Preslia, Praha, 65:335-340, 1993

Sex ratios in dioecious *Rumex tuberosus* populations along a successional gradient

Poměr počtu samičích a samčích rostlin u *Rumex tuberosus* podél sukcesního gradientu

Leoš K l i m e š

Department of Plant Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 145, CZ-379 82 Třeboň, Czech Republic

Klimeš L. (1993): Sex ratio in dioecious *Rumex tuberosus* populations along a successional gradient. - Preslia, Praha, 65:335-340.

K e y w o r d s : *Polygonaceae*, *Rumex tuberosus*, dioecy, sex ratio, succession.

Sex ratio in dioecious *Rumex tuberosus* populations was studied in the Ropotamo National Park, Bulgaria, on sixteen plots, differing in their successional stage. Females prevailed in all populations ($P<0.05$), except one with equal ratio, which colonizes an early successional stage. The female-biased sex ratio increased in closed-canopy vegetation reaching its maximum in the woods. Possible causes of female dominance are discussed.

Introduction

The genus *Rumex* includes about 150 species distributed in all climatic zones except the wet tropics. Most *Rumex* species are monoecious. However, some dozens of species belonging to the subgenera of *Acetosa* Mill. and *Acetosella* (Meisner) Rech. f. are dioecious or polygamous.

The expected equal sex ratio (Fisher 1930) has been found in germinating seeds of *Rumex acetosa* (Rychlewski et Zarzycki 1975); in adults it is quite rare.

Ramet sex ratios (based on number of inflorescences) have been studied in five species of *Rumex*: *R. arifolius* All. (Zuk 1963), *R. hastatulus* Baldw. (Smith 1963, Conn 1981), *R. thyrsiflorus* Fingerh. (Zuk 1963, Zarzycki et Rychlewski 1972, 1982), *R. acetosella* L. (Löve 1944, Harris 1968, Putwain et Harper 1972, Lovett Doust et Lovett Doust 1985, 1987, Escarré et al. 1987, Escarré et Houssard 1991) and *R. acetosa* L. (Sprecher 1913, Raunkiaer 1918, Correns 1922, 1928, Löve 1940, 1944, Zuk 1963, Zarzycki et Rychlewski 1972, Korpelainen 1991); female ramets prevail in most populations. Their proportion in *R. acetosella* decreased during a succession (Escarré et Houssard 1991). In contrast, the proportion of females increased in time during a period of 7 years in a population of *R. thyrsiflorus* (Zarzycki et Rychlewski 1982).

Sex ratio of distinct individuals (genets) was studied in *R. acetosella*, *R. acetosa* (Korpelainen 1991) and *R. thyrsiflorus* (Zarzycki et Rychlewski 1972) only. Females prevailed in most populations. The correlation between ramet and genet sex ratios in 15 populations of *R. thyrsiflorus* is highly significant ($r^2 = 0.665$, $P<0.0005$, $n = 15$; based on data in Table III by Zarzycki et Rychlewski 1972).

In spite of the extensive research, the cause of the prevalence of female genets in the field is still unclear. Pollination with a large amount of pollen results in an increased percentage of seeds later developing into females in *R. acetosa* (Zarzycki et Rychlewski 1972). It seems, however, that this factor is hardly responsible for the extreme variation in the sex ratios found in natural populations. Higher mortality of males is another possible cause of female-biased sex ratio in *R. acetosa* (Korpelainen 1991). In other genera niche partitioning among sexes was responsible for variation in the sex ratio (Cox 1981).

The aim of the present study was to compare populations of the dioecious *R. tuberosus* along a successional gradient, in order to detect the trend in the genet sex ratio.

Material and methods

Sixteen populations of *R. tuberosus*, a perennial dioecious herb with south-European distribution, were studied in the Ropotamo National Park, E. Bulgaria (42°22'N, 27°44'W), in five natural habitats differing in their successional status (Table 1). The earliest stage, with sparse *R. tuberosus*, is represented by an open plant assemblage on sandy dunes. It is dominated by *Artemisia campestris* L. var. *sericea* (Nos. 1-3). If the stand is not much disturbed, scattered *Paliurus spina-christi* L. shrubs establish there step by step (Nos. 7-12). They buffer microclimatic conditions and enable establishment of several *Viciaceae* species which enhance nitrogen availability. Many meadow species colonize the stand at

Table 1. Sex ratio of genets of sixteen *Rumex tuberosus* populations and some characteristics of vegetation studied in the Ropotamo National Park, E. Bulgaria. Plant density classes are defined as follows: 'very low' - <0.01, 'low' - 0.01 to 0.1, 'high' - 0.1 to 1 individuals/m^2.

