Genetical and ecological mechanisms regulating the sex ratio in populations of "Rumex thyrsiflorus" Fingerh. "(Polygonaceae)" = Genetische und oekologische Mechanismen zur Regulierung der Geschlechtsverhältnisse bei Populationen von "Rumex thyrsiflorus" ...

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Objekttyp: **Article**

Zeitschrift: **Veröffentlichungen des Geobotanischen Institutes der Eidg. Tech. Hochschule, Stiftung Rübel, in Zürich**

Band (Jahr): **87 (1986)**

PDF erstellt am: **29.05.2024**

Persistenter Link: https://doi.org/10.5169/seals-308776

Veröff.Geobot.Inst.ETH, Stiftung Rübel, Zürich **87** (1986), 132-140

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Genetische und oekologische Mechanismen zur Regulierung der Geschlechtsverhältnisse bei Populationen von *Rumex thyrsiflorus* Fingerh. *(Polygonaceae)*

by

Jerzy RYCHLEWSKI and Kazimierz ZARZYCKI

1. INTRODUCTION

Frequencies of male and female plants are nearly equal in populations of some dioecious species, e.g. Spondias nigrescens or Bernardia nicaraguensis (OPLER and BAWA 1978), Juniperus communis (FALINSKI 1980). However, species in which one sex prevails are much more frequent. Male-biased sex ratio was reported e.g. for Chamaelirium luteum (MEAGHER 1980, 1981) or Clematis gentianoides (GODLEY 1976). On the other hand,

female plants always dominate e.g. in Rumex acetosa (CORRENS 1922, ZARZYCKI and RYCHLEWSKI 1972) or Triplaris americana (MELAMPY and HOWE 1977). However, only rarely is the sex ratio skewed in favour of females so strongly as in some populations of Rumex thyrsiflorus (RAUNKIAER 1918, ZUK 1970b, ZARZYCKI and RYCHLEWSKI 1972). Recent studies on the population biology of dioecious plants revealed some variability in mechanisms regulating the sex ratio (e.g. GODLEY 1964, 1976, PUTWAIN and HARPER 1972, LLOYD 1973, CONN and BLUM 1981). Rumex thyrsiflorus appeared to be a good object for studying the sex ratio, a comparison between the primary ratio in seeds and the secondary in populations being of particular interest. The present paper deals with a long-term study on the subject.

ACKNOWLEDGEMENTS

The authors wish to express their gratitude to Professors E. Pogan, A. Lomnicki (Jagellonian University, Cracow, Poland) and K. Urbanska (Geobotanical Institute, Zurich, Switzerland) as well as to Dr. M. Guzikowa (Polish Academy of Sciences, Cracow) for their kind criticism and suggestions during preparation of the manuscript. The technical assistance of Miss A. Sidor is also gratefully acknowledged.

2. REPRODUCTION

2.1. SEX DETERMINATION IN RUMEX THYRSIFLORUS

Rumex thyrsiflorus reproduces only by seed. Female flowers are pollinated by the wind, the pollen sometimes being transported over long distances, about 100 m or more.

The mechanism of sex determination in R. thyrsiflorus follows the 'Drosophila'-type and an equal proportion of both sexes in the progeny is to be expected. Female plants (2n=14), are homogametic and produce egg cells with the chromosome constitution 6a+X. Heterogametic males (2n=15) shed pollen with two types of grains: 6a+X, determining female, and 6a+YY, determining male sex, both in equal proportion. The resulting primary sex ratio of seeds should be 1:1.

2.2. SEX RATIO IN POPULATIONS AND IN SEEDS

The predominance of female plants in Rumex thyrsiflorus and in related R. acetosa in natural populations has been known for many years. Sex ratio in these populations most frequently oscillated around 1:3, but in old grassland communities the prevalence of females was significantly higher, attaining in some populations the ratio 1:6 or even 1:12 (ZARZYCKI and RYCHLEWSKI 1972). To get better assessment of this phenomenon, studies on the primary sex ratio in seeds from these populations were undertaken. The first results (l.c.) seemed to confirm our expectation that the sex ratio in seeds should be 1:1. Further studies, however, revealed this problem to be more complex.

