

Structure and dynamics of *Saxifraga hirculus* L. populations

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Summarized data of many-year investigations of *Saxifraga hirculus* L. population dynamics, performed in the Kurtuvėnai Regional Park (Šiauliai and Kelmė districts) in 1999–2005 are presented. This plant is protected by international and national legal acts in many of the European countries. The results have shown that *S. hirculus* populations consist of individuals of different size, which in most cases have a single orthotropic floral shoot and a number of plagiotropic runners. The absolute majority of *S. hirculus* individuals in natural populations are of vegetative origin. The basic reasons for the rarity of the individuals of generative origin are the massive death of floral shoots from unknown factors and seed misformation, as well as specific *S. hirculus* seed germination requirements for the light and open substrata. In the study site, *S. hirculus* population is characterized by sprout number fluctuations expressed unevenly in different places of the population, mainly because of changes in the hydrological regime of the habitat (floods caused by beaver dams). In significantly flooded places these changes become disastrous and result in *S. hirculus* perishing. The hydrological changes of the habitat modify also the morphometric traits of essential structural elements of *S. hirculus* individuals. In the conditions of ecological stress (the higher level of water) nearly all indices gradually become lowered. The annual tendencies of *S. hirculus* morphometric changes are analogous to the development of floral shoots and runners. It takes several years for the initial state of a *S. hirculus* population to recover after normalization of the hydrological regime.

Key words: *Saxifraga hirculus*, many-year dynamics, structure of population, vegetative reproduction, Lithuania

INTRODUCTION

Saxifraga hirculus (Marsh saxifrage, *Rosidae*, *Saxifragaceae*) is a perennial rhizomatous herbaceous plant 10–50 cm high. In the botanical geographical respect, *S. hirculus* is a meridional alpine arctic continental species of a circumpolar distribution (Rothmaler et al., 1986). In the non-polar regions the distribution of *S. hirculus* is very fragmentary (Hulten, 1971, cit. from Dahlgaard, Warncke, 1995). In Lithuania, *S. hirculus* is a post-glacial relict; it occurs more often in the southeastern part of the country, although isolated habitats are known in Middle and West Lithuania (Lapelė, 1992).

S. hirculus is protected by international and national legal acts in numerous European countries (Lapelė, 1992; Ingelög et al., 1993). It is on the lists of Bern Convention Appendix I (1996) and Annex II of Habitats Directive (92/43/EEC). In Lithuania, *S. hirculus* has been protected since 1962. The indication of the prewar researchers (Dagys ir kt., 1934) that *S.*

hirculus was a frequent plant in Lithuania might have been not quite correct, because at that time the floristic picture of our country was only vaguely known. On the other hand, it is quite possible that at that time the number of habitats suitable for this species to flourish was larger, because the anthropogenization level of the country was much lower than at present. Today, *S. hirculus* is ascribed to Category 2 plants (rapidly becoming extinct) in the Lithuanian Red Book (Dėl į Lietuvos..., 2005). To our knowledge, no specific *S. hirculus* studies have been performed in Lithuania. As to the other countries, most abundant data have been collected about *S. hirculus* population structure (Ohlson, 1986; Olesen, Warncke, 1990) and reproductive processes (Dahlgaard, Warncke, 1995; Ohlson, 1988, 1989; Olesen, Warncke, 1989a, 1989b, 1989c).

The major goals of the present work were as follows: 1) to study the structural elements of the populations of *S. hirculus*; 2) to assess the impact of hydrological regime changes of the habitat on *S. hirculus*

population; 3) to summarize the recent data on many-year dynamics of *S. hirculus* population.