No.	Habitat	*R. tuberosus* density	Successional status	Females/males	Total number of plants	Chi^2 (H_0: females : males = 1:1)	Heterogeneity Chi^2 (DF)
1	*Artemisia*	low	early	1.26	52	0.69n.s.	10.58 (5) n.s.
2	dunes	low	stage	1.57	90	4.44*	
3		low		1.58	116	5.83*	
4	Wood	high	medium	1.35	195	4.30*	
	margin	high	stage	2.57	150	29.04***	
6		high		2.26	124	18.58***	
7	*Paliurus*	high	medium	4.00	85	30.60***	5.19 (5) n.s.
8	shrub	high	stage	2.85	104	24.04***	
9		high		2.77	49	10.79***	
10		high		3.59	78	24.82***	
11		high		1.94	94	9.57**	
12		high		2.32	199	31.36***	
13	*Quercus* wood	very low	late stage	8.22	83	50.31***	2.34 (3) n.s.
14	Meadow	low	late	8.90	307	194.89***	
15	steppe	low	stage	8.42	113	69.49***	
16		high		7.87	337	201.54***	

* - P<0.05, ** - P<0.005, *** - P<0.001, n.s. - non-significant

that stage and the density of *R. tuberosus* increases rapidly. *R. tuberosus* plants remain abundant also on the wood margins (Nos. 4-6). *Paliurus* shrubs are followed in succession by *Crataegus* sp., *Fraxinus ornus* L. and several *Quercus* species (e.g. *Q. cerris* L., *Q. frainetto* Ten.). Trees and shrubs are suppressed on exposed windward slopes (Nos. 14-16) resulting in predominance of steppe grasses. In close woods, the dense *Ruscus aculeatus* L. populations outcompete most herbs, including *R. tuberosus* (No. 13).

The pairwise population distances ranged from 50 m to 1000 m. Meadow and wood populations were well isolated by hedges and/or woods, the studied wood margin populations were situated along the Ropotamo river, far from the other populations. Individual populations of *R. tuberosus* in dunes and shrubs were at least 100 m apart in each case. Nevertheless, they were not so well isolated since those sites were located in an open dune area.

The *R. tuberosus* populations were examined in May 1991, when the flowering periods, which takes about 2 weeks, was nearly over. The area of the individual populations was 200 m^2 to ca. 3 ha. All individuals found in the area were examined. Genets, which were usually identical with clumps, were used as basic units (individuals). If more than one inflorescence was found per clump, underground connections between ramets were traced to distinguish genets. Separation of individual clumps was possible without examining underground organs in most cases because the large distance between individual clumps ruled out the underground integration.

Departures of female/male genet ratio from unity in each of the 16 populations were chi-square tested.

Results

The proportion of females in the *R. tuberosus* populations varied between 56 and 90 %. If the population were grouped according to their habitats (Table 1), five groups of populations were found: (1) *Artemisia* dunes (females : males = 1.47), (2) Wood margins (1.61), (3) *Paliurus* shrub (2.67), (4) *Quercus* wood (8.22), and Meadow steppe (8.40). Splitting of the habitats (1) and (2), and (4) and (5) is possible as the test value for heterogeneity between groups of habitats remains non-significant. However, the difference in the sex ratios among the first two groups is only slight in contrast to the third group. The order of the groups of habitats corresponds with successional status of the surrounding vegetation (see Olson 1958, Syers et Walker 1969a, b, Walker et al. 1980 for vegetation analyses of dune series).

The proportion of females showed a great variation among and a little variation within habitats (Table 1).

