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Reproductive strategies of *Caltha palustris* L. under various living conditions

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Abstract

Reproductive effort and strategies of *Caltha palustris* were compared for four phytocoenoses located in the southern Biebrza basin: sedge reedswamp (*Caricetum gracilis*), sedge-moss community (*Caricetum limoso-diandrae*), willow-birch brushwood (*Salix cinerea-Betula pubescens*), and alder-bog forest (*Carici elongatae-Alnetum*), The individuals of analysed populations were found to differ with respect to their biomass allocation to generative and vegetative reproduction. Three types of reproductive strategies were distinguished: generative (G), vegetative (V) and intermediate (G/V). The individuals growing in the alder-bog forest had the highest reproductive effort (V strategy), while those from sedge reedswamp – the lowest (G strategy).

Key words: Caltha palustris, reproductive effort, vegetative and generative diaspores, biomass allocation

INTRODUCTION

Only a very few plant and animal populations grow in a "competition vacuum". Diversified habitat conditions and competition cause each population to evolve an optimal life strategy. Under favourable growth conditions and at the absence of strong competition the best strategy would lie in the allocating maximum biomass and energy to reproduction (Cody 1966). To the contrary, populations that experience adverse environmental conditions and strong competition pressure would sacrifice more energy to competitive ability and establishment. It may lead to the formation of a few, relatively

large propagation organs. They are usually very costly, but also highly adaptable to variable environment (Falińska 1979, Gębczyński 1985). However in the reality most populations have compromising strategies, either they produce a large number of offspring (r-strategy) or a few propagules well-adapted to their environment (K-strategy) (MacArthur 1962, Stearns 1976, Pianka 1981). It also means that an individual having allocated more energy to some strategy element has to sacrifice less to others (Begon and Mortimer 1981). Especially populations of herb perennials exhibit a large spectrum of various reproductive strategies (Falińska 1986). For these plants the analysis of effectiveness of both reproduction types (Bostock and Benton 1983), and variation in their reproductive effort (Harper and Ogden 1970, Falińska 1979, 1981) seems crucial.

The paper aims to determine the type of reproductive strategy and to assess reproductive effort of *Caltha palustris* populations under various environmental conditions.

The work attempts to answer the following questions:

1. What per cent of individual biomass is allocated to their reproduction?
2. To what extent the type of reproductive strategy in *Caltha* populations is stable, and to what modified by their environment?
3. What is intra and interpopulational variation regarding biomass allocation to reproduction?

MATERIAL AND METHODS

STUDY AREA

Four *Caltha palustris* populations growing in four phytocenoses were selected. The studies were conducted in the southern (lower) Biebrza basin, with pronounced zonation of plant communities (Oświt 1973) and large typical phytocenoses. The study areas were selected regarding: 1) large *Caltha* frequency, 2) location of analysed population in a representative phytocoenose within a successive zone of vegetation parallel to the river course. Following phytocoenoses (association nomenclature after Pałczyński 1975) and vegetation zones (after Oświt 1973) were sampled:

Population 1. *Caricetum gracilis* (Graebn. et Hueck 1931) R. Tx. 1937 – sedge reedswamp – zone I (immersed vegetation).

Population 2. *Caricetum limoso-diandrae* (Tołpa 1956) Pałcz. – sedge-moss community – zone IV (emmersion communities, rich in low sedges and brown mosses).

Population 3. *Salix cinerea-Betula pubescens* – willow-birch brushwood (contact community between alder-bog forest and moss bog).

Population 4. *Carici elongatae-Alnetum* Koch 1926 – zone V (alder-bog forests).

SAMPLING

In order to assess the density of *Caltha palustris* clumps in all phytocoenoses 100 m^2 plots were constructed. In the reedswampp community 3 such plots were selected so as to vary with the water level during spring floods (A, B, C – from the lowest to the highest). The plots were mapped (1 : 50 scale), all *Caltha* clumps located, and generative shoot number was determined. Single individuals and their aggregations derived through development of regenerative buds were considered clumps.