MATERIALS AND METHODS

The investigations of *S. hirculus* populations were carried out in the Šona landscape preserve in the Galvydiškės village environs, Kurtuvėnai Regional Park (Šiauliai and Kelmė districts). At the study site, *S. hirculus* is distributed over a territory of about 500 m² on a marshy bank of the Juodupis rivulet. The most abundant groups of *S. hirculus* plants grow at a distance of 20–50 m from the Juodupis rivulet. The geographical co-ordinates of the *S. hirculus* habitat: 55°47'01" N, 22°58'16" E. Analysis of geobotanical descriptions performed in 10² m plots has shown *S. hirculus* to be a component of the *Caricion davallianae* Klika 1934 community ascribed to the *Scheuchzerio-Caricetea nigrae* (Nordhagen 1936) R. Tx. 1937. The bush height is not pronounced, with rather frequent single not high *Salix cinerea* L. and *Betula pubescens* Ehrh. and *B. × aurata* Borkh. The mean projection covering of the herbage overground part is about 80%. The most stable and abundant community species are *Carex rostrata* Stokes, *C. lasiocarpa* Ehrh., *C. nigra* (L.) Reichard, *C. dioica* L., *Filipendula ulmaria* (L.) Maxim, *Galium uliginosum* L., *Caltha palustris* L., *Equisetum fluviatile* L., *Menyanthes trifoliata* L., *Oxycoccus palustris* Pers. The moss carpet is almost uninterrupted, with *Tomenthypnum nitens* (Hedw.) Loeske, *Aulacomium palustre* (Hedw.) Schwaegr., *Sphagnum teres* (Shimp.) Ångstr. and *S. warnstorffii* Russow prevailing.

The many-year dynamics of *S. hirculus* populations was studied by the repeated annual cartographic calculation method in eight permanent plots from 1999 till 2004. The area of the study plots was 0.25 m². The boundaries of the study plots were marked with wooden pegs. The cartographic calculation in the permanent plots was performed annually once per vegetation season in the period of the most intensive *S. hirculus* flowering at the end of August. The basic criteria of *S. hirculus* population assessment in the plots were: the number of floral shoots, the number and length of runners, the number of generative structures (flowers, buds and fruits), the height

of floral shoots, the number of leaves, the length and width of the longest leaf. The height of floral shoots and the length of runners were measured from the surface of moss carpet.

All data of the biometric measurements of morphological traits were treated statistically. Calculations were performed using Microsoft Excel software. Student's t test was employed to assess many-year changes of *S. hirculus* traits.

RESULTS AND DISCUSSION

Structural elements of populations of *S. hirculus*

As mentioned in Introduction, *S. hirculus* is a perennial rhizomatous plant (Fig. 1). Thin (0.6–0.8 mm in diameter) *S. hirculus* rhizomes run at a depth of 3–10 cm in the moss cover. Their length is 5–10 cm. Every year, at the beginning of summer, from the terminal or lower buds of the rhizomes on the surface of moss cover, usually a single orthotropic leafy floral shoot with flowers and several (one to 6) lateral, also leafy, runners appear; the latter run plagiotropically over the surface of moss cover. Rather often than not, only runners appear from the buds. The formation of lateral shoots proceeds gradually throughout the whole summer, therefore in autumn they differ in length. In autumn, after seed dispersion, the floral shoots of *S. hirculus* deteriorate, and the lateral plagiotropic shoots are partly covered with moss. The next year such *S. hirculus* runners do not develop leaves and function as rhizomes, and from axillary buds of the upper leaves again orthotropic floral shoots and plagiotropic runners appear. Thus, gradually complex *S. hirculus* individuals of various sizes are formed; their separate parts are interconnected, but later, following decomposition of the oldest rhizome parts, they separate from one another and function independently. It is impossible to detect visually the communicative ties among separate shoots in the perpetual plots in a long-term investigation, therefore in the present paper not separate individuals but floral shoots and runners are regarded as structural elements of *S. hirculus* populations.

In natural populations, the absolute majority of *S. hirculus* individuals are undoubtedly of vegetative ori-

Table 1. Statistical parameters of morphometric traits of *S. hirculus* flowering individuals in 1999

Trait	Mean	Median	Minimum	Maximum	Variance	Coef. of variation, %	Standard error
Height of floral shoots, cm	26.86	28.00	15.50	35.00	24.16	18.32	0.93
Length of longest leaf, mm	26.66	27.00	15.00	50.00	85.01	24.78	1.63
Width of longest leaf, mm	3.81	4.00	3.00	6.00	0.67	34.58	0.15
Number of leaves	16.75	16.50	8.00	27.00	17.23	21.52	0.78
Number of flowers	3.04	3.00	1.00	6.00	1.72	43.14	0.26
Length of runners, cm	3.65	4.00	0.20	9.00	5.59	64.80	0.39

