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NOTES AND COMMENTS

Sex ratios in populations of *Geranium sylvaticum* in European Russia

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Introduction

Flowers of *Geranium sylvaticum* L. are normally hermaphroditic and have 10 stamens. Some flowers have reduced non-functional anthers or do not have anthers at all; these flowers are called female flowers. Flowers with 1–9 functional anthers are classified as intermediate (Asikainen & Mutikainen 2003). Such a reduction probably prevents self-fertilization and lets female flowers produce more seeds, or seeds with greater nutrient stores, which increases the population's fitness (Asikainen & Mutikainen 2003, 2005; Ramula & Mutikainen 2003). A negative correlation has been found between the frequency of female flowers and seed production of hermaphroditic flowers in *G. sylvaticum* populations (Asikainen & Mutikainen 2003). Given the importance of sex ratio to the reproductive biology of this species, this pattern warrants further investigation.

Finnish researchers have investigated the frequency of female flowers in 23 *Geranium sylvaticum* populations in Finland (Asikainen & Mutikainen 2003). The proportion of female flowers in these populations varied from 0.4 to 27.2% (11.5% on average) and was apparently dependent on habitat conditions; female flowers are less frequent in southern populations (Asikainen & Mutikainen 2003). Low numbers of 'intermediate' flowers were found in very low frequency (less then 1%) in less than half of the Southern Finland populations, and only one population had 42% of intermediate-type flowers. Northern populations, in contrast, showed higher frequencies of intermediate flowers. Sex ratio variation among populations may also be explained by ecological factors that affect the relative seed fitness of the two gender morphs (Asikainen & Mutikainen 2003).

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As *G. sylvaticum* is widely distributed in Europe and Asia, we decided to investigate other populations of this species to determine whether the latitudinal distribution pattern of flower type observed in Finland is a general pattern. We also attempted to check whether sex ratio variation between populations is caused by habitat conditions.

Materials and methods

The investigations were carried out during June and July 2003–2005 in the northern part of the Tver' region (N 58°15′, E 34°30′; 564 plants from 21 populations, Fig. 1) and in the northern part of the Murmansk region on the Barents Sea shore (N 69°10′, E 36°00′; 274 plants from four populations, Fig. 1). During this project, we followed the ecological definition of populations, as described in Waples and Gaggiotti (2006). We counted the number of fertile stamens for one flower from each flowering plant in the population. It was important to investigate flower buds instead of open flowers because anthers easily drop from the stamen filaments in the latter stages of flower development and this could cause an erroneous count of fertile stamen number. In addition, we inferred some characteristics of habitat conditions (light intensity, moisture, soil acidity and degree of soil mineralization) from modified Ellenberg tables (Hill *et al*. 1999), using lists of the most frequent vascular plant species in the locality.

The statistical analysis of our data was carried out in R statistical environment (R Development Core Team 2004). We used the standard deviation (SD) of the mean to show data variance around mean values.

Results

The regions investigated in the present study have obvious differences in the values of some edaphic factors

Fig. 1 Map of the investigated area. Crosses mark the investigated populations: 1, Tver′ region; 2, Murmansk region.

calculated from the Ellenberg tables. We observed low soil mineralization in the Murmansk region (2.0–3.0 points on the Ellenberg tables) compared to medium or high mineralization in the Tver′ region (3.5–7.5 points). Soil was moderately acid in the Murmansk region (3.0–5.0) and weakly acid or neutral in the localities from the Tver′ region (5.0–7.5).

We found no female flowers in any of the investigated populations in the Tver′ region; and we found only one female flower in the four investigated populations in the Murmansk region (Table 1).

The proportion of hermaphroditic flowers in the temperate Tver′ region is lower on average (mean ± SD: 57 ± 6%) than in the arctic Murmansk region (97 ± 0.5%) (Table 1). The proportion of hermaphroditic flowers in the Tver′ region depends on edaphic factors: we found a significant positive association between the proportion of hermaphroditic flowers in the population and moisture (Multiple r-squared = 0.21, $F = 5.18$, $P = 0.034$; Fig. 2), and a significant negative association between the frequency of hermaphroditic flowers and soil pH (multiple r-squared = 0.35, $F = 10.34$, $P = 0.005$; Fig. 3).

The proportion of 'intermediate' flowers in the population varies from 9 to 84% in the Tver′ region (43 ± 6% in average) and from 0 to 4% (1.5 ± 1%) in the Murmansk region (Table 1).

Discussion

In general, our data on the sex ratio in different populations of *G. sylvaticum* in European Russia corresponds poorly with the published data of Asikainen and Mutikainen (2003) on Finnish populations. Female flowers were much rarer in our study than was reported by Asikainen and Mutikainen (2003) for southern Finland. The proportion of hermaphroditic flowers was much more lower in the temperate region than in the arctic region, which is contrary to Asikainen and Mutikainen's (2003) findings. The Murmansk region is the only area where our results resemble the Finnish data (Asikainen & Mutikainen 2003) with respect to the low frequency of 'intermediate' flowers.