In each analysed population in spring 1986, 50 *Caltha* clumps with at least 1 generative shoot were selected at random and labeled. This enabled to conduct parallel cytological studies on the species. In the end of May 1986 at the population fruiting stage all labeled clumps were dug out, bagged after the excess soil was removed from the rizosphere, and brought to the laboratory. Each clump was divided into individuals, which were divided into roots, leaves, generative shoots, vegetative diaspores and fruits. Every organ was measured, then dried at $t = 85°C$ to the constant weight and weighed.

Following parameters were determined:

1. Clump density per 100 m^2.
2. Individual number in 50 clumps.
3. Individual number per clump.
4. Number of clumps with and without generative shoots.
5. Number of clumps and shoots with vegetative diaspores.
6. Number of individuals with and without generative shoots.
7. Number of generative shoots per one individual.
8. Vegetative diaspore number.
9. Biomass of clumps and their parts.
10. Growth form of generative shoots.
11. Seed number.

EXPERIMENT

In order to determine the germinability and germination rate of *Caltha* seeds, 1000 seeds from each population were sown onto 20 Petri dishes (50 seeds per dish). The experiment has been conducted twice, on seeds collected in the beginning (4 populations) and at the end (3 populations) of dissemination. The seeds were sown 14 days after their collection. Similarly, from each population 500 seeds were sown into trays filled with flood-plain forest soil, located in the experimental garden of the Białowieża Geobotanical Station W.U.

CALCULATION OF "REPRODUCTIVE EFFORT"

Energy contribution to reproduction is termed as plant "reproductive effort" (Harper and Ogden 1970). Its value is calculated from the % ratio of seed biomass (or energy) to that of the whole mature plant. In the present

paper the former contained also biomass of fruits (pericarp and seeds), and vegetative diaspores. The reproductive effort was assessed by three methods: a) traditionally, i.e. biomass of fruits and vegetative diaspores to that of clump or individual; b) traditionally, but excluding root biomass; c) biomass of generative shoots was added to that of propagation organs, as their main function is associated directly both with generative and vegetative reproduction. The reproductive effort was calculated for clumps and individuals with generative shoot(s).

RESULTS

NUMBER OF INDIVIDUALS WITH GENERATIVE SHOOTS AND VEGETATIVE DIASPORES

Fairly large differences between populations in the number of individuals, and those of generative shoots and vegetative diaspores were found.

The number of individuals in 50 clumps was 118 and 104 (reedswamp and brushwood populations), and 83 and 88 (moss-community and alder-bog populations). The mean number of individuals per one clump equaled to 2.36-2.08 and 1.66-1.76, respectively. The maximum number of individuals (13) in one clump was found in brushwood population. The proportion of individuals with no generative shoots was 31-33% in reedswamp, brushwood and alder-bog populations, and 8.4% in moss-community population (Table 1).

Table 1

Number of individuals and generative shoots (G.S) in *Caltha palustris* populations

Population	Number of individuals in 50 clumps			Number of individuals per a clump	Max. number of individuals in a clump	G.S. number in 50 clumps	G.S. number per an individual
	without G.S.	with G.S.	Σ				
1	39 (33%)	79	118	2.36	7	89	1.13
2	7 (8%)	76	83	1.66	5	78	1.03
3	33 (32%)	71	104	2.08	13	80	1.13
4	27 (31%)	61	88	1.76	5	65	1.07

1-4 As in Fig. 1.

The smallest number of generative shoots per 50 clumps was found for alder-bog population (65), whereas the biggest – in reedswamp population (89). The number of generative shoots per an individual was similar in all populations and ranged from 1.03 to 1.13 (Table 1). Only in 5% of individuals were two or more generative shoots (max. 3) encountered (Fig. 1).