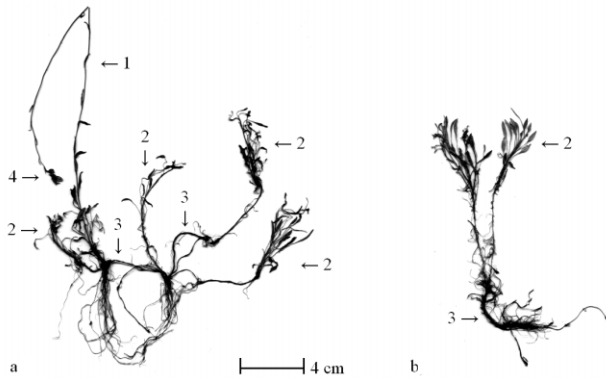


Fig. 1. Flowering (a) and vegetative (b) individuals of *Saxifraga hirculus* (herbarium specimens). 1 – floral shoot; 2 – runners; 3 – previous year runners turned into rhizomes; 4 – flower

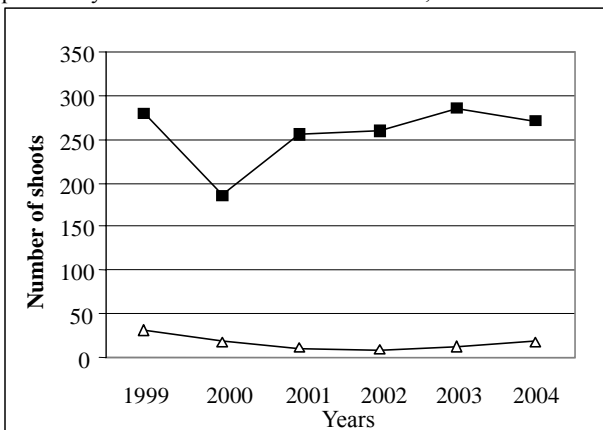


Fig. 2. Many-year variation in number of floral *S. hirculus* shoots (△) and total number of shoots and runners (■)

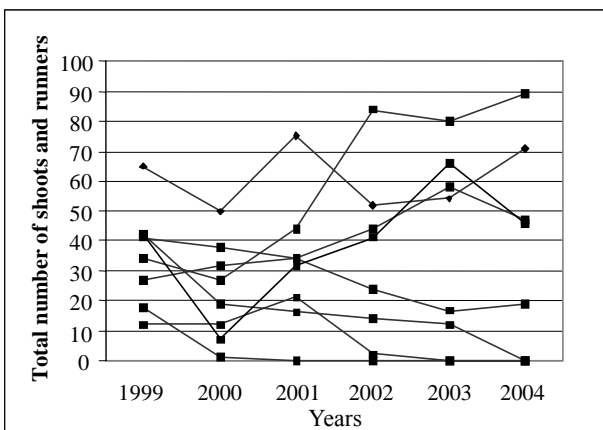


Fig. 3. Total number of shoots and runners of *S. hirculus* in each of 8 permanent quadrats from 1999 to 2004

gin. Investigations in different places of Lithuania so far have failed to detect a seedling or juvenile individual originated from seed. Studies in the Labanoras Regional Park (unpublished data) have shown that usually 19.7 ± 3.0 seeds are formed in a *S. hirculus* boll. In the 31 bolls examined, the minimum number of seeds was 2 and the maximum 84. *S. hirculus* seeds are dark brown, about 1 mm long and 0.5 mm wide. One seed weighs on average 0.062 mg. In laboratory conditions, *S. hirculus* seeds begin germinating eight

days after sowing. Seeds germinated well on different substrata (filter paper, sand, turfy soil). Turfy substratum was the best for *S. hirculus* seeds to germinate (germination 50%). According to the J. M. Olesen and E. Warncke's (1990) data, laboratory germination of seeds can reach up to 95% in optimal conditions.

