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Biological properties of *Majanthemum bifolium* (L.) F. W. Schm. polycormones under various ecological conditions

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Abstract

Majanthemum bifolium (L.) F. W. Schm. populations exhibit a two-level organisation. Individuals in the biological sense (polycormones) consists of a number of basic units-above-ground shoots joined by durable rhizomes. The role of the individual in the population and plant community depends on its age, size and individual area which is the exponent of the number and biomass of the produced organs. It is considered that there exist both intra- and interpopulation differences in the number of above-ground shoots and length of rhizomes as well as in the structure of the developmental phases and age states of the above- and underground parts of the polycormones. In all populations the greater part of the biomass falls to underground organs. A more favourable ratio of shoot biomass to that of rhizomes is, however, found in the polycormones of *Dentario glandulosae-Fagetum* and *Carici elongatae-Alnetum* where the presence of nitrogen in nitrate form was disclosed. With increase of participation of young age classes of shoots more of the total biomass falls to the above-ground parts.

Key words: *Majanthemum bifolium, populations, polycormones, individual area, development phases, age states, biomass proportions*

INTRODUCTION

Under the conditions of forest ecosystems rhizome caulophytes are an abundantly represented morphological-developmental type of perennial (Łukasiewicz 1962). To this group of plants belongs also *Majanthemum bifolium* (L.) F. W. Schm. The latter species is characteristic by the short duration of its above-ground shoots joined by underground organs of high durability. The age limit of the rhizomes attains usually four years; adventitious roots begin to appear on one-year-old segments of the underground shoots, and gradually die back on three-year-old segments (Leszczyńska 1970, 1976).

In up-to-date studies on the different properties of *Majanthemum bifolium* populations (Falińska 1974, 1979, Tumidajowicz 1977, Czarnecka 1985 and others), as individual of this species was conventionally treated each spatially delimited, independently rooted above-ground shoot (Rabotnov 1969). The assumption for *M. bifolium* of the ecological definition of population as a group of individuals of one species constituting a component of a phytocenosis of a definite ecosystem (Falińska 1977) leads to the necessity of defining the morphological-physiological unit ranking as individual. In the present investigations as individual (polycormone) of *M. bifolium* was adopted a multi-shoot and multi-root "morphological whole and physically uninterrupted organisms being an ontogenetic unit which may be considered as the elementary source of the phytogenic field" (Smirnova et al. 1976).

The aim of the study was to define these morphological-developmental properties of *Majanthemum bifolium* polycormones which are decisive for the role of the individual in the structure and functioning of the population and plant community. The following characters were taken into account: 1) age of the unit with rank of individual and calendar age of its particular parts, 2) developmental phases of the above-ground and underground parts of polycormones, 3) size of the individual expressed in the number of above-ground shoots and length of rhizomes, 4) the area occupied by the individual, 5) state and proportions of the biomass of the above- and underground parts of individuals. The information obtained served as basis for defining the structure of the age states, the biomass proportion of the above-ground shoots and rhizomes in the populations and for forecasting the further development of the *M. bifolium* populations developing under different ecological conditions.

MATERIAL AND METHODS

MATERIAL COLLECTION

Majanthemum bifolium polycormones were collected once at the height of the vegetation season (second 10 days of July 1982) in several forest communities of the Roztocze National Park. The following phytocenoses were investigated: upland mixed fir forest (*Abietetum polonicum* (Dziub. 1928) Br. Bl. et Vlieg. 1939) and Carpathian beech forest (*Dentario glandulosae*-

-*Fagetum* (Klika 1927 em. Mat. 1964)) together with the transition zone between these phytocenoses and subboreal moist mixed coniferous forest (*Querco-Piceetum* (Mat. 1952) Mat. et Pol. 1955) and alder forest (*Carici elongatae-Alnetum* Koch. 1926) also with the transition zone between these associations. The geobotanical characteristic of these associations is given by Izdebski and Popiołek (1969) and Izdebski (1972). The plant material was collected close to transects laid out for observations of the population properties of *M. bifolium* (Czarnecka 1985).