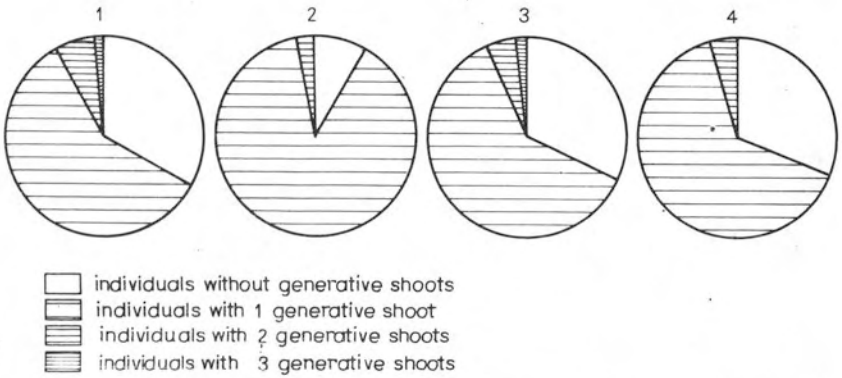


Fig. 1. The proportion of individuals with generative shoots in *Caltha palustris* populations. 1 – sedge reedswamp population, 2 – sedge-moss community population, 3 – willow-birch brushwood population, 4 – alder-bog forest population

The proportion of clumps with vegetative diaspores also varied, from 34% in moss-community population, 70% – in brushwood population, to 96% in alder-bog population. On average there were 1.0-1.33 vegetative diaspores per one shoot. In moss-community population all vegetative diaspores were single on the shoots, in brushwood population 16% of shoots and in alder-bog population 33% had 2 diaspores (Table 2).

