

REPRODUCTIVE EFFORT AS AN ELEMENT OF LIFE STRATEGY OF *LYTHRUM SALICARIA* L. POPULATIONS

Bożenna Czarnecka, Magdalena Franczak, Katarzyna Nowak

Department of Ecology, Maria Curie-Skłodowska University in Lublin, Poland
e-mail: boczar@biotop.umcs.lublin.pl; mpele@biotop.umcs.lublin.pl

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S u m m a r y

The aim of the study was to compare some life strategy traits of individuals of Purple Loosestrife *Lythrum salicaria* within three meadow populations existing under various habitat conditions. The study attempted to answer the following questions: Do different habitat conditions affect the biomass allocation between particular organs of individuals? Can the individuals belonging to different populations of the same species realise their own unique reproductive strategy, in other words, can their reproductive effort represent various levels? In the case of *L. salicaria* the reproductive effort, measured by the participation of inflorescence biomass in the biomass of aboveground parts of genets, exhibits similar values (14.2-15.1%) in all the study populations, despite their habitat conditions. This fact proves that at the population level, the reproductive effort is relatively stable. Great differences are visible in the case of particular individuals within each of the populations. Specific genets in a population, depending on the habitat microstructure and the biotic relations with other individuals both of their own and other species, may realise their own reproductive strategies, being a part of their life strategies.

Key words: reproductive effort, biomass allocation, life strategy, trade-off, clonal plant, *Lythrum salicaria*

INTRODUCTION

Life history of a species, also referred to as its lifestyle, comprises the entire course of events in the life of an individual (genet) connected with successive stages of its development and growth, until its death (Harper, 1977). The genet survival in a population, affected by a set of unique habitat conditions, is determined by a set of life history traits. Temporal pattern of its growth and reproduction is shaped by such features as, among others, growth rate, size, body mass, vegetative offspring and number of generative propagules produced per one generative episode, and the number of

such episodes during the ontogeny (Stearns, 1992). Each individual is affected by a different selection force, resulting from natural selection, both under the influence of habitat conditions, which change with different rate, and under the pressure of intra- and interspecific competition. These limitations condition the shaping of such a combination of life history traits which becomes a life strategy. At the level of an individual, a web of evolutionary trade-offs is formed, which is a result of the drive to reach maximum size and reproduction success on the one hand, and to adapt to the environment and last in time on the other (Silvertown and Lovett Doust, 1993; Crawley, 1997).

In clonal species of the iterative growth type which multiply their basic structures, i.e. shoots, rhizomes and roots, and thus expand the genet, a particularly important element of life strategy is the biomass allocation to vegetative and generative parts of plants. The part of the biomass (energy) used to produce generative organs, in relation to the total biomass (energy) of an individual, is defined as reproductive effort (Harper and Ogden, 1970).

The aim of the present study is to compare some life strategy traits of individuals of Purple Loosestrife *Lythrum salicaria* within three populations existing in different types of meadow vegetation occurring in habitats of various resource abundance. The study attempts to answer the following questions: Do different habitat conditions affect the division of energy between particular organs of individuals? Can the individuals belonging to different populations of the same species realise their own unique reproductive strategy, in other words, can their reproductive effort represent various levels?

MATERIALS AND METHODS

The study was carried out in the Szum river valley in the Central (Tomaszów) Roztocze region, near

Górecko Kościelne. The study area comprised hydrogenic habitats, within the inundation terrace and occupied by communities of variously moist meadows of the *Molinio-Arrhenatheretea* class. Their vegetation was dominated, first of all, by macroforbes: *Filipendula ulmaria*, *Lythrum salicaria*, *Lysimachia vulgaris*, *Cirsium rivulare*, *C. oleraceum*.

Purple Loosestrife *Lythrum salicaria* L. (Lythraceae) is a perennial clonal plant belonging to rhizocaulophytes (Łukasiwicz, 1962). Genets of *L. salicaria* are compact and usually consist of several, maximum a dozen, of ramets. Therefore, the species takes part in the formation of both fine-grained and coarse-grained spatial mosaic. The calendar age of genets is estimated as exceeding 10 years. Strong, well-shaped underground organs enable the individuals to last long in the once occupied area. Therefore, *L. salicaria* realises its dynamics in time rather than in space, and belongs to the promoters of succession within meadow communities (Falińska, 1991, 2003).