These differences could perhaps be explained by the different sizes of the populations (the Russian populations investigated in the present study are much smaller than the Finnish populations) because it is known from other plant species that variance in sex ratio increases inversely with population size (*Plantago maritima* investigations by Nilsson & Agren 2006). We may also have encountered temporal (Agren & Willson 1991) or longitudinal variation in the frequency of female flowers in populations of *G. sylvaticum*. Finally, the bias in the sex ratio in the populations could be explained if the Finnish researchers examined open flowers instead of flower buds (some anthers can drop from the stamen filaments leading to inflated estimates of intermediate and female flowers). However, Eija Asikainen (pers. comm. 2006) stated that in their investigations all stamens were accurately counted several times during flowering.

Thus, the geographical variation in female flower frequency in populations of *G. sylvaticum* seems to have more complex patterns than has been previously reported (Asikainen & Mutikainen 2003, 2005; Ramula & Mutikainen 2003). The frequency of female plants in gynodioecious populations may vary widely over relatively short distances (Couvet *et al*. 1990). Some stochastic processes could influence the sex ratio in small gynodioecious populations (Nilsson & Agren 2006). We hope that further investigations throughout the range of *G. sylvaticum,* with due attention to the stages of flower development, will provide further information on sex in *G. sylvaticum* populations.

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Table 1 Frequency of plants of different sexes

Region	Population number	No. plants	No. plants of a given sex† Female	'Intermediate'	Hermaphroditic
Tver' region	1	6	0 (0)	4 (66.7)	2 (33.3)
	2	18	0 (0)	15 (83.3)	3 (16.7)
	3	20	0 (0)	15 (75)	5 (25)
	4	16	0 (0)	11 (68.8)	5 (31.2)
	5	18	0 (0)	12 (66.7)	6 (33.3)
	6	40	0 (0)	15 (37.6)	25 (62.5)
	111	17	0 (0)	7 (41.2)	10 (58.8)
	201	26	0 (0)	5 (19.2)	21 (80.8)
	202	36	0 (0)	5 (13.9)	31 (86.1)
	203	28	0 (0)	4 (14.3)	24 (85.7)
	204	59	0 (0)	18 (30.5)	41 (69.5)
	205	14	0 (0)	3 (21.4)	11 (78.6)
	206	31	0 (0)	7 (22.6)	24 (77.4)
	207	18	0 (0)	6 (33.3)	12 (66.7)
	208	9	0 (0)	0 (0)	9 (100)
	209	8	0 (0)	1 (12.5)	7 (87.5)
	210	61	0 (0)	7 (11.5)	54 (88.5)
	211	33	0 (0)	0 (0)	33 (100)
	212	28	0 (0)	0 (0)	28 (100)
	213	23	0 (0)	2 (8.7)	21 (91.3)
	214	61	0 (0)	0 (0)	61 (100)
Murmansk region	221	108	1 (0.9)	3 (3.7)	104 (96.3)
	222	108	0 (0)	2 (1.9)	106 (98.1)
	223	41	0 (0)	0 (0)	41 (100)
	224	18	0 (0)	0 (0)	18 (100)

†Number of plants of a given sex (ratio of the number of plants of a given sex to the total plant number in the population [%]).

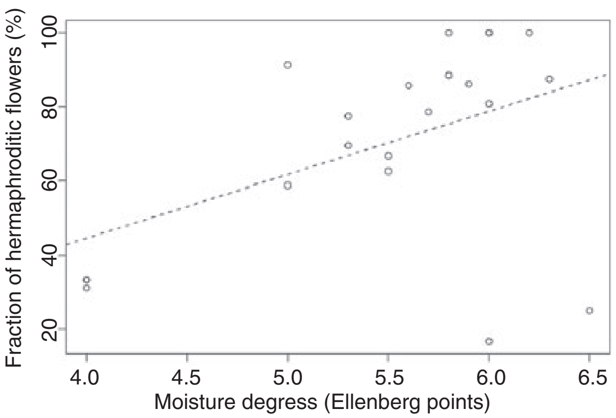

Fig. 2 Correlation between the proportion of hermaphroditic flowers in the population and the moisture level in the Tver' region. The dashed line is a linear regression ($y = 17x - 23.5$).

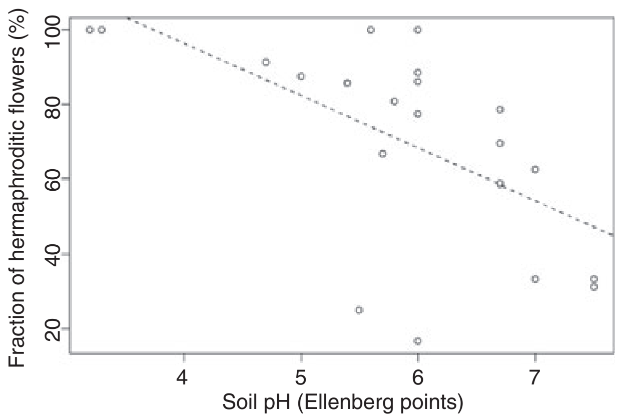

Fig. 3 Correlation between the proportion of hermaphroditic flowers in the population and soil pH in the Tver' region. The dashed line is a linear regression ($y = -14x + 152.5$).

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