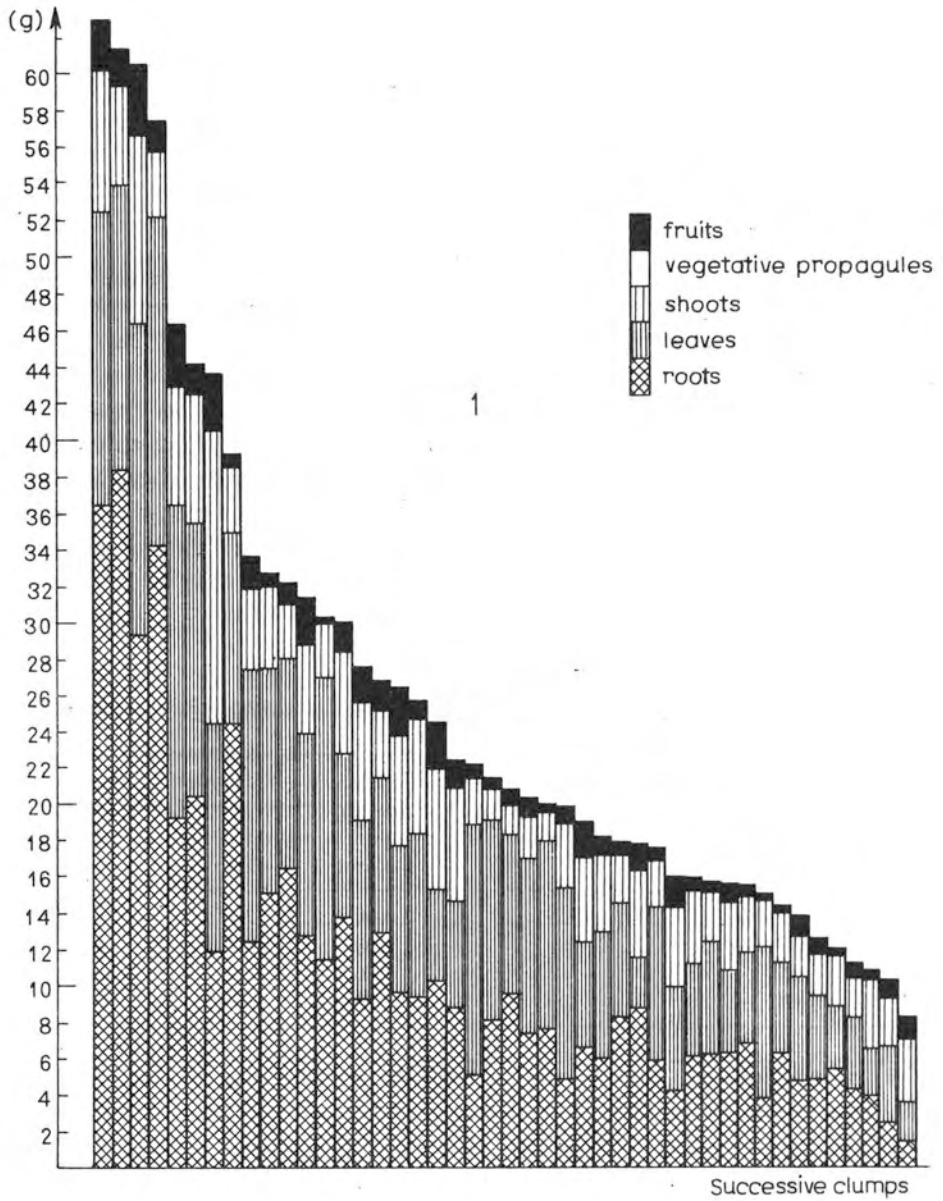
Table 2

Number of clumps and shoots with vegetatvie diaspores (V.D.) in *Caltha palustris* populations

Population	Number of clumps with V.D. and number of V.D. (in 50 clumps)	Proportion of clumps with V.D. (%)	V.D. number per a shoot	Proportion of shoots	
				with 1 V.D. (%)	with 2 V.D. (%)
1	0 → 0 V.D.	0	0.00	0.0	0.0
2	17 → 23 V.D.	34	1.00	100.0	0.0
3	35 → 43 V.D.	70	1.16	83.8	16.2
4	48 → 80 V.D.	96	1.33	66.7	33.3

The proportion of clumps no generative shoots also varied among populations, being the smallest in reedswamp and brushwood populations (9.4 and 37%), whereas the biggest in alder-bog population (almost 80%) (Table 3).

The differentiation of growth forms is worth noting (Table 4). Reedswamp population consisted of only orthotropic forms, while alder-bog population enclosed merely plagiotropic individuals. In two other populations both growth forms were present.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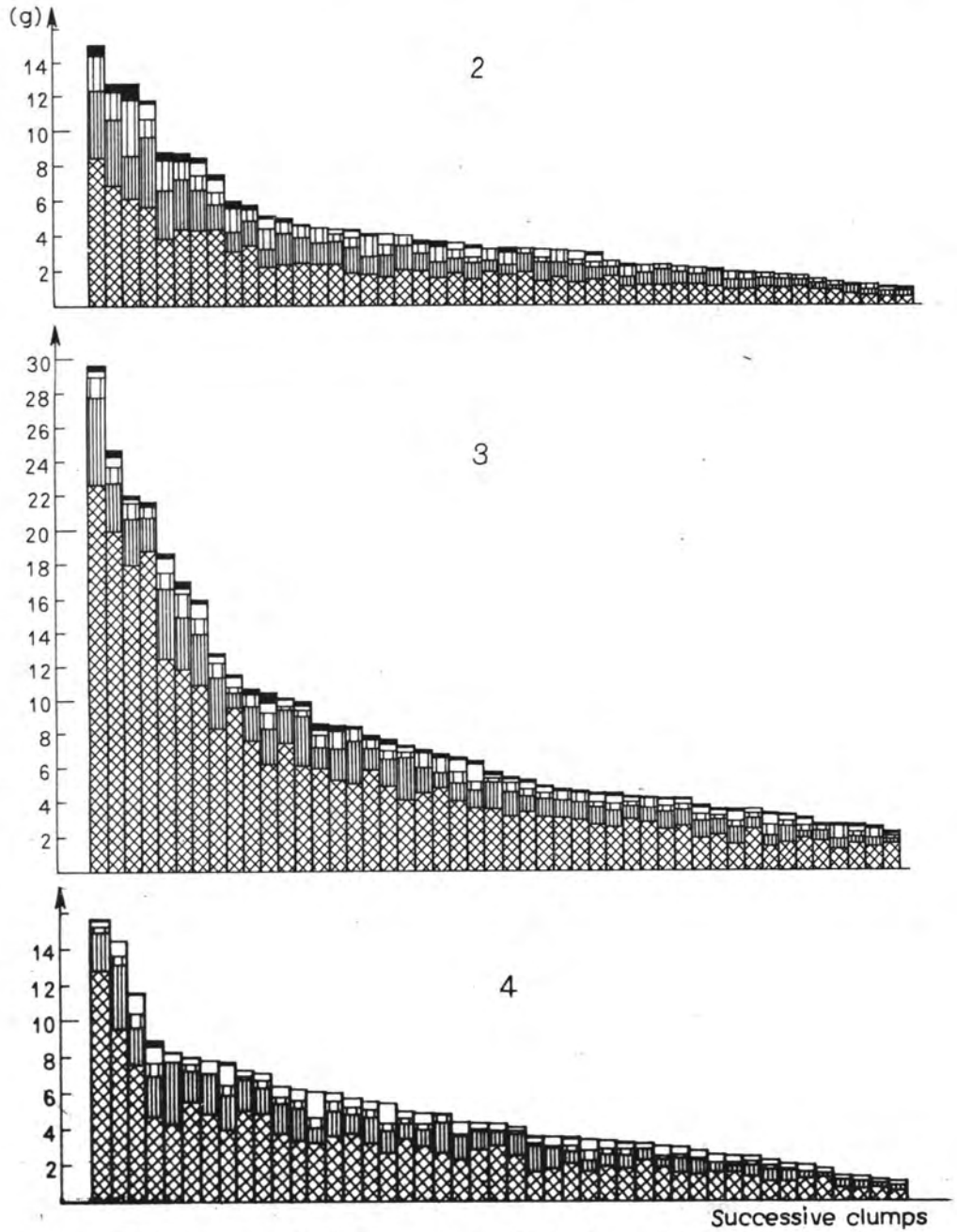

