·9	28	17·8	3·0
	III	26	21·5	4·1	14	13·5	4·7	23	18·8	9·2	21	20·3	5·6	26	23·8	4·2
Start of flowering (days)	I	24	123·0	15·6	23	112·0	21·3	15	159·9	13·4	13	150·2	18·8	17	144·5	20·5
	II	17	185·9	10·7	19	158·8	13·2	3	197·0	1·0	0	—	—	3	197·0	13·5
	III	28	151·5	13·9	14	154·7	22·5	25	171·6	19·2	27	158·7	13·1	26	163·4	14·3
Plant weight (mg)	I	23	803·8	101·2	20	448·2	151·7	6	996·7	66·3	8	927·2	108·0	11	940·3	62·2
	II	17	469·4	72·2	15	393·4	67·6	3	642·3	25·9	0	—	—	3	617·7	41·0
	III	28	718·7	109·9	14	559·1	125·8	20	860·3	225·3	27	803·4	157·6	25	832·9	144·9
Number of capsules per plant	I	24	6·4	4·7	21	21·5	9·2	15	3·6	4·2	13	3·3	3·3	17	1·1	1·0
	II	17	7·3	5·1	15	19·8	7·5	3	0·3	0·6	0	—	—	3	1·0	1·0
	III	28	10·3	7·4	14	24·9	7·7	25	5·4	5·1	27	5·3	1·6	26	1·7	0·8
Number of seeds per capsule	I	23	101·6	63·9	21	76·4	40·8	12	42·8	49·2	12	13·4	19·4	16	33·1	36·8
	II	16	100·7	91·3	19	23·8	19·3	1	10·0	—	0	—	—	2	55·0	48·1
	III	28	84·8	54·3	13	66·4	32·2	23	90·5	54·5	27	27·3	31·4	26	49·5	39·0

(b) Mean square (MS) and *F*-values of the two-way ANOVAs in the measured traits. In each trait the effects of treatment, population, the interaction treatment × population, and the error term are given. By ordinary model is meant an analysis with the interaction term included. In the reproductive traits one cell in the matrix of the model was missing, population U2 in treatment II. An ordinary two-way ANOVA with the effect of interaction included cannot be estimated when one cell is missing. In these cases three models were estimated: (i) without interaction term, (ii) with treatment II excluded, and (iii) with population U2 excluded

		Treatment (df=2)*		Population (df=4)†		Treat. × Pop. (df=8)‡		Error	
	Model	MS	*F*	MS	*F*	MS	*F*	df	MS
Size at day 35 (mm)	Ordinary	1312·9	55·50	184·4	7·802	38·01	1·608	373	23·64
Size at day 55 (mm)	Ordinary	7375·6	192·51	355·9	9·289	133·56	3·486	345	38·31
Start of flowering (days after planting)	No interaction	35 108	116·66	8906	29·593	—	—	247	300·95
	Excluded treatment	23 897	81·53	7037	24·010	1748	5·965	202	293·09
	Excluded population	25 142	91·02	7423	26·872	1312	4·750	202	276·21
Plant weight (mg)	No interaction	703 748	36·09	895 104	45·90	—	—	213	19 502
	Excluded treatment	164 491	8·20	860 743	42·90	79 404	3·958	172	20 062
	Excluded population	510 774	30·73	852 302	51·27	86 104	5·180	173	16 622
Number of capsules per plant (log)	No interaction	1·063	13·58	6·740	86·11	—	—	241	0·0783
	Excluded treatment	1·691	21·81	5·230	67·46	0·0419	0·540	200	0·0775
	Excluded population	0·812	9·73	6·943	83·18	0·0871	1·043	196	0·0835
Number of seeds per capsule (sq. root)	No interaction	68·30	6·10	220·79	19·73	—	—	232	11·19
	Excluded treatment	66·18	6·67	196·96	19·85	28·81	2·903	191	9·92
	Excluded population	35·09	3·27	65·55	6·11	36·13	3·367	188	10·73

*When (one) treatment excluded, df=1.
†When (one) population excluded, df=3.
‡When (one) treatment excluded, df=4; when (one) population excluded, df=6.