In order to conduct the biometrical analysis and to estimate the biomass, the total number of 90 generative individuals of *L. salicaria* were collected in the growing season of the year 2006. The genets came from three meadow patches (30 plants out of each), differing in habitat conditions, vegetation composition and population density. The patches of *Cirsium rivulare* (A) and *Lythro-Filipenduletum ulmariae* (B) occupy eutrophic habitats on a flat inundation terrace, supplied with highly mineralised waters (300-350 mg dm⁻³). The vegetation of the third of the analysed patches, *Lysimachio vulgaris-Filipenduletum* (C), occupies poorer soils, supplied with acidic, lowly mineralised (100-130 mg dm⁻³) seeping waters, typical of neighbouring mires; it is characteristic of a high participation of *Carex acutiformis*, too. Population density of *L. salicaria* in particular patches was as follows: patch A – 1.00 genet m⁻², patch B – 4.25 genets m⁻², and patch C – 3.05 genets m⁻². Measurement comprised the following morphological features: stem height (1 cm accuracy), number of branches, leaves and inflorescences, and inflorescence length (0.5 cm accuracy). Aboveground parts of plants were subsequently divided into the stem, leaves and the inflorescence part. The material thus divided was dried and weighed with the 0.0001 g accuracy. In order to determine the reproductive effort, the participation of inflorescence biomass in the total biomass of an individual's aboveground parts was measured. The results were analysed statistically with the Shapiro-Wilk, Levene and Kruskal-Wallis tests.

RESULTS

The differences between the study populations of *Lythrum salicaria* were significant ($0.001 < p < 0.05$) in case of all the features subjected to biometrical analy-

sis. Most of them do not exhibit the Gaussian distribution, with the exception of stem height (all populations), number of shoot branches (patch A, i.e. *Cirsium rivulare* population), and leaves (patch A and patch B – *Lythro-Filipenduletum ulmariae*). Genets from patch B are characteristic of the lowest mean height of ramets, while all the remaining analysed vegetative parameters reach their highest values here (Tab. 1). The average number of leaves per individual is twice as high as in the case of patch C (*Lysimachio vulgaris-Filipenduletum* population). As far as the generative features are concerned, individuals from patch B have shown the highest number of inflorescences (Tab. 2, Fig. 1). In all the populations, the inflorescence length is negatively correlated with their number; patch A: $r = -0.33$; patch B: $r = -0.10$; patch C: $r = -0.29$. The genets of *L. salicaria* occupying patch A exhibit the intermediate values of all the parameters in respect to the remaining populations. The only exception is the average inflorescence length which reaches its lowest value in this population. The lowest variability among all the analysed features was observed in patch B.

The comparison of the aboveground parts of plants additionally indicates the biggest size of genets in patch B (statistically significant differences between the populations), and the smallest size in patch C (Fig. 2). The average percentage of biomass coming from particular aboveground parts of plants was similar in all the populations and was contained within the following ranges: stem – 49.8-52.1%, leaves – 33-36% and inflorescence – 14.2-15.1%. The individuals of *L. salicaria* coming from the C population exhibit the lowest value of the coefficient of variation in the case of the stem and inflorescence biomass (Tab. 3). The greatest variability in the biomass allocation was observed for the individuals of the A population. The reproductive effort of the B and C populations showed similar values (15.1 and 14.9%), while its slightly smaller value (14.2%) was noted in the population coming from the *Cirsium rivulare* patch (Tab. 4). Great differences are visible in particular individuals within each of the populations; population A: 8-times different, population B: ca. 4-times, population C: ca 3-times.

DISCUSSION

One of the most important evolutionary trade-offs undertaken by clonal species is the share of biomass spent on vegetative growth and generative reproduction. In the case of *Lythrum salicaria*, habitat differences are reflected in the diverse size and genet architecture in particular populations, which further influence the biomass of an individual and its reproductive effort. Purple Loosestrife occurs in the patch of macroforbes *Lythro-Filipenduletum ulmariae* (patch B), where the individuals are frequently branched, and therefore producing the highest number of inflorescences. Despite its highest

Table 1
Vegetative traits of individuals in the *Lythrum salicaria* populations.