There could be several reasons why in natural *S. hirculus* populations the number of individuals of generative origin is extremely low, if any. In all years of our investigations we found a very significant (up to 50%) damage of flower shoots which were broken or gnawed off, more rarely just dried off. Another reason is that *S. hirculus* seeds need light to germinate (under laboratory conditions, seeds of this plant never germinate in the dark). The study habitats were characterized by a very dense projective herbage and moss carpet. Even if seedlings do appear, they massively perish as soon as the first year of their life, being unable to compete with mosses or other herbaceous plants. It is possible to conclude that the best conditions for *S. hirculus* seeds to germinate and seedlings to survive could be open pioneering substrata not occupied by moss or other plants. This conclusion is in agreement with the data of M. Ohlson's (1989) from Sweden.

Many-year dynamics of *S. hirculus* floral shoot and runner number

One of the most objective indices of *S. hirculus* population dynamics is the change of floral shoots and runners in the course of several years. During the six years of the present investigation, in eight plots of observation the number of *S. hirculus* shoots varied (Figs. 2 and 3). At the beginning of the study, in 1999, in eight plots 281 shoots were found (the minimum number of shoots per plot was 12 and the maximum 65, with 28 floral shoots). In 2000, the number of *S. hirculus* shoots in the study plots decreased by even 33.8% (total number 186, minimum 1, maximum 50, floral shoots 15). In 2001, the number of *S. hirculus* shoots increased by 15.8% (total number 256, minimum 0, maximum 75, floral shoots 6). In 2002, the number of shoots remained practically the same (total 261, minimum 0, maximum 84, floral shoots 7). In 2003, the number of shoots increased by 4.7% and the total number (287) exceeded the 1999 level (minimum 0, maximum 80, floral shoots 13). In 2004, the total number of *S. hirculus* shoots decreased to 270 (minimum 0, maximum 89), however, the number of floral shoots was significantly higher (19).

The change of the number of floral shoots (a significant decrease in 2000 through 2002) shows that the *S. hirculus* population was exposed to an ecologically unfavourable, stressogenic situation. This observation is strongly supported by considerable changes of shoot numbers in separate plots. Over the period of observation, in three plots from eight, *S. hirculus* shoots massively perished, and the plants themselves most probably died. At the same time, in the other plots the total

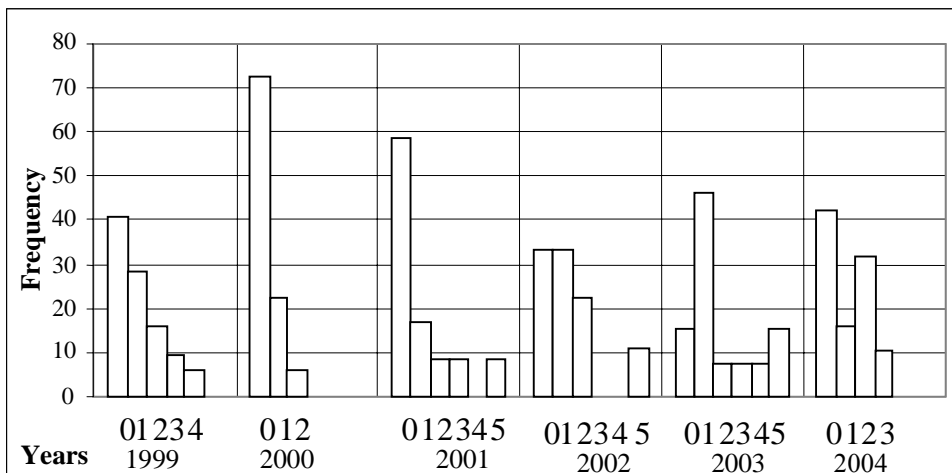
Table 2. Significance of t-test for dependent samples of *S. hirculus* flowering individuals

Year	Height of floral shoots, cm	Length of longest leaf, mm	Width of longest leaf, mm	Number of leaves	Number of flowers
1999/ 2000	*	**	**	NS	*
1999/ 2001	NS	NS	**	NS	*
1999/ 2002	NS	NS	NS	NS	NS
1999/ 2003	**	NS	NS	NS	NS
1999/ 2004	*	**	*	NS	**
2000/ 2001	NS	NS	NS	NS	**
2000/ 2002	**	NS	NS	NS	NS
2000/ 2003	NS	NS	NS	NS	**
2000/ 2004	NS	NS	NS	*	*
2001/ 2002	*	NS	NS	NS	NS
2001/ 2003	NS	NS	NS	NS	*
2001/ 2004	NS	NS	NS	*	NS
2002/ 2003	NS	NS	NS	NS	NS
2002/ 2004	NS	*	NS	NS	NS
2003/ 2004	NS	NS	NS	NS	**

* $p < 0.05$; ** $p < 0.01$; NS – $p > 0.05$ (not significant).