Owing to differences in number and morphology of the sex chromosomes in R. thyrsiflorus it was possible to determine the gender of seedlings and to establish a primary proportion of sexes (l.c.). It has been found that the sex ratio in seed samples originating from various wild populations was slightly female-biased (as a rule 1.1-1.6, Fig. 1) and only rarely deviated in favour of males (0.9). An average prevalence of females in seeds from nature might be expressed with the ratio 1:1.25 (RYCHLEWSKI and ZARZYCKI 1981). (Two forms of expression of the sex ratio are used interchangeably. E.g. the ratio M:F = 1:1.25 means the same as the short form F/M = 1.25, both pointing to the female-biased ratio.)

The constant predominance of female seeds might result from a higher mortality of male zygotes or embryos; empty or underdeveloped seeds observed in low numbers do not permit the exclusion of this possibility. The prevalence of female seeds might also result from differential fertilisation influenced by the sex chromosomes. It has been shown that two Y chromosomes in R. thyrsiflorus are almost entirely heterochromatic and late replicating; the male-determining sperms with two Y chromosomes might be less successful in fertilisation than those with X chromosomes (ZUK 1969, 1970a). No direct evidence of the selective fertilisation and its nature is available to date; however, the results of experiments with pollination under low and high pollen densities in R. acetosa (CORRENS 1922, RYCHLEWSKI and ZARZYCKI 1975) seem to favour this hypothesis. Similar results have recently been obtained by the present authors in R. thyrsiflorus: under low pollen density nearly equal proportions of male and female seeds were set. On the other hand, the proportion of

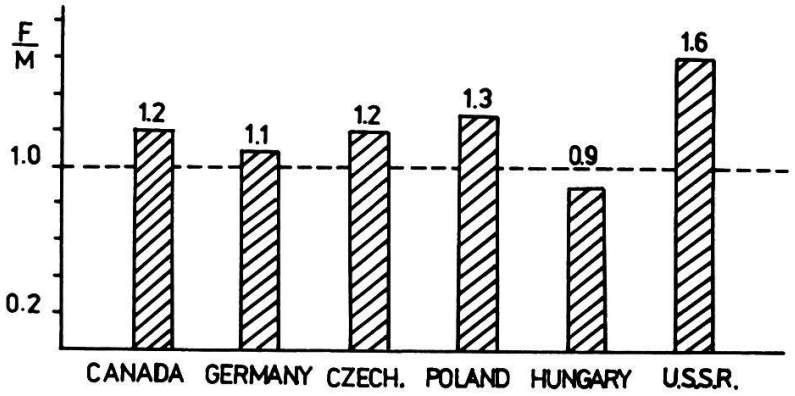

Fig. 1. Rumex thyrsiflorus: Sex ratio in seed samples from natural populations.
Abb. 1. Rumex thyrsiflorus: Geschlechtsverhältnis in Samenproben aus natürlichen Populations.