Discussion

It seems that the growth habit of *R. tuberosus* makes this species a convenient model for studies of sex ratio. (*R. tuberosus* is closely related to *R. acetosa* and *R. thyrsiflorus*; it belongs to the same subsection *Acetosa* - Löve et Kapoor 1967). It was easy to distinguish individual genets of *R. tuberosus* within the stands because, first, the density of the species was much lower (ca 0.001 to 1/m^2) than in other species which have been studied (usually 10 to 50 individuals/m^2 - Putwain et Harper 1972, Zarzycki et Rychlewski 1972) and, second, vegetative multiplication results in clearly defined clumps which are easily separable and it occurs much less frequently than in *R. acetosella*, for instance. Thus, it is possible to count genets instead of ramets in *R. tuberosus*.

Sex ratio in *R. tuberosus* was slightly female-biased in the early successional stages. In the habitats with later stages of vegetation, populations of *R. tuberosus* were markedly female-biased.

Female-biased ramet and genet sex ratios in dioecious *Rumex* species have been found repeatedly by numerous investigators. Even more extreme values were found by Zarzycki et Rychlewski (1972) (*R. acetosa*: 13.6 and *R. thyrsiflorus*: 12.2) and by Korpelainen (1991) (*R. acetosella*: 9.1 but also all males). Nevertheless, it is still difficult to interpret these observations because it was often impossible to distinguish individual genets within a stand since vegetative multiplication and fragmentation of old rhizomes are very common. In *R. acetosella*, for instance, vegetative multiplication is sometimes the only mode of reproduction (Putwain et al. 1968).

Abundant pollination may result in high female proportion (Correns 1922, Rychlewski et Zarzycki 1975). It has been reported from related species that fertilization by male-determining gametes is diminished because pollen tubes with Y-chromosome determining male sex are outcompeted in style by pollen tubes determining female which grow faster (Correns 1922, Zuk 1970, Rychlewski et Zarzycki 1975, Zarzycki et Rychlewski 1982). Because *Rumex* species are wind-pollinated it is likely that stigmatic pollen loads increase with density. As density is always low abundant pollination may be uncommon in *R. tuberosus*. Female preponderance was found both in populations with high (No. 16) and low (No. 13) densities.

Putwain et Harper (1972) suggested that an important factor causing shifts in the sex ratio is intraspecific competition. In *R. acetosa* they found that competition between the sexes resulted in female-biased sex ratio of about 2 which is similar to that found frequently in the field. However, density of *R. tuberosus* is usually very low and thus intraspecific competition can be ruled out.

Escarré et al. (1987) and Escarré et Houssard (1991) found that male ramets of *R. acetosella* show greater clonal growth than female ramets because of lower energetic cost of sexual reproduction. In *R. tuberosus* and other *Rumex* species with generative reproduction prevailing, other factors should be considered.

Putwain et Harper (1972) and Korpelainen (1991, 1992) suggested that the major factor causing the shift in the sex ratio from young to old populations is differential mortality of the sexes. The decreasing stem heigth and the increasing proportion of male genets with a single inflorescence in the late successional stages are more apparent in males than in females of *R. tuberosus* (Klimeš, unpubl.). If mortality is higher in small plants than in tall plants, it could account for the observed pattern in the sex ratios. Differences in the competitive abilities and survival of the *R. tuberosus* sexes should be examined to test this hypothesis.

Acknowledgments

I am indebted to Hana Končalová and Jan van Groenendael for their comments.

Souhrn

Poměr počtu samičích a samčích rostlin byl studován v 16 populacích dvoudomého druhu šťovíku *Rumex tuberosus* L. v národním parku Ropotamo v Bulharsku. Ve všech populacích převládaly průkazně samičí rostliny s výjimkou jedné populace, v časném

sukcesním stádiu, kde byl poměr vyrovnaný. Převaha samičích rostlin narůstala podél sukcesního gradientu. Nejvyšší poměr samičí:samčí rostliny byl zjištěn v lese. Pravděpodobné příčiny převahy samičích rostlin v pozdějších sukcesních stádiích jsou diskutovány.

References

Conn J. S. (1981): Phenological differentiation between sexes of *Rumex hastatulus*: Niche partitioning or different optimal reproductive strategies? - Bull. Torrey Bot. Club, Lancaster, 108:374-378.

Correns C. (1922): Geschlechtsbestimmung und Zahlenverhältnis der Geschlechter beim Sauerampfer (*Rumex acetosa*). - Biol. Zentralbl., Leipzig, 42:465-480.