Table 3. Significant among between morphometric traits of *S. hirculus* flowering individuals

Trait	Height of floral shoots, cm	Length of longest leaf, mm	Length of lamina of longest leaf, mm	Width of longest leaf, mm	Number of leaves	Number of flower
Height of floral shoots, cm	1	0.2194	0.4021	0.3606	0.1245	0.4239
	$p = -$	$p = 0.220$	$p = 0.020$	$p = 0.039$	$p = 0.490$	$p = 0.014$
Length of longest leaf, mm		1	0.3546	0.6355	0.3444	0.0983
		$P = -$	$p = 0.043$	$p = 0.000$	$p = 0.050$	$p = 0.586$
Length of lamina of longest leaf, mm			1	0.3993	0.4199	0.4011
			$p = -$	$p = 0.021$	$p = 0.015$	$p = 0.021$
Width of longest leaf, mm				1	0.3454	0.1138
				$p = -$	$p = 0.049$	$p = 0.528$
Number of leaves					1	-0.1682
					$p = -$	$p = 0.349$

Fig. 4. Frequency distribution of runners per floral shoot in *S. hirculus* from 1999 to 2004

number of shoots varied, increasing in one year and decreasing in another. An exception was the year 2000 when the number of *S. hirculus* plants was notably lower. It is important that the number of floral shoots in the *S. hirculus* population studied is not large in general as compared with the Swedish scientist's data where even up to 52 floral shoots are growing in the plot of 0.25 m² in optimal