Fig. 2. Biomass allocation in successive *Caltha* clumps. 1-4 As in Fig. 1

Table 3

Clump density and proportion of clumps without generative shoots (G.S.) in *Caltha palustris* populations

Population	Clump number per 100 m²	Proportion of clumps without G.S. (%)
1 A	106± 25.9	9.4
1 B	186± 31.1	37.1
1 C	440± 67.7	34.5
2 A	519± 53.0	37.6
2 B	661± 66.8	39.0
3	531± 57.5	29.9
4	1070±193.1	79.2

± – 95% confidence limits.

Table 4

Number of seeds, vegetative diaspores, and proportion of growth forms of generative shoots in *Caltha palustris* populations

Population	Seed number in 50 clumps	Vegetative diaspore number in 50 clumps	Proportion of growth forms of generative shoots (%)	
			orthotropic	plagiotropic
1	111 864	0	100	0
2	21 508	23	76	24
3	18 957	43	6	94
4	10 004	80	0	100

BIOMASS ALLOCATION TO ORGANS

The clumps were the heaviest in reedswamp population (mean clump weight more than 28 g), and the lightest in moss-community and alder--bog populations (4-5 g). In brushwood population mean clump biomass amounted to c. 8 g (Table 5, Figs. 2-3). In the clumps of analysed populations 1.6-5.8% were allocated to fruit, 2.9-7.8% – to vegetative diaspores, 5.3-16.1% – to shoots, 19.5-32.8% – to leaves, and 48.4-69.4% – to roots. The biomass allocated to reproduction oscillated between 4.5% and 9.4%.