The date of collection was choosen according to the indications concerning the morphology and development of above- and underground parts of the plants (Łukasiewicz 1962, 1976) and the growth phenology of underground organs of herbaceous plants (Tumidajowicz 1971). In *M. bifolium* permanent underground shoots (rhizomes and adventitious roots) develop about 2 months later than the above-ground parts so that their maximal growth falls to July. In the latter period of 1982 the above-ground shoots were still in full development on account of the favourable meteorological conditions. Only those polycormones were chosen for examination for which it could be ascertained that the continuity of the rhizomes had not been interrupted during removal of litter and the soil layer underneath it. The *M. bifolium* polycormones removed in this way (54 individuals of this species) were transferred to the laboratory for further examination.

LABORATORY ELABORATION

The underground parts of the polycormones were thoroughly cleaned from soil remains under a mild flow of tap water. After preliminary drying of the roots and rhizomes the *M. bifolium* individuals were placed on sheets of filter paper in possibly natural position (Fig. 1).

Biometric evaluation of the polycormones comprised the following determinations: 1) of the number of above-ground shoots belonging under various ecological conditions to one polycormone, 2) of the number of above-ground shoots in the particular development phases and of various calendar ages, 3) of the rhizome length in the particular development phases and at various calendar ages.

These data allowed to assay the age of the individual in the biological sense and the age of the basic units composing the individual. Pyramids of development phases were also plotted both for the above- and underground parts of the polycormones as well as pyramids of age states in reference to the *M. bifolium* populations in various phytocenoses. For this purpose the classification of age states of Smirnova et al. (1976) was adapted to the properties of the species under investigation.

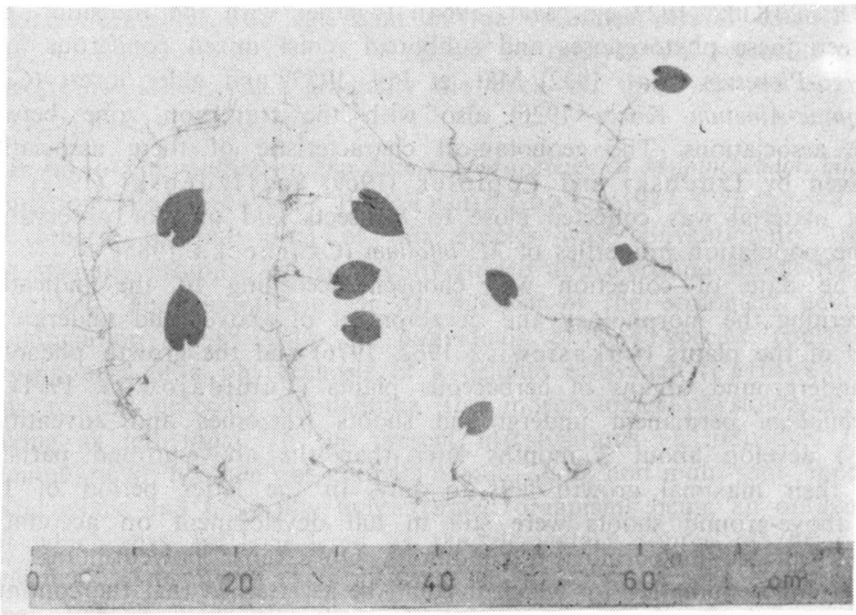

Fig. 1. Area occupied by a *Majanthemum bifolium* polycormone from the *Querco-Piceetum* population

The knowledge of the number of schoots and rhizome sections in the particular development phases served as basis for determining the proportions of young and old "partial shoots" of *M. bifolium* individuals and the ratio of young actively growing rhizome segments to "communicating" rhizomes on the basis of coefficients δ_1 and δ_2 (Gatsuk et al. 1980). These coefficients have the form:

$$\delta_1 = \frac{p-P}{p+P}, \qquad \delta_2 = \frac{p_1-P_1}{p_1+P_1},$$

where P denotes the number of young (regenerative) shoots of the individual, p — the number of old shoots, P_1 — the number of actively growing rhizomes, p_1 — the number of "communicating" rhizomes.