Patch	Stem height [cm]				Number of shoot branches				Number of leaves			
	$\bar{x} \pm SD$	Sk	K	V [%]	$\bar{x} \pm SD$	Sk	K	V [%]	$\bar{x} \pm SD$	Sk	K	V [%]
A	98.2 ± 16.6	-0.19	0.40	16.90	6.7 ± 3.3	0.31	-0.09	49.25	195.5 ± 79.8	0.14	-0.46	40.82
B	93.3 ± 13.2	0.33	0.51	14.15	8.7 ± 4.9	0.39	-0.59	56.32	297.9 ± 100.8	0.41	-0.60	33.84
C	104.8 ± 15.5	-0.10	-0.52	14.79	6.2 ± 5.1	0.51	-0.89	82.26	127.1 ± 55.6	1.32	1.87	43.74

\bar{x} – arithmetic mean, SD – standard deviation, Sk – skewness, K – kurtosis, V – coefficient of variation

Table 2
Generative traits of individuals in the *Lythrum salicaria* populations.

Patch	Number of inflorescences				Inflorescence length [cm]			
	$\bar{x} \pm SD$	Sk	K	V [%]	$\bar{x} \pm SD$	Sk	K	V [%]
A	11.6 ± 8.6	1.53	3.27	74.14	5.3 ± 2.2	2.08	4.92	41.51
B	17.6 ± 8.6	1.97	5.84	48.86	6.2 ± 2.0	1.00	1.06	32.26
C	8.1 ± 5.3	0.84	0.54	65.43	9.2 ± 4.2	0.57	0.03	45.65

Table 3
Biomass allocation in generative individuals of *Lythrum salicaria* populations (in g).

Patch	Stem biomass				Leaf biomass				Inflorescence biomass			
	$\bar{x} \pm SD$	Sk	K	V [%]	$\bar{x} \pm SD$	Sk	K	V [%]	$\bar{x} \pm SD$	Sk	K	V [%]
A	4.78 ± 3.36	1.59	2.41	70.29	3.22 ± 1.71	1.07	1.13	53.10	1.27 ± 0.96	2.40	8.17	75.59
B	6.49 ± 3.66	2.94	11.24	56.39	3.94 ± 1.53	0.61	-0.26	38.83	1.94 ± 1.32	2.12	5.96	68.04
C	3.97 ± 2.05	1.25	1.09	51.50	2.53 ± 1.30	0.69	-0.84	51.38	1.17 ± 0.65	0.48	-1.24	55.55

Table 4
Reproductive effort in the *Lythrum salicaria* populations (in %).

Patch	$\bar{x} \pm SD$	min.	max.
A	14.20 ± 8.13	5.72	47.79
B	15.14 ± 5.00	7.04	27.39
C	14.82 ± 3.28	6.96	20.56