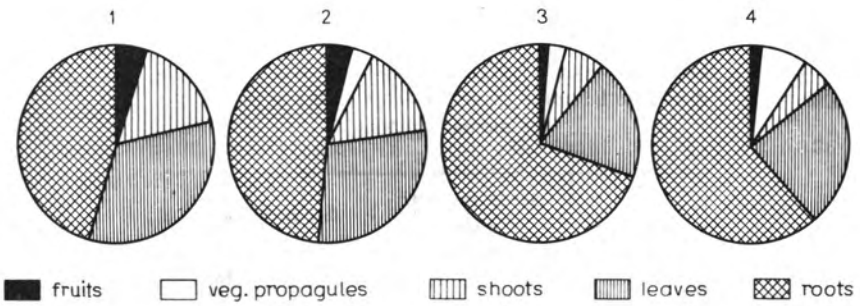

Fig. 3. Biomass allocation to individual organs in *Caltha* clumps. 1-4 As in Fig. 1

Table 5

Mean clump biomass and biomass allocation to individual organs in *Caltha palustris* populations

Population	Mean clump biomass (g)	Biomass allocation to individual organs (%)					
		F	V.D.	F+V.D.	S	L	R
1	28.06	5.3	0.0	5.3	16.1	32.8	45.8
2	4.12	4.1	3.4	7.5	15.3	28.7	48.4
3	8.15	1.6	2.9	4.5	6.6	19.5	69.4
4	4.90	1.6	7.8	9.4	5.3	24.1	61.2

F – fruits, V.D. – vegetative diaspores, S – shoots, L – leaves, R – roots.

SEED PRODUCTION AND GERMINABILITY

The analysed populations highly differed in seed production. *Caltha* individuals in reedswamp population produced sixfold more seeds than those in alder-bog population (Table 4). Similar proportions were obtained for seed number per one individual and per one shoot.

On Petri dishes early collected seeds germinated after 16-22 days, while the late ones after 14 days. Seeds derived from sedge communities (reedswamp and moss-community populations) germinated better (64-68%) than those from the other two populations (45%). The difference between early and late collected seeds was noticed. The former germinated better and faster than the latter (Table 6). The seeds from sedge communities showed higher dynamics of their germination.

Also in trays in the experimental garden (near-natural conditions) seeds from sedge communities exhibited the highest germinability (8-15%), whereas those from alder-bog and brushwood germinated worse (4-6%) (Table 6).

Table 6

Germinability (%) of *Caltha palustris* seeds on Petri dishes (in laboratory), and in trays with soil (in experimental garden)

Population	Seeds on Petri dishes		Seeds in trays	
	early	late	early	late
1	64	–	15	–
2	68	40	8	8
3	45	30	5	6
4	45	39	4	6

Only in reedswamp population no individuals with vegetative diaspores were found. In alder-bog, brushwood and moss-community populations the number of vegetative diaspores amounted to 80, 43 and 23, respectively (Table 2). In order to compare the number of produced seeds and vegetative diaspores the latter were also given in Table 4.

REPRODUCTIVE EFFORT

It was found that the total biomass of fruits from 50 *Caltha* clumps was 7-17 times bigger in reedswamp populations than in the others (Table 7). Similar results were obtained regarding fruit biomass per one shoot and per

Table 7

Reproductive effort (R.E.) of a clump and of an individual with a generative shoot in *Caltha palustris* populations

Population	Biomass of fruits (F) and vegetative diaspores (V.D.) in 50 clumps (g)		Clump R.E. (%)			R.E. of an individual with a generative shoot (%)		
	F	V.D.	(a)	(b)	(c)	(a)	(b)	(c)
1	68.02	0.00	5.74	9.56	39.98	7.11	12.36	49.33
2	8.24	6.85	7.99	15.03	44.68	15.28	27.17	53.94
3	5.95	11.08	5.40	15.14	37.63	9.36	25.85	50.50
4	3.65	17.15	10.85	25.96	39.62	13.76	31.83	48.25

(a) – R.E. calculated traditionally.
(b) – R.E. calculated traditionally, but excluding root biomass.
(c) – Including generative shoot biomass.

one individual. The differences in the biomass of vegetative diaspores were not so pronounced, but in alder-bog population it was doubled compared to that in moss-community population.