For the selected most vigorous polycormones from fir forest and moist mixed coniferous forest phytocenoses the occupied area was determined. As measure was assumed the surface area outlined by the vertical projection of the space of influence of these individuals on other components of the herb layer and on the abiotic environment. At the same time schematic drawings were prepared indicating the development phases of above- and underground polycormone shoots (Fig. 2). All the *M. bifolium* polycormones separated into above- and underground parts (the latter for some chosen individuals from both phytocenoses were separated according to age classes), were dried at 105° C and weighed, in order to determine the proportions of biomass in the above-ground shoots and rhizomes.

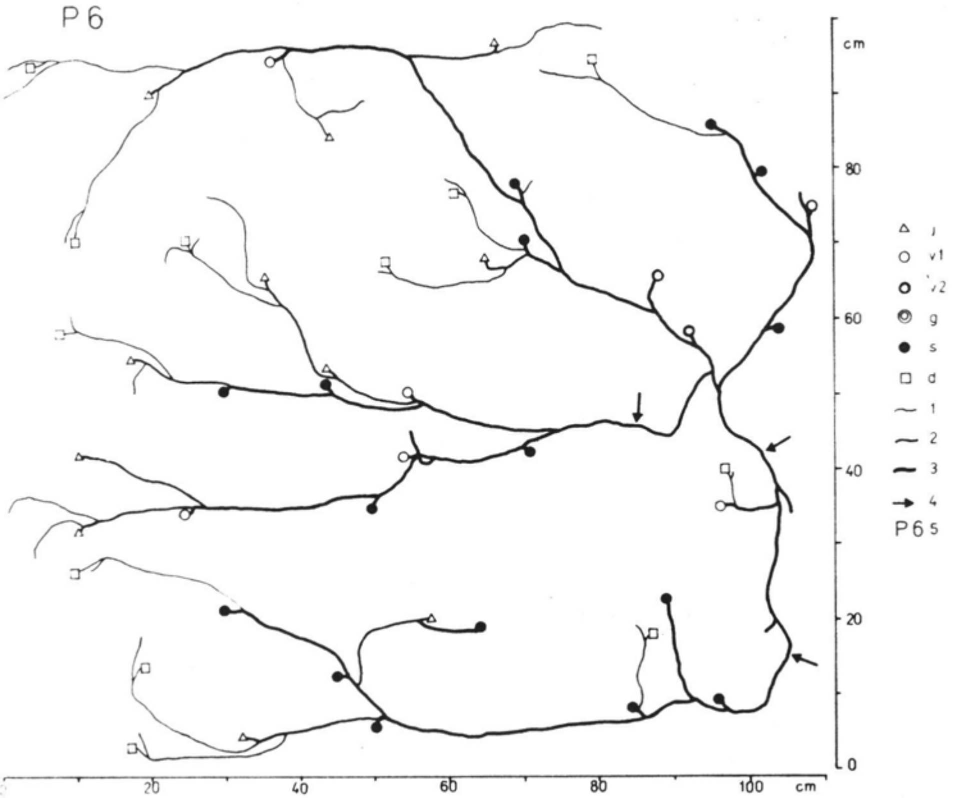

Fig. 2. Area occupied by the *Majanthemum bifolium* polycormone from the *Abietetum polonicum* population; j — juvenile shoots; v1 — virginal (1) shoots; v2 — virginal (2) shoots; g — generative shoots; s — senile shoots; d — regenerative buds ("makings" of next year's above-ground shoots); 1 — juvenile rhizomes; 2 — virginal rhizomes; 3 — senile rhizomes; 4 — points of disintegration of the polycormone; 5 — number of the polycormone

RESULTS

AGE OF INDIVIDUAL

The particular parts of multi-shoot and multi-root *M. bifolium* individuals exhibit various calendar ages and unequal development phases. Among shoots the following age classes are represented:

Fig. 3. Fragment of a *Majanthemum bifolium* polycormone from the ecotonel population between *Abietetum polonicum* and *Dentario glandulosae-Fagetum*; points of the disintegration marked by arrows

— juvenile (1-year-old) shoots without a trace of bygone year's shoot,
— virginal 1 (2-year-old) shoots with remains of the bygone year's shoot but no trace of an older one,
— virginal 2 (3-year-old) shoots with remains of the bygone year's shoot and a distinct trace of an older one,
— generative 2- and 3-year-old flowering (fruiting) shoots with always remains of the bygone year's shoot alone or together with a trace of an older one,
— senile (4-year-old and in some few cases older) shoots, remains of bygone year's shoots and older ones or only remains of older shoots without any distinct trace of the bygone year's one.