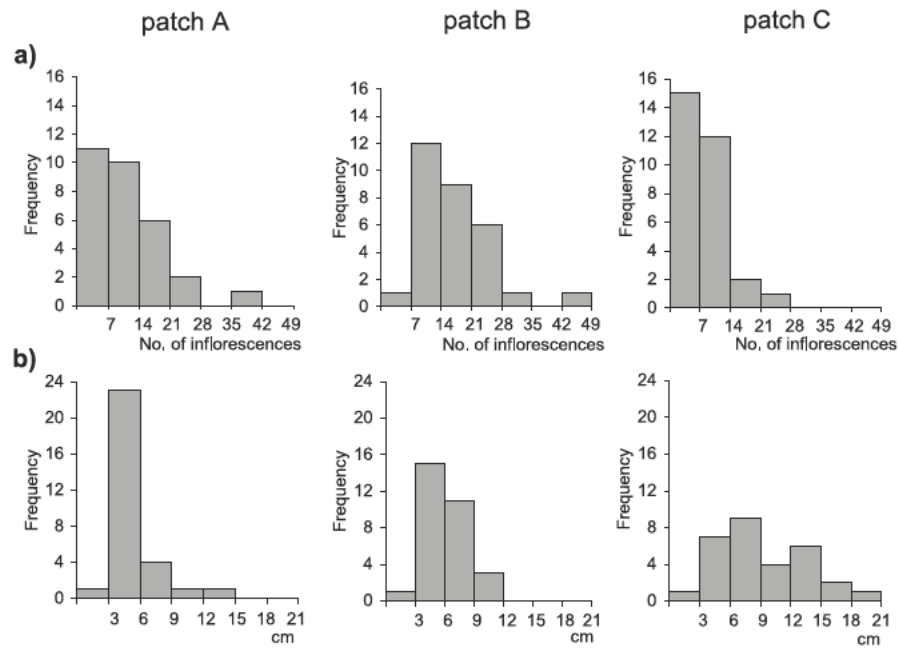


Fig. 1. Distribution of number of inflorescences (a) and inflorescence length (b) in 30 generative individuals in the *Lythrum salicaria* populations in patches A, B and C.

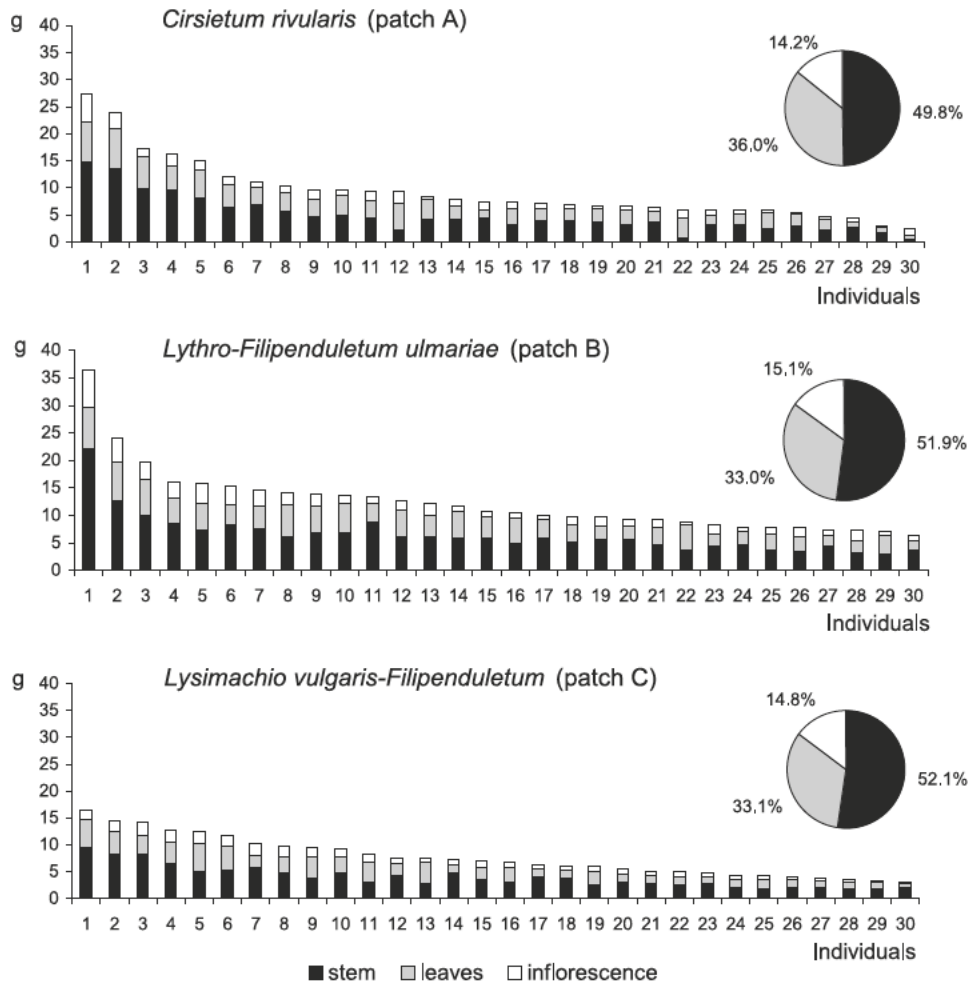


Fig. 2. Differentiation of the biomass allocation in 30 generative individuals in the *Lythrum salicaria* populations in patches A, B and C; cyclogram – the entire sample (in %).