Correns C. (1928): Bestimmung, Vererbung und Verteilung des Geschlechtes bei den höheren Pflanzen. - Handb. Vererbungsw, 2:1-138.

Cox P. A. (1981): Niche partitioning between sexes of dioecious plants. - Amer. Natur., Chicago, 117:295-307.

Escarré J. et Houssard C. (1991): Changes in sex ratio in experimental populations of *Rumex acetosella*. - J. Ecol., Oxford, 79:379-387.

Escarré J., Houssard C. et Briane, J. P. (1987): Évolution du rapport des sexes de populations de *Rumex acetosella* le long d'une succession postculturale. - Can. J. Bot., Ottawa, 65:1668-2675.

Harris W. (1968): Environmental effects on the sex ratio of *Rumex acetosella*. - Proc. New Zealand Ecol. Soc., Wellington, 15:51-54.

Korpelainen H. (1991): Sex ratio variation and spatial segregation of the sexes in populations of *Rumex acetosa* and *R. acetosella* (*Polygonaceae*). - Pl. Syst. Evol., Wien etc., 174:183-195.

Korpelainen H. (1992): Patterns of phenotypic variation and sexual size dimorphism in *Rumex acetosa* and *R. acetosella*. - Bot. Helvet., Basel, 102:109-120.

Löve A. (1940): Cytogenetic studies in *Rumex*. - Bot. Notiser, Lund, 93:157-169.

Löve A. (1944): Cytogenetic studies on *Rumex* subgenus *Acetosella*. - Hereditas, Lund, 28:289-296.

Löve A. et Kapoor B. M. (1967): A chromosome atlas of the collective genus *Rumex*. - Cytologia, Tokyo, 32:328-342.

Lovett Doust J. et Lovett Doust L. (1985): Sex ratios, clonal growth and herbivory in *Rumex acetosella*. - In: White J. [red.], Studies on plant demography: A Festschrift for John L. Harper, p. 327-341, Academic Press, London.

Lovett Doust L. et Lovett Doust J. (1987): Leaf demography and clonal growth in female and male *Rumex acetosella*. - Ecology, Durham, 68:2056-2058.

Olson J. S. (1958): Rates of succession and soil changes on southern Lake Michigan sand dunes. - Botanical Gazette, Chicago, 119:125-170.

Putwain P. D. et Harper J. L. (1972): Studies in the dynamics of plant populations. V. Mechanisms governing the sex ratio in *Rumex acetosa* and *R. acetosella*. - J. Ecol., Oxford, 60:113-129.

Putwain P. D., Machin D. et Harper, J. L. (1968): Studies in the dynamics of plant populations. II. Components and regulation of a natural population of *Rumex acetosella* L. - Ibid., 56:421-431.

Raunkiaer C. (1918): Über die verhältnismässige Anzahl männlicher und weiblicher Individuen bei *Rumex thyrsiflorus* Fingerh. - Det. Kgl. Danske Vidensk. Selskab. Biol. Medd. 1, Kobenhavn, 7:3-17.

Rychlewski J. et Zarzycki K. (1975): Sex ratio in seeds of *Rumex acetosa* L. as a result of sparse or abundant pollination. - Acta Biol. Cracov., Kraków, 18:101-114.

Smith B. W. (1963): The mechanism of sex determination in *Rumex hastatulus*. - Genetics, Princetown, N.J., 48:1265-1288.

Sprecher A. (1913): Recherches sur la variabilité des sexes chez *Cannabis sativa* L. et *Rumex acetosa* L. - Ann. Sci. Nat. Bot., Paris, Sér. 9., p. 255-352.

Syers J. K. et Walker T. W. (1969a,b): Phosphorus transformations in a chronosequence of soils developed on wind blown sand in New Zealand. I, II. - J. Soil Sci. London 20:57-64 et 219-224.

Walker J., Thompson C. H., Fergus I. F. et Tunstall B. R. (1980): Plant succession and soil development in coastal sand dunes of subtropical Eastern Australia. - In: Shugart H. H., Botkin D. et West D. [red.], Forest succession: concepts and applications, p. 107-131, Springer, New York.