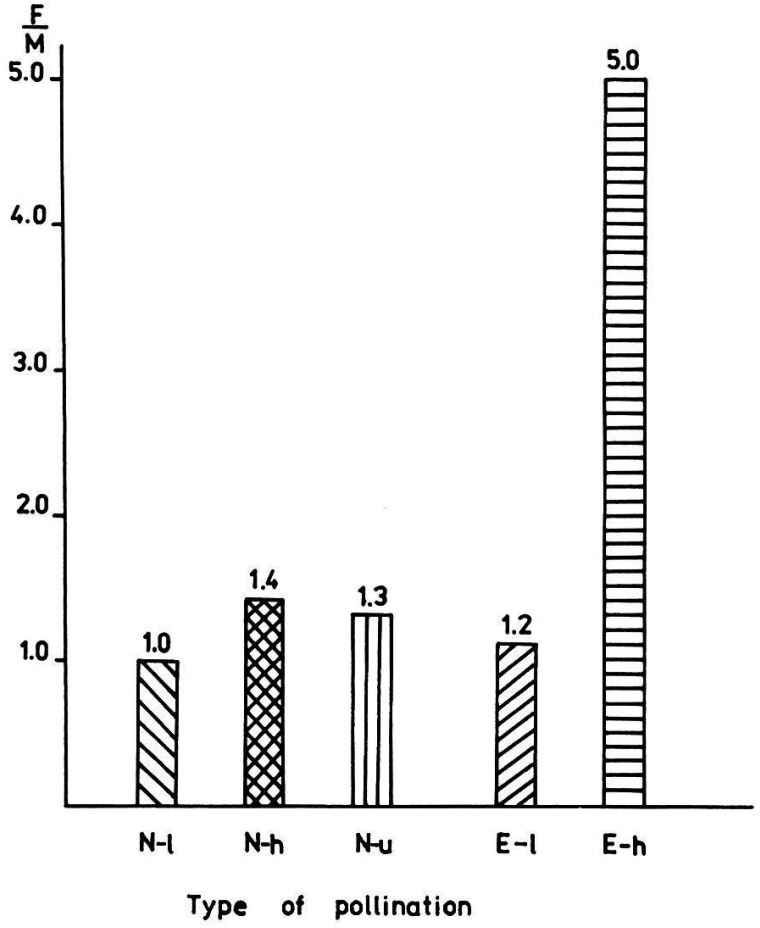

Fig. 2. Rumex thyrsiflorus: Sex ratio in seed samples after natural (N) and experimental (E) pollinations under low (l) and high (h) pollen density. u = uncontrolled.
Abb. 2. Rumex thyrsiflorus: Geschlechtsverhältnis in Samenproben nach natürlicher (N) und künstlicher (E) Bestäubung bei niedriger (l) und hoher (h) Pollendichte. u = unkontrolliert.

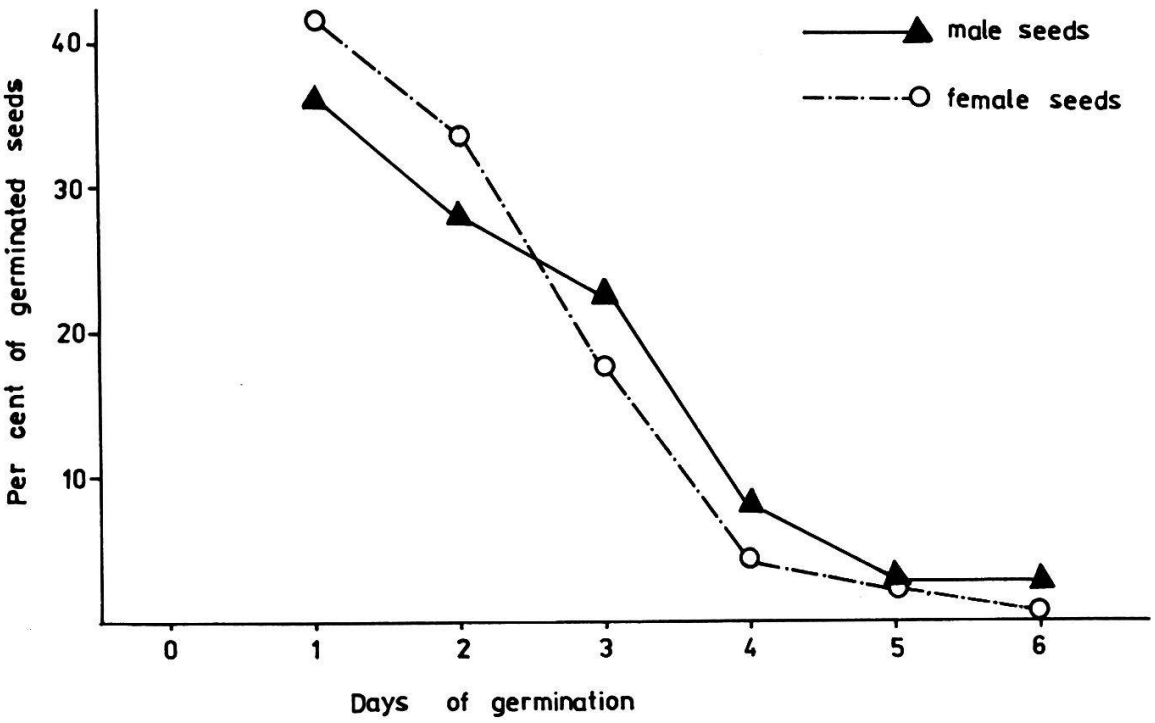

Fig. 3. Rumex thyrsiflorus: germination of male and female seeds during six consecutive days.
Abb. 3. Rumex thyrsiflorus: Keimung männlicher und weiblicher Samen während sechs aufeinanderfolgenden Tagen.

female seeds significantly increased under conditions of considerably high pollen density. Natural pollination, when high pollen density was anticipated, resulted only in a moderately female-biased ratio (Fig. 2). Female-biased ratio was obtained also by CONN and BLUM (1981) in progeny of R. hastatulus under high pollen density. However, in their studies the prevalence of females was not as marked as in our experiment. CORRENS (1922) and LEWIS (1942) explained these findings with a competition of pollen, depending on a differential rate of growth of pollen tubes in two types of pollen grains. This effect might also be due to the differential genetic activity of sex chromosomes in both types of male gametes (ZUK 1970b). Be it as it may, the genetic determination of sex in R. thyrsiflorus promotes the female-biased ratio and any prevalence of male seeds seems to be rather incidental.