density among all three analysed populations, the inflorescence biomass in this patch is greater by 52% and 66% than in the remaining patches of *Cirsium rivularis* (patch A) and *Lysimachio vulgaris-Filipenduletum* (patch C), respectively. In patch C, in turn, there occur individuals of the tallest stems. This fact is connected with the habitat conditions, that is, with considerable solum moisture and, first of all, with a dense and tall herb layer, which reinforces the interspecific competition, particularly on the part of *Carex acutiformis*. Additionally, the shading caused by the entering of willow-alder shrubs makes the individuals of *L. salicaria* 'run to the sun' (Falińska, 1990). Tall ramets raise inflorescences above the herbaceous layer also because of pollinators, especially the *Lepidoptera*. Yet, despite the fact that in the patch of *Lysimachio vulgaris-Filipenduletum* generative ramets are the tallest and inflorescences the longest, their size does not affect the reproductive effort in this population.

The percentage of biomass spent on reproduction is different not merely across the individuals of different species, but often among the plants of the same one (Harper, 1977). The reproductive effort may depend on genet age, size and sex, as well as on habitat conditions of a population, its density, the succession stage of a community, abundance of nutrient resources and light conditions, and on the influence of competition, although these relationships are not always unambiguous (Harper and Ogden, 1970; Gaines et al. 1974; van Andel and Vera, 1977; Newell, 1978; Samson and Werk, 1986; Werpachowski, 1989; Powelson and Lieffers, 1992; Verburg and Grava, 1998; Hemborg and Karlsson, 1999; Pino et al. 2002).

In the case of *L. salicaria* the reproductive effort measured by the participation of inflorescence biomass in the biomass of aboveground parts of genets, exhibits similar values (14.2-15.1%) in all the study populations, despite their habitat conditions. This fact proves that at the population level, the reproductive effort is relatively stable. In *L. salicaria* populations the biomass percentage spent on reproduction is not connected with the number of generative ramets, produced by a genet, similarly to other populations occurring in hydrogenic habitats, e.g. *Caltha palustris* (Werpachowski, 1989) and *Senecio rivularis* (Czarnecka, 1995).

The study shows that, at the level of a whole population, different habitat conditions are not decisive for the differentiation of the matter and energy allocation pattern between vegetative and generative structures. However, particular genets in a population, depending on the habitat microstructure and the biotic relations with other individuals both of their own and other species, may realise their own reproductive strategies, being a part of their life strategies (Harper, 1977; Southwood, 1988; Kozłowski, 1992).

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Wysilek reprodukcyjny jako element strategii życiowej populacji *Lythrum salicaria* L.

Streszczenie

Celem badań było porównanie wybranych cech strategii życiowej osobników krwawnicy pospolitej *Lythrum salicaria* w trzech populacjach łąkowych, bytujących w zróżnicowanych warunkach siedliskowych. Poszukiwano odpowiedzi na następujące pytania: Czy odmienne warunki środowiskowe wpływają

na sposób podziału materii między poszczególne organy? Czy osobniki różnych populacji tego samego gatunku mogą realizować własną strategię reprodukcyjną, tzn., czy ich wysilek reprodukcyjny może kształtować się na zróżnicowanym poziomie? U *L. salicaria* wysilek reprodukcyjny mierzony udziałem biomasy kwiatostanów w biomase części nadziemnych genetów przyjmuje zbliżone wartości (14,2-15,1%) we wszystkich badanych populacjach, niezależnie od warunków środowiskowych. Dowodzi to, że wysilek reprodukcyjny na poziomie populacji jest wartością względnie stałą. Natomiast poszczególne osobniki w każdej z badanych populacji, w zależności od mikrostruktury siedliska i oddziaływań biotycznych z innymi osobnikami własnego, jak i innych gatunków, mogą realizować własną strategię reprodukcyjną, będącą częścią ich strategii życiowej.