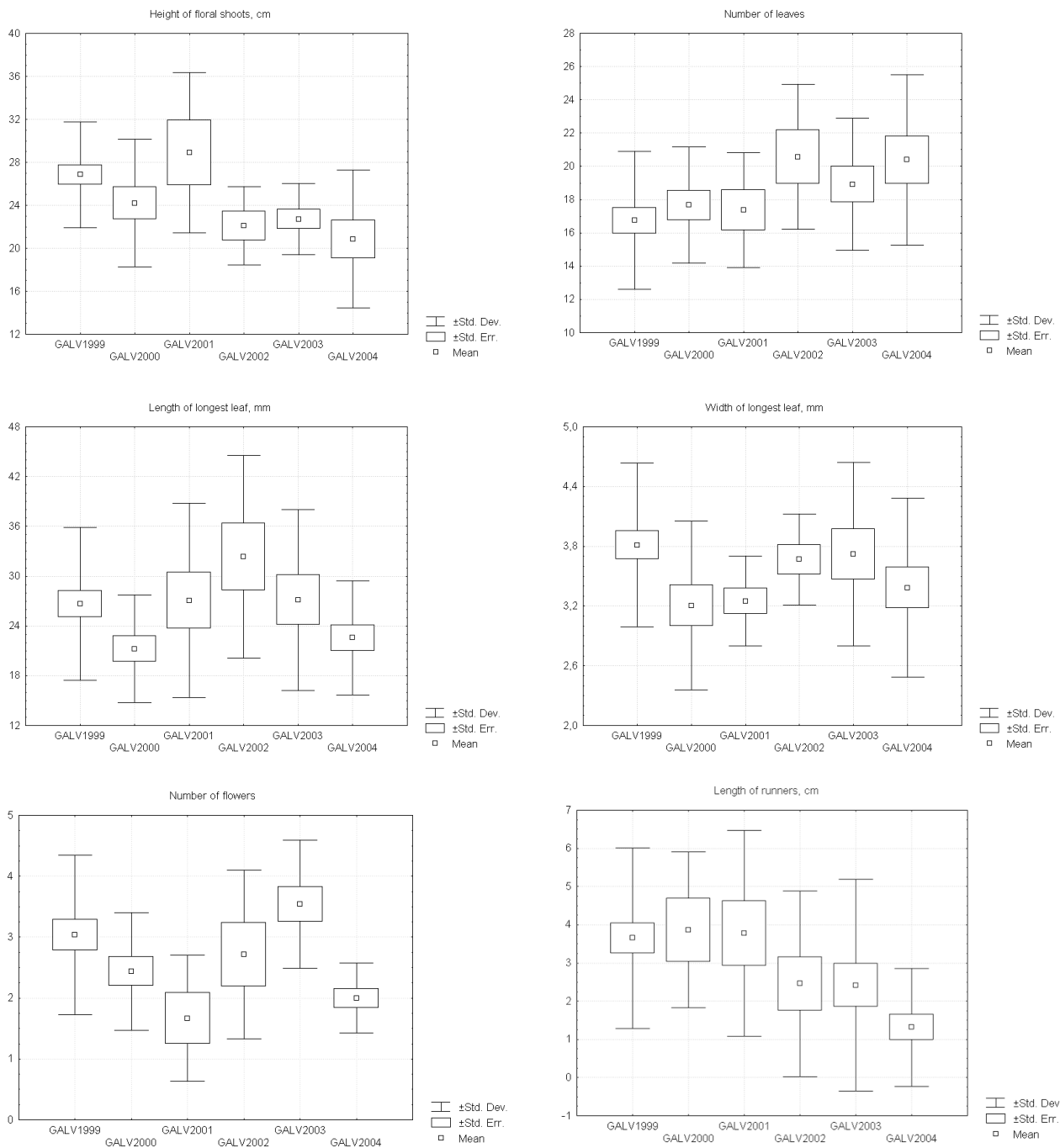


Fig. 5. Many-year variation in morphometric traits of *S. hirculus* flowering individuals

conditions – 4–7 m from a spring (Ohlson, 1986).

Thus, *S. hirculus* populations are characterized by minor and medium fluctuations of shoot numbers, which are unevenly expressed in separate places. In some places of the population, the medium fluctuations grow into catastrophic and are manifested through *S. hirculus* extinction. The main reason for the fluctuation and catastrophic changes in *S. hirculus* population shoot number is the changed hydrological regime of the habitat, evoked by a dam erected by beavers across the Juodupis rivulet in 2000, which caused a 20–25 cm water level increase in the *S. hirculus* habitat. The level of flooding in the study plots varied: in August 2000, the

three plots closest to the rivulet were covered with an about 20 cm water layer; the other plots, more remote from the rivulet, were covered with a 2–10 cm layer. It was in these most significantly flooded plots (about 20 cm above moss level) that in 2000 from 50% to 95% of *S. hirculus* shoots perished. Although the next year workers of the Regional Park destroyed the dam and the hydrological regime was restored to its initial level, *S. hirculus* individuals were severely damaged and before 2005 became totally extinct. At the same time, in the less flooded spots of the habitat where the water layer reached 2–10 cm above the ground level, the number of shoots, though decreased by 25%, as

soon as the next year was not only restored but even exceeded the initial level by 30%. Thus, *S. hirculus* populations possess well developed mechanisms allowing a rapid restoration after short-term stresses caused by hydrological regime fluctuations. The number of floral shoots recovers much slower. In 1999, floral shoots comprised about 11% of all shoots in a population. After the flooding, during three years the percentage of floral shoots was constantly decreasing (2000 – 9.7%, 2001 – 4.7% and 2002 – 3.5%). Only in 2003 the portion of floral shoots in the *S. hirculus* population began to increase, however, even after four years following the flooding (in 2004) these shoots comprised only 7% of the whole population.

The major restorative factor of *S. hirculus* population after stress was vegetative reproduction. According to Ohlson (1986), in Sweden about 60–70% of *S. hirculus* generative individuals have 2–3 runners, whereas in our study, in 1999 more than 40% of the individuals had no runners at all, 28% had one, about 15% two, nearly 10% three, and more than 6% had four runners (Fig. 4), *i.e.* there were 1.13 ± 0.22 runners per individual. In 2000, because of the above-discussed extreme changes in the hydrological regime, there was nearly no vegetative propagation in the *S. hirculus* population, and the average number of runners per individual reached only 0.33 ± 0.14 . That year, more than 70% of all *S. hirculus* generative individuals had not a single runner at all. After the hydrological regime was normalized, the vegetative propagation of *S. hirculus* gradually became very intensive. In 2001, there were on average 0.92 ± 0.40 runners per individual, whereas in 2002 this index reached 1.33 ± 0.53 , in 2003 1.92 ± 0.49 , and in 2004 1.10 ± 0.25 . The latter value shows that the *S. hirculus* population restored its development to the level before the change of the hydrological regime. In future, also the increased number of floral shoots can be expected.