The values of reproductive effort (R.E.), calculated by three methods (a, b, c), are presented in Table 7.

a. R.E. as a ratio of biomass of vegetative diaspores and fruit to the clump biomass was the smallest in reedswamp and brushwood populations (less than 6%), slightly higher in moss-community population (8%), and the highest in alder-bog population (more than 10%). Calculated per one individual it was bigger in moss-community and alder-bog populations (15 and 13%), while smaller in reedswamp and brushwood populations (9 and 7%).

b. R.E. as a ratio of total reproductive biomass to the vegetative biomass of above-ground parts was the lowest in reedswamp population and the highest in alder-bog forest, both for one clump and one individual.

c The highest R.E. was obtained for the total of generative shoot biomass and that of propagation organs. However, in that case no statistically significant differences between populations were found by the variance analysis.

REPRODUCTIVE STRATEGIES

The populations were divided into three types with different reproductive strategies regarding the differences in biomass allocation to individual organs, especially to fruits and vegetative diaspores (Table 5, Fig. 4), as well as in the number of seeds and vegetative diaspores (Table 4).

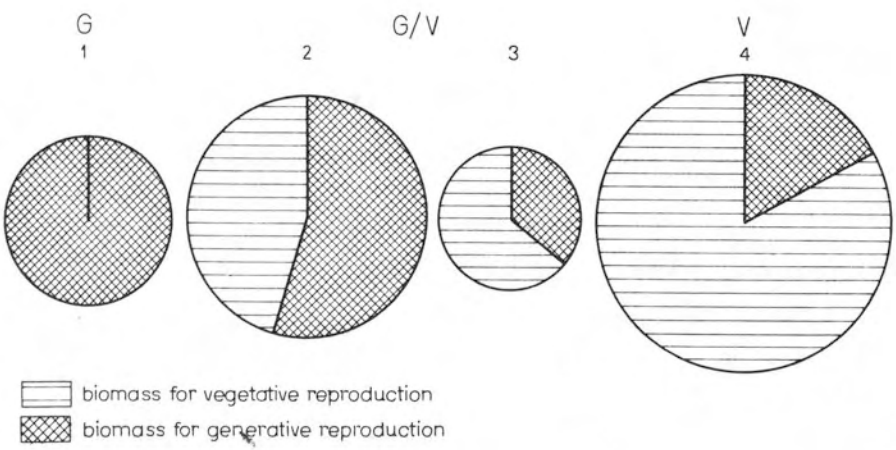

Fig. 4. Reproductive strategy types in *Caltha palustris* populations. G – generative reproduction, G/V – generative and vegetative reproduction, V – vegetative reproduction. 1-4 As in Fig. 1

Type 1 – (G) strategy (reedswamp population). Individuals reproduce only generatively and produce many highly germinable seeds. The number of generative individuals and shoots is the highest (Table 1), while the mean reproductive effort of one clump and individuals with generative shoots, the biomass allocated to reproduction and clump density are lowest (Table 3).

Type 2 – (V) strategy (alder-bog population). Vegetative reproduction dominates. The number of vegetative diaspores is the highest, while that of weakly germinating seeds – the lowest. Biomass allocation to vegetative reproduction is five times bigger than its allocation to fruits (Table 5, Fig. 4). The reproductive effort calculated by a and b methods is the highest. Nearly all clumps contain shoots with vegetative diaspores (Table 2), while their number per one shoot is the highest. Clump density is 2-10 times bigger than in other populations.

Type 3 – (G/V) strategy (moss-community and brushwood populations). Individuals reproduce generatively and vegetatively. Both the seed number (Table 4), and biomass allocated to fruits and vegetative diaspores (Table 5, Fig. 4) are similar in these populations.

Such classification at the same time reflects their distribution in space, in parallel vegetation zones. It is a natural arrangement and three last populations occur in neighbour phytocoenoses. The similarities were observed within the populations of open sedge communities (reedswamp and moss community), and those from brushwoods and alder-bog forests, especially regarding biomass allocation to underground and above-ground organs (Figs. 2 and 3, Table 5) e.g. the former allocate 45% of their biomass to roots, the latter – 60%.