The youngest shoots are usually distributed in the most external part of the area occupied by the plant. As we move towards the centre the proportion of shoots in more advanced development stages increases (Figs. 1, 2, 4a, 5a).

The underground parts of *M. bifolium* polycormones — thin and delicate rhizomes 1 to 1.5 mm in diametre — spread horizontally or archwise in the upper soil layer at a depth of several centimetres. Filamentous, wavy or twisted adventitious roots spread radially from the rhizome nodes. The internodes, generally 1.5 to 3 cm long are much shorter close to the base of the above-ground shoots.

Age classes of the rhizomes can be distinguished on the basis of the colour, degree of rooting and distribution. Juvenile rhizomes (current year's) are distributed furthest at the periphery, they are cream-white and have few adventitious roots. These rhizome segments do not end in above-ground shoots or, less frequently, they have "buds", for the next year's shoot below which there always is a short side branching which develops in the following vegetation season into a rhizome increment. Virginal rhizomes (2-year-old) are cream coloured segments profusely rooted ending in juvenile above-ground shoots without any trace of the last year's one. Three-year-old rhizomes light brown in colour with sparse brownish rootlets (gradual dying back) ending in above-ground shoots with remains of the foregoing year's shoot. On these segments of underground shoots sometimes the beginning of disintegration can already be noticed (Fig. 3). Four year-old rhizomes and older ones are brownish segments poorly rooted having still on one side an above-ground shoot with remains of the foregoing year's and older ones or, more frequently, with only remains of the latter shoots, and, on the other side exhibiting always traces of rot. The last two classes (3- and 4-year-old and older) can be considered jointly as senile rhizomes because of the dying back of adventitious roots and the rhizomes themselves.

Units ranking as individuals determined by the age of the oldest part of the plant which has survived to the moment of observations attain usually 3–4 years.

SIZE AND AREA OF INDIVIDUALS

The differences in the number of above-ground shoots and proportions between shoots in the particular developmental phases and calendar age are noticeable also within one population as well as between populations. The greatest mean number of shoots is found on polycormones of the fir forest populations. They are successively much less abundant in the following phytocenoses: moist mixed coniferous forest, transition zone to fir forest, Carpathian beech forest, alder forest, transition zone between mixed coniferous forest and alder and beech forest (Table 1).

The mean joint length of all rhizome segments in the populations of the studied phytocenoses varies within very wide limits: from 351.9 ±