Our observations suggest that a great excess of pollen does not occur very frequently in natural populations of R. thyrsiflorus. As a result only slight, although statistically significant, prevalence of female

seeds set in nature is found (Fig. 1). The field observations support this opinion.

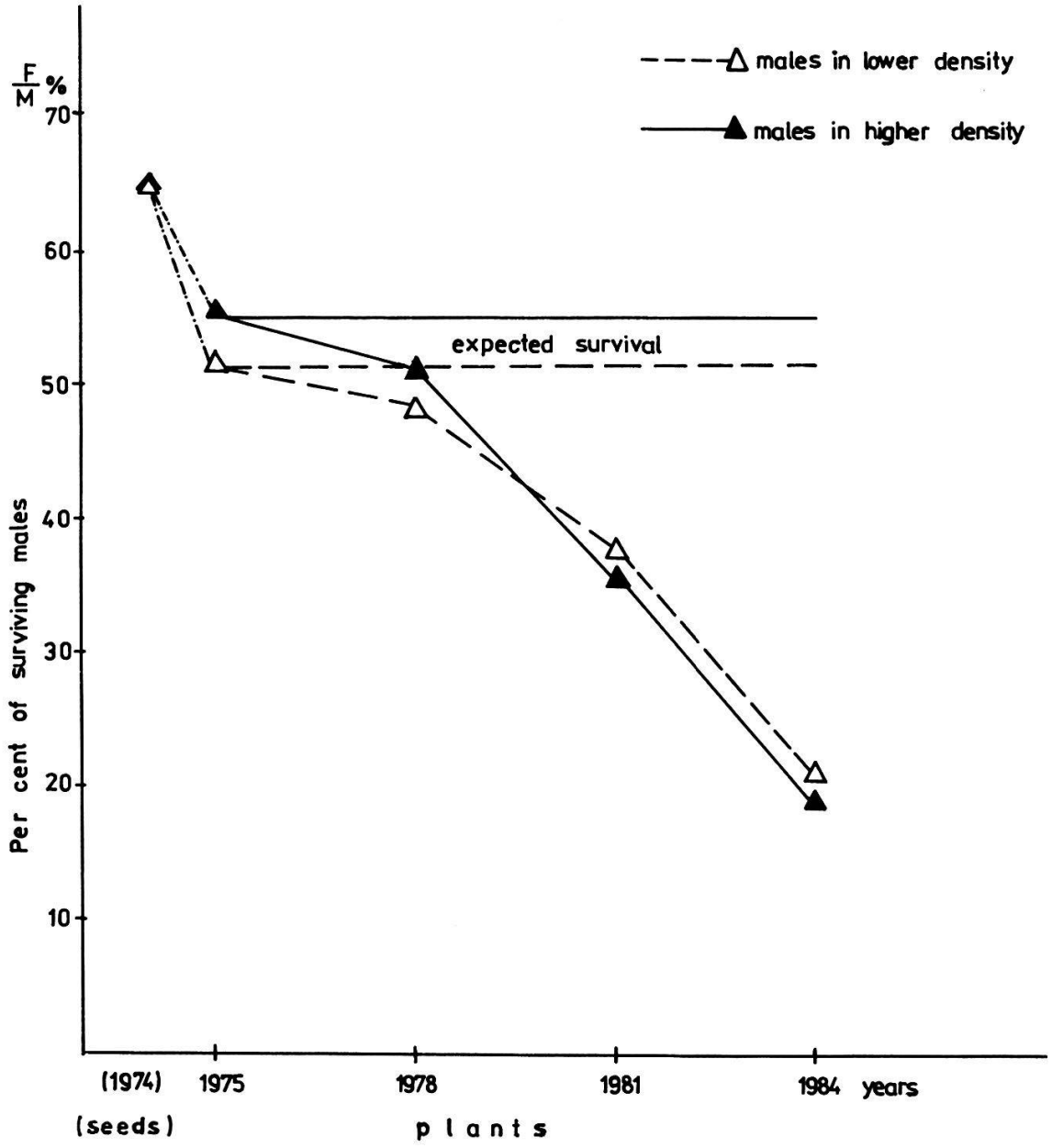

Fig. 4. Rumex thyrsiflorus: Survival of male plants as a percentage of surviving female plants in conditions of low and high density.