Many-year dynamics of *S. hirculus* morphometric traits

Changes of morphometric traits are an important index of many-year dynamics of a population (Naujalis, 1995). In the beginning of the study (in 1999), the statistic indices of the major morphometric traits of the *S. hirculus* population showed the values presented in Table 1: the average height of floral shoots reached 26.86 ± 0.93 cm, they had 16.75 ± 0.78 leaves and 3.04 ± 0.26 flowers. The length of the longest leaf was 26.66 ± 1.63 mm and width 3.81 ± 0.15 mm. The length of runners was found to be the most unstable among the evaluated traits (it varied from 0.2 to 9.0 cm, the coefficient of variation being 65%), followed by the number of flowers (1 to 6, the coefficient of variation 43%). The least variation was shown by the floral shoot height (the coefficient of variation 18.32%). The variations of the other traits were close to 20–30%. In Sweden, floral shoots of *S. hirculus* are somewhat shorter – 19–24 cm (Ohlson, 1986).

The many-year dynamics of the morphometric traits is presented in Fig. 5. Student's test was employed to assess the annual changes of the traits (Table 2). The analysis showed that changes of *S. hirculus* morphometric traits were statistically reliable only in some of the years. Statistically significant changes were most numerous ($p < 0.05$) while comparing the number of flowers in floral shoots. In 2000, one floral shoot had on average 2.44 ± 0.24 and in 2001 1.67 ± 0.42 flowers. Thus, in the period 1999–2001 this number decreased nearly by half. Later, two years in turn, this index significantly increased, in 2002 reaching 2.71 ± 0.59 and in 2003 even 3.54 ± 0.29 . The latter value was an absolute maximum in the whole *S. hirculus* population studied. In 2004, the average number of flowers again decreased to 2.00 ± 0.16 . Thus, the tendency of annual changes of floral shoot number was analogous to that of changes in runner numbers, though the tempos of changes were somewhat slower in floral shoots, because their minimum number was established in 2001. Undoubtedly, the main reason for *S. hirculus* floral shoot number changes is the unstable hydrological regime of the habitat.

Similar tendencies were shown also by leaf length and width values, however, almost in all cases changes of these parameters were not statistically reliable (Table 2). The most significant changes of these two indices ($p < 0.002$) were found in 1999/2000 when leaf length decreased by nearly 20% (to 21.24 ± 1.57 mm) and leaf width 15% (to 3.21 ± 0.21 mm). The next year, both leaf morphometric indices somewhat increased, but in 2004 decreased again, and in comparison with the 1999 *S. hirculus* population parameters these values were 12–15% lower and the change was statistically reliable ($p < 0.05$).

Changes of *S. hirculus* leaf number were insignificant and statistically not reliable over almost the whole study period.

Thus, generally speaking, the annual changes of *S. hirculus* morphometric traits were analogous to those of floral shoot and runner numbers.

Various morphometric traits can be used to determine the condition of *S. hirculus* populations, but they are not always correlated (Table 3). The highest, medium positive correlation was found between leaf length and width ($r = 0.63$). *S. hirculus* floral shoot height is weakly correlated with a number of traits such as lamina length ($r = 0.40$), leaf width ($r = 0.36$) and flower number ($r = 0.43$). A similar weakly positive correlation ($r = 0.40$) was shown by lamina length and leaf width, lamina length and flower number, as well as lamina length and leaf number. A somewhat lower correlation ($r = 0.35$) was found between leaf length and leaf number as well as between leaf length and lamina length. The correlation among the other traits was statistically not reliable ($p > 0.05$). Thus, only a complex of traits can be a reliable index of the condition of a *S. hirculus* population.