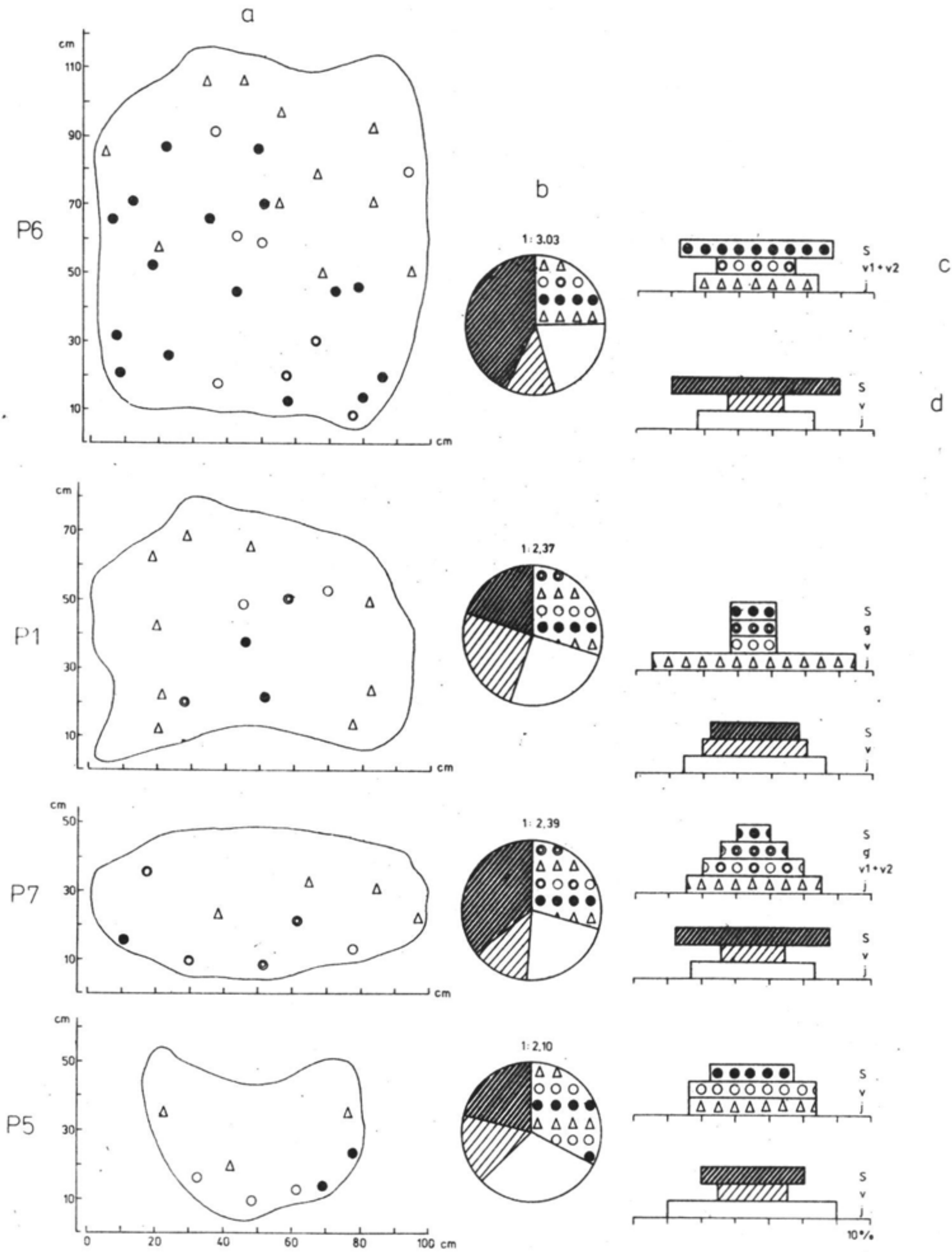

Fig. 4. Properties of chosen *Majanthemum bifolium* polycormones in the *Abietetum polonicum* population; a — area occupied by the polycormone; b — proportion of above-ground parts and of juvenile, virginal and senile rhizomes in the polycormone biomass; c — pyramids of developmental phases of above-ground shoots; d — pyramids of developmental phases of rhizomes; j — juvenile shoots and rhizomes; v — virginal shoots and rhizomes; s — senile shoots and rhizomes; g — generative shoots. Polycormone ordered according to number of above-ground shoots