Zarzycki K. et Rychlewski J. (1972): Sex ratios in Polish natural populations and in seedling samples of *Rumex acetosa* L. and *R. thyrsiflorus* Fing. - Acta Biol. Cracov., Kraków, 15:135-151.

Zarzycki K. et Rychlewski J. (1982): Ekologiczne i genetyczne mechanizmy reguljace proporcje plci w populacjach dwupiennego szczawiu rozpierzchlego (*Rumex thyrsiflorus* Fingerh.). - Wiad. Ekol., Warszawa, 28:199-208.

Zuk J. (1963): An investigation on polyploidy and sex determination within the genus *Rumex*. - Acta Soc. Bot. Polon., Warszawa, 22:5-67.

Zuk J. (1970): Structure and function of sex chromosomes in *Rumex thyrsiflorus*. - Ibid., 39:539-564.

Received 6 September 1993
Accepted 13 December 1993

Urbanska K. M.

Populationsbiologie der Pflanzen

Uni Taschen Bücher 1631, Gustav Fischer Verlag, Stuttgart, Jena 1992, 374 str., 105 obr., 57 tab. Cena 39,80 DEM.

Populační biologie rostlin se dá bez pochyby označit za disciplínu s největším rozvojem v uplynulých 15 letech. Tento rozvoj byl zahájen v roce 1977 vydáním Harperova díla „Population biology of plants". Celý rozvoj se odehrával především v anglosaských státech, tedy tam, kde je pravidlem mezi ekology spíše nižší stupeň taxonomických znalostí. Proto také v dosavadních příručkách populační biologie jsou zanedbány taxonomické relace. Nově publikovaná příručka prof. Urbanské alespoň částečně (je psána německy) vyplňuje tento nedostatek.

Krystyna M. Urbanska je profesorkou na Curyšské technické universitě a v minulých letech se věnovala biosystematickému studiu (známé jsou např. její práce o skupině *Cardamine pratensis* či o rodu *Antennaria*). Její biosystematický přístup se v této nové příručce odráží především v poměrně vyváženém uvádění příkladů z různých taxonomických skupin. Autorka ukazuje, jaká je skutečně vysoká rozmanitost v životních cyklech jednotlivých rostlin a jak je obtížné dělat generalizace založené na několika málo známých příkladech. Recenzovaná kniha má ještě dva klady: prvním z nich je propojení na populační genetiku (nikoliv pouze v teoretické rovině); druhým kladem je to, že autorka díky svému polskému původu a díky jazykové oblasti, kde pracuje, dokázala využít podstatně širší soubor literárních zdrojů, než je obvyklé v knihách anglosaských autorů.

Předností recenzované příručky je i její didaktická hodnota: vhodně volený grafický doprovod (ilustrace, fotografie) je kombinován s četnými tabulkami, důležité teze jsou zvýrazněny v rámečcích. Z hlediska anglicky psaných příruček se kniha může zdát více popisná a statičtější. Uvedené přednosti však bohatě převyšují tento nedostatek. Abych ukázal blíže obsah knihy, uvádím dále názvy jednotlivých kapitol:

1. Úvod. 2. Rozšiřování rostlin. 3. Biologie diaspor v půdě. 4. Klíčení a ecese semenáčků a mladých rostlin. 5. Růst a vývoj. 6. Biologie klonálně rostoucích rostlin. 7. Regenerace. 8. Rozmnožování: koncepce, typy, chápání. 9. Semenné rozmnožování. 10. Vegetativní rozmnožování. 11. Populační biologie a populační genetika rostlin. 12. Populační genetika a demografie rostlin.

Práce je zakončena bohatým seznamem citované literatury (37 stran!) a rejstříkem. Z hlediska našich čtenářů, zejména mladší generace, je určitým záporem knihy skutečnost, že je psána německy; v některých případech, ne však důsledně, je anglický termín uveden v závorce. Knihu doporučuji k prostudování většině našich čtenářů se zájmem o populační biologii zejména kvůli jinému pohledu, než který je vlastní pro anglicky psané příručky. Svou knihou prof. Urbanska dokázala, že v současné době již prakticky neexistuje žádná hranice mezi populační ekologií, evoluční biologií a biosystematikou. Recensovanou knihu je možno doporučit jako základní příručku pro výuku uvedených směrů na vysokých školách.

F. Krahulec