CONCLUSIONS

1. *S. hirculus* is a plant protected by international and national legal acts in many European countries. *S. hirculus* populations comprise individuals of different size. Each individual consists of one orthotropic floral shoot and several plagiotropic runners. At first, the shoots are interconnected, but later, when the oldest rhizome parts die, the shoots separate from each other and begin functioning independently.

2. *S. hirculus* population stability is based on new shoots annually appearing early in summer from the overwintered buds. The absolute majority of naturally occurring *S. hirculus* plants is of vegetative origin. The main reasons for the rarity of generatively originated individuals are the massive damage of flowers by unknown factors and the lack of fruits as well as the specific *S. hirculus* seed requirements of the light and of open substrata.

3. *S. hirculus* populations are characterized by annual fluctuative minor and medium changes of the number of floral shoots and runners, unevenly expressed in separate places of the population. The main reason for such changes is a change in the hydrological regime of the habitat. In some places of a population, the fluctuative changes grow into catastrophic ones resulting in the death of *S. hirculus* plants.

4. Changes of the hydrological regime exert an influence on variations of the morphometry of essential structural elements of *S. hirculus* individuals. Under conditions of ecological stress (water level increase), practically all indices of generative individuals become gradually lower. The tendencies of annual changes in morphometric traits are analogous in both floral shoots and runners. The condition of the *S. hirculus* population after normalization of the hydrological regime of the habitat should return to the initial level within a period of several years.

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Saxifraga hirculus L. POPULIACIJŲ STRUKTŪRA IR DINAMIKA

Santrauka

Straipsnyje apibendrinti 1999–2005 m. tarptautiniais ir nacionaliniais įstatymais daugelyje Europos šalių saugomo augalo *Saxifraga hirculus* populiacijų daugiamečio kintamumo tyrimų, atliktų Kurtuvėnų regioniniame parke (Šiauliu ir Kelmės r.), duomenys. Tyrimų rezultatai parodė, kad *S. hirculus* populiacijos sudarytos iš įvairaus dydžio sudėtinių individų, kuriuos paprastai sudaro vienas ortotropinis generatyvinis ūglis ir keletas plagiotropinių vegetatyvinių ūglių. Rudenį generatyviniai *S. hirculus* ūgliai nunyks, o šoniniai plagiotropiniai ūgliai dalinai apauga samanomis ir kitais metais funkcionuoja kaip šakniastiebiai, iš kurių žiemojančių pumpurų išauga nauji ūgliai. Absoliuti dauguma *S. hirculus* individų gamtinėse populiacijose yra vegetatyvinės kilmės. Pagrindinės generatyvinės kilmės individų retumo priežastys yra masinis generatyvinių ūglių pažeidimas nenustatytais veiksniais ir vaisių nesusidarymas bei specifiniai *S. hirculus* sėklų dygimo poreikiai šviesai ir atviriems substratams. Tirtose vietovėse *S. hirculus* populiacijai yra būdingi smulkaus ir vidutinio masto fluktuaciniai ūglių skaičiaus po-

kyčiai, kurie netolygiai pasireiškia atskirose populiacijos vietose. Pagrindinė tokių pokyčių priežastis – augimvietės hidrologinio režimo pasikeitimas (patvanka dėl bebrų užtvankos). Ženkliai apsemtose vietose šie fliktuaciniai pokyčiai perauga į katastrofinius, pasireiškiančius *S. hirculus* žūtimi. Augimvietės hidrologinio režimo pasikeitimas turi įtaką ir *S. hirculus* individų esminių struktūros elementų morfometriniams požymiams.

Ekologinio streso sąlygomis (pakilus vandens lygiui) praktiškai visi generatyvinių individų rodikliai palaipsniui sumažėja. *S. hirculus* populiacijos būklė po hidrologinio režimo normalizacijos turėtų atsistatyti per keletą metų. *S. hirculus* kasmetinių morfometrinių pokyčių tendencijos yra analogiškos generatyvinių ir vegetatyvinių ūglių raidai.

Raktažodžiai: *Saxifraga hirculus*, daugiametė dinamika, populiacijos struktūra, vegetatyvinis dauginimasis, Lietuva