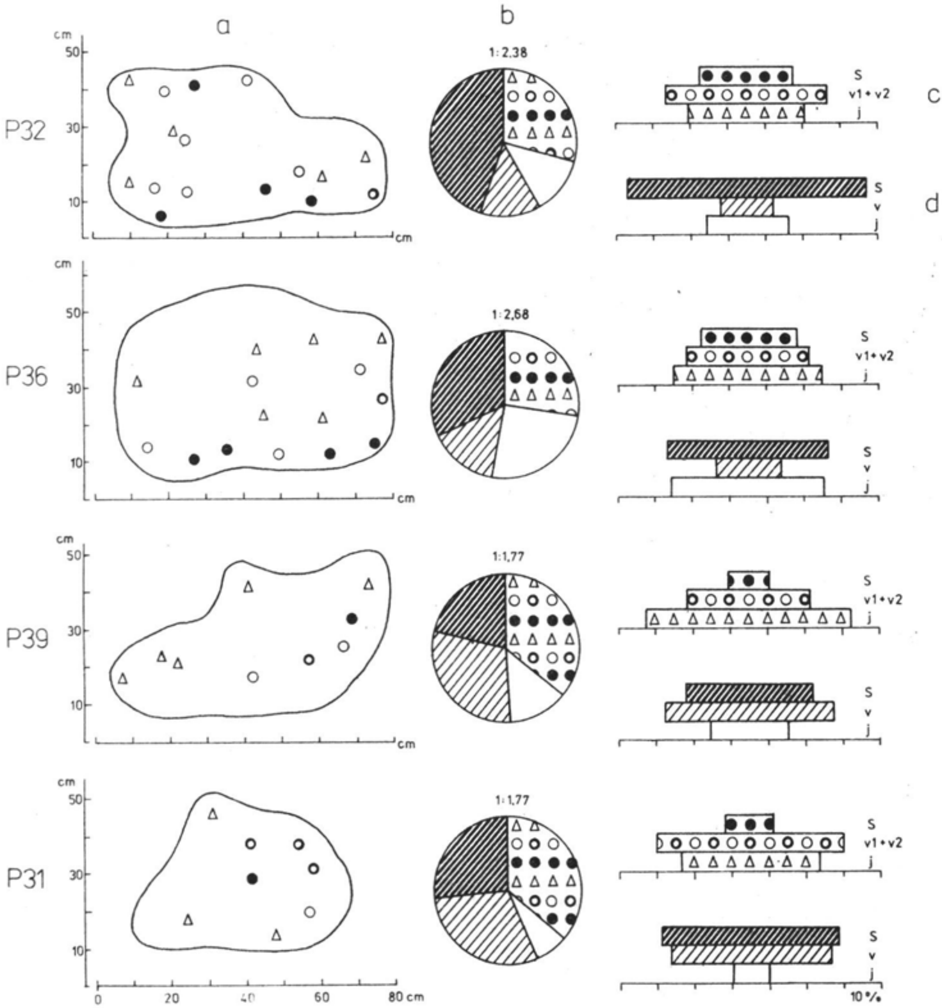

Fig. 5. Properties of chosen *Majanthemum bifolium* polycormones in the *Querco-Piceetum* population; notations as in Fig. 4

± 279.1 to 69.8 ± 40.3 cm. Its value is highest in the *Abietetum polonicum* population, where the sum of lengths of the rhizomes of the particular polycormones shows also the widest range of variability. Second as regards the mean length of underground shoots of *M. bifolium* individuals is the population of the transition zone between fir and beech forest. Lower values are noted in populations of the phytocenoses *Dentario glandulosae-Fagetum* and *Querco-Piceetum*, and the lowest in the populations of the transition zone mixed coniferous forest-alder forest and alder forest (Table 2). The greatest annual rhizome increment is found in the populations

Number of above-ground shoots of *Majanthemum bifolium*

Ecosystem	Total (j + v1 + v2 + g + s)				Juvenile shoots (j)			
	x̄ ± s	min.	max.	%	x̄ ± s	min.	max.	%
Abietetum polonicum	11.62 ± 9.31	5	35	38.7	4.50 ± 3.27	1	11	21.5
Ecotone	6.67 ± 4.37	2	13	47.5	3.17 ± 2.41	1	7	25.0
Dentario glandulosae-Fagetum	4.00 ± 1.26	1	6	40.0	1.60 ± 1.02	1	3	50.0
Querco-Piceetum	6.87 ± 4.01	2	16	41.8	2.87 ± 1.49	1	6	36.4
Ecotone	4.00 ± 1.66	1	7	37.5	1.50 ± 1.00	0	3	43.7
Carici elongatae-Alnetum	4.33 ± 1.88	2	7	50.0	2.17 ± 1.34	0	4	23.1

Rhizome length of *Majanthemum bifolium*

Ecosystem	Total rhizome length, cm			Juvenile length,	
	x̄ ± s	min.	max.	%	x̄ ± s
Abietetum polonicum	351.9 ± 279.1	136.1	1008.8	37.5	131.9 ± 35.8
Ecotone	227.1 ± 169.8	24.0	468.5	38.6	87.7 ± 56.6
Dentario glandulosae-Fagetum	120.6 ± 47.2	43.1	227.1	46.5	56.1 ± 21.9
Querco-Piceetum	127.9 ± 84.2	31.2	363.0	23.3	29.8 ± 35.6
Ecotone	73.8 ± 45.0	32.6	162.4	15.8	11.7 ± 12.9
Carici elongatae-Alnetum	69.8 ± 40.3	24.1	142.9	11.3	7.9 ± 7.5

of the fir forest and transition zone between the latter forest and beech forest (33.8 and 33.2 cm, respectively), and the smallest in the alder forest (as little as 20.5 cm).