Abb. 4. Rumex thyrsiflorus: Das Ueberleben der männlichen Pflanzen als Prozentanteil der überlebenden weiblichen Pflanzen in niedriger und hoher Dichte.

2.3. GERMINATING BEHAVIOUR AND DIFFERENTIAL MORTALITY

Under laboratory conditions seeds of Rumex thyrsiflorus start germinating two or three days after being sown. Female seedlings appear in majority during the first two days of germination, whereas mostly male seeds germinate already on the third day (Fig. 3). Thus the female seedlings may have an initial advantage in overgrowing of the habitat.
Our long-term experimental studies suggest, however, that a factor most significantly influencing the sex ratio in populations of R. thyrsiflorus seems to be the differential survival rate. The experimental populations derived from seeds, the sex ratio of which was 1:1.5. The seedlings were planted in two densities. All individuals in plots were tallied for sex in nine following seasons. Irrespective of the density of the plot, the mortality of male individuals was always higher than that of females and in subsequent years a constant decrease of the sex ratio could be observed (Fig. 4). The conditions of this experiment do not allow any conclusion to be drawn concerning the density-dependent differential mortality of plants of a given sex. However, the higher survival rate of female plants seems to be evident under both conditions.
ZUK (1970b) has observed Y-hyperploid male and female plants in R. thyrsiflorus to be shorter and to die off earlier than normal males. He attributed it to a depressive effect of Y-chromosomes. Such phenotypic effects of Y-chromosomes seem rather probable, in spite of the conclusion being drawn from the aneuploid plants, that had an abnormal chromosome constitution.

3. CONCLUDING REMARKS

The differential survival in Rumex thyrsiflorus seems to be the most important factor in modifying the sex ratio in wild populations. In this respect R. thyrsiflorus differs from some other dioecious species in which genetic effects are supposed to be of no significance to the adult sex ratio in populations (e.g. in Chamaelirium luteum, MEAGHER 1981).
A simulated model of population dynamics and the problem of sex struc-

ture-dependent strategy in R. thyrsiflorus will be the subject of a separate study.

SUMMARY

Sex in Rumex thyrsiflorus is differentiated according to the 'Drosophila'-type. In wild populations of R. thyrsiflorus female plants prevail as a rule, but the proportion of males vs. females, expressed as a sex ratio (M:F), oscillates in different populations between 1:1.5 and 1:12 (most frequently 1:3). Mean sex ratio in seeds set in nature is 1:1.25, close to the theoretical 1:1. A similar ratio was found in seeds set under low pollen density, but an experimental high pollen density resulted in a significant prevalence of females (1:5). During the first two days of germination under laboratory conditions the females appear with a slightly higher frequency (ca. 75%) than the males (ca. 64%). Ten year observation of the survival rate of the plants of both sexes in experimental populations revealed a markedly higher mortality of male individuals. The differential survivorship seems to play the main role in the regulation of the sex ratio in populations of R. thyrsiflorus.

ZUSAMMENFASSUNG

Das Geschlecht unterscheidet sich in Rumex thyrsiflorus nach dem Drosophila-Prinzip. Bei natürlichen Populationen von R. thyrsiflorus überwiegen in der Regel die weiblichen Pflanzen. Das Verhältnis zwischen männlichen und weiblichen Individuen, bezeichnet als Geschlechtsverhältnis (M:F), pendelt in verschiedenen Populationen zwischen 1:1.5 und 1:12 (am häufigsten 1:3). Das Durchschnitts-Geschlechtsverhältnis bei Samen, die im Freien ausgesät wurden, beträgt 1:1.25, liegt also nahe beim theoretischen Wert von 1:1. Ein ähnliches Verhältnis fand man bei Samen, die bei geringer Pollendichte ausgesät worden waren. Bei einer experimentell hohen Pollendichte herrschen die weiblichen Pflanzen vor (1:5). Während der ersten zwei Tage der Keimung entwickelten sich im Labor ca. 75% weibliche gegenüber von nur 64% männlichen Pflanzen. Die Beobachtung der Ueberlebensrate von Pflanzen beiderlei Geschlechts in experimentellen Populationen während zehn Jahren liess eine bedeutend höhere Sterblichkeit der männlichen Individuen erkennen. Die unterschiedlichen Ueberlebenschancen scheinen die Hauptrolle zu spielen bei der Regulierung der Geschlechtsverhältnisse von Rumex thyrsiflorus.

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