DISCUSSION AND CONCLUSIONS

Caltha palustris individuals can produce both vegetative and generative diaspores on one shoot. As a typical caulophyte it forms annually regenerative, relatively short-lived (1-2 years) shoots (Łukasiewicz 1962). All this makes the population studies on the species difficult. The assessement of the reproductive effort does not seem easy if the *Caltha* clump is considered a modular structure composed of modules-individuals. The problem has been discussed by Watson (1984), Watson and Casper (1984), and Bazzaz et al. (1987).

The origin of a clump as an aggregation ("mini-clone", Falińska 1981) of genets is associated with a vegetative propagation of one among them. The vegets become independent functionally already in their first year, they

produce their own biomass and stop to translocate assimilates with the mother individual. This means that already in the first season new individuals derived from the mother plant lose the direct contact through vascular strands, although they still form well-distinguished clump. Similar tendencies have found in other species by Noble and Marshall (1983), and Hartnett and Bazzaz (1983). Considering all this, it seems that the most objective assessement of R.E. concerns the level of an individual with one generative shoot.

The results obtained have proved that in spite of big differences in reproductive effort values calculated by methods *a* and *b*, general trends have been maintained, hence both techniques can be applied interchangeably. The populations with similar reproductive effort can differ in the number of produced seeds and even in the type of reproductive strategy, which has been also found for *Plantago major* (Lotz and Spoormakers 1988).

Reedswamp population with clumps and individuals 4-7 times bigger than in other populations has the lowest reproductive effort. It has been confirmed by other observations on annual species, larger individuals require relatively smaller reproductive effort to produce large seed number (Lee and Hamrick 1983, Samson and Werk 1986, Klinkhamer and De Jong 1987).

Calculated values of reproductive effort are comparable to those obtained by Falińska (1979) in the Białowieża Forest. *Caltha* individuals from natural populations and those cultivated in the experimental garden allocated, respectively, 20 and 30% of their biomass to reproduction. It seemed to indicate that *Caltha* individuals exhibited high plasticity of their reproductive strategies, formed in the course of their evolution and conditioned geneticaly. The differences in the values of reproductive effort (different reproductive strategies) result from modifying effect of the environment (Seischab et al. 1985, Southwood 1988). Especially interspecific competition is very important. It should be concluded that under natural conditions individuals use their reproductive potential only partly.

Therefore, *Caltha palustris* can be considered as a species resistant to stress, which responses to changes in the environment by modifying reproductive strategy (Grime 1979).

Also big differences in reproductive strategies between forest populations and those from open communities (Falińska 1979) have been confirmed. However, in Białowieża populations vegetative reproduction prevailed in meadow and spring populations, whereas those from alder-bog and flood-plain forests reproduced mainly generatively. It has been probably caused by the differences in the level of stagnant water above the ground and the age of compared phytocoenoses. All this again proves that each individual, population or species has its own specific life strategy (Begon and Mortimer 1981).

The paper has showed that *Caltha palustris* can occupy various niches and form populations which differ in reproductive strategies and the values of reproductive effort.

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Strategie reprodukcyjne Caltha palustris L. w różnych warunkach bytowania

Streszczenie

Porównano wysiłek reprodukcyjny i strategie rozrodcze *Caltha palustris* w czterech fitocenozach z południowego basenu Biebrzy: szuwaru turzycowego (*Caricetum gracilis*), mechowiska turzycowego (*Caricetum limoso-diandrae*), zarośli wierzbowo-brzozowych (*Salix cinerea-Betula pubescens*) oraz olsu (*Carici elongatae-Alnetum*). Stwierdzono, że osobniki badanych populacji różnią się pod względem wielkości biomasy przeznaczonej na reprodukcję generatywną i wegetatywną. Wyróżniono trzy typy strategii rozrodczych: strategię generatywną (G), wegetatywną (V) oraz pośrednią (G/V). Największym wysiłkiem reprodukcyjnym charakteryzowały się osobniki z populacji olsowej (typ strategii (V)), a najmniejszym z szuwaru turzycowego (typ (G)).