The area occupied by *M. bifolium* (Fig. 2) is the exponent of the number of above-ground shoots produced and number of rhizome segments and their joint length. The size of the area occupied varies both for polycormones from the same and from different ecological conditions.

Individuals of the fir forest population with the largest number of above-ground shoots and joint length of different-aged rhizome segments (Tables 1 and 2) occupy also the largest area, varying as rule within the limits of 0.5 to 1.0 m^2 (Fig. 4a). In the population of mixed coniferous forest ranking second as regards the number of above-ground shoots per one individual, although exceeded in the sum of rhizome length by the population of the transition zone between fir forest and beech forest (Tables 1 and 2), the areas occupied by the most prominent polycormones amounted from 0.25 to 0.5 m^2 (Fig. 5a).

The surface determining the vertical projection of the space of influence of the individuals is usually oval (Figs. 4a and 5a), although some

Table 1

polycormones in various environmental conditions

Virginal shoots (v1 + v2)			Generative shoots (g)				Senile shoots (s)			
$\bar{x} \pm s$	min.	max.	%	$\bar{x} \pm s$	min.	max.	%	$\bar{x} \pm s$	min.	max.
2.50 ± 2.11	1	8	4.3	0.50 ± 0.87	0	2	35.5	4.12 ± 4.70	0	16
1.67 ± 1.32	0	4	—	—	—	—	27.5	1.83 ± 1.57	0	4
2.00 ± 1.41	0	4	—	—	—	—	10.0	0.40 ± 0.49	0	1
2.50 ± 1.69	0	7	0.9	0.06 ± 0.24	0	1	20.9	1.44 ± 1.27	0	4
1.75 ± 1.20	0	4	—	—	—	—	18.8	0.75 ± 1.00	0	3
1.00 ± 0.41	0	2	—	—	—	—	26.9	1.17 ± 1.07	0	3

Table 2

polycormones in various environmental conditions

rhizomes cm		Virginal rhizomes length, cm				Senile rhizomes length, cm			
min.	max.	%	$\bar{x} \pm s$	min.	max.	%	$\bar{x} \pm s$	min.	max.
21.4	348.7	20.1	70.7 ± 57.1	14.3	166.0	42.4	149.3 ± 137.0	34.4	494.1
5.8	164.4	22.5	51.0 ± 44.1	0.0	130.3	38.9	88.4 ± 81.0	11.8	173.6
29.1	94.4	24.0	29.0 ± 17.1	0.0	52.4	29.5	35.5 ± 17.9	14.0	59.1
0.0	148.1	27.1	34.6 ± 17.6	9.5	73.7	49.6	63.5 ± 46.4	18.7	174.3
0.0	41.1	22.4	16.5 ± 14.6	0.0	39.1	61.8	45.6 ± 10.7	2.8	106.8
0.0	19.6	38.5	26.9 ± 22.3	0.0	70.9	50.2	.35.0 ± 28.9	12.8	94.9

polycormones, especially younger ones, spread distinctly in one direction. With ageing (prevalence of the dying back process over renewal) the oldest part of the polycormone gradually dies. Owing to the interruption of continuity of the rhizomes, division occurs into several smaller units (Figs. 2 and 3) which begin to form new rhizome segments and new above-ground shoots. Disintegration and intensive growth of new units as the result of the process of renewal over that of dying leads to an increase of the areas and further to their overlapping. This produces large *M. bifolium* agglomerations within which the rhizomes of various polycormones interwine so that it is very difficult to distinguist the particular units ranking as individuals.

STRUCTURE OF DEVELOPMENT PHASES AND AGE STATES

Majanthemum bifolium individuals even when originating from the same phytocenoses differ considerably in their percentual proportion of above--ground and underground shoots at the given development phase. This may be seen from the development pyramids for shoots and rhizomes (Figs. 4 and 5).

In the populations from *Abietetum polonicum* the differences in the share of juvenile virginal and senile shoots between the particular polycormones may reach 20–30 per cent, the range of variability being widest for the oldest shoots. Moreover, all polycormones do not produce generative shoots (Fig. 4c). In individuals of *M. bifolium* from the *Querco-Piceetum* phytocenosis the widest range of variations is observed in the class of juvenile shoots and the smallest in the senile class. None of the polycormones included in the comparative observations of this phytocenosis formed generative shoots (Fig. 5c).

M. bifolium polycormones also show considerable differences in the proportion of the particular development phases of the rhizomes (Figs. 4d and 5d). In the fir forest population the smallest share of juvenile (current year's) rhizomes, expressed in the sum of lengths of the particular segments, noted in an individual occupying the largest area. Only the polycormone with the smallest area of all showed a preponderance of youngest rhizomes (Fig. 4a, d). For instance, polycormones developing under the conditions of mixed moist coniferous forest were as a rule characterised by a lower percentual proportion of the juvenile rhizome class and a higher one of senile rhizomes (Fig. 5d).

Plotting of pyramids of age states on the basis of all the collected polycormones allows to evaluate the age structure of the *M. bifolium* populations growing under different ecological conditions (Tables 1 and 2, Figs. 6 and 7).

As far as the decreasing proportion of juvenile shoots is concerned the examined populations can be ordered as follows: alder forest, transition zone between fir forest and Carpathian beech forest, moist mixed coniferous forest, fir forest and the transition zone between mixed coniferous forest and alder forest. The share of shoots of "mean" calendar age (2- and 3-year-old, virginal) varies within the limits of 20–50 per cent, being lowest in the beech forest population and highest in that from the fir forest. Intermediate values were noted successively for the populations of the transition zone mixed coniferous forest-alder forest, mixed coniferous forest, transition zone fir forest-beech forest and alder forest. As regards 4-year shoots and older ones the differences are widest between the fir and beech forest populations (differences within limits of 25%). The transition zone fir forest-beech forest population is in this respect close to the *Abietetum polonicum* population (Table 1, Fig. 6a), whereas in the phytocenosis moist mixed coniferous forest-alder forest and the transition zone between these two communities the populations show differences of barely a few per cent in the proportion of oldest above-ground shoots (Table 1, Fig. 7a).

Table 3

Scale of δ_1 and δ_2 coefficients variability in the *Majanthemum bifolium* populations

Ecosystem	Coefficient δ_1		Coefficient δ_2	
	min.	max.	min.	max.
Abietetum polonicum	−0.67	+0.67	−0.18	+0.78
Ecotone	−0.60	+0.11	−0.71	+0.27
Dentario glandulosae-Fagetum	−1.00	−0.20	−0.14	+0.08
Querco-Piceetum	−1.00	0.00	0.00	+0.78
Ecotone	−1.00	+0.43	+0.14	+0.78
Carici elongatae-Alnetum	−1.00	0.00	+0.33	+0.75

The proportion between the number of young ("renewal" shoots) shoots and old shoots reflects the value of the coefficient δ_1 (Table 3). To the category of "renewal" shoots may be classified juvenile (one-year) and virginal 1 (2-year) ones. It may, namely, be supposed that in the next vegetation season new above-ground shoots will arise from the regenerative buds in their place. Shoots of the remaining age classes may be considered as old. Index δ_1 calculated for the particular polycormones of the *Abietetum polonicum* populations varies in rather wide limits indicating the presence of individuals with prevalence of "renewal" shoots and of those in which old shoots dominate. A similar tendency, with a narrower range of variability, is illustrated by the population of the transition zone from fir to beech forest. On the other hand, in *Dentario glandulosae-Fagetum* young shoots markedly prevail in all polycormones. The populations of the second pair of neighbouring phytocenoses, *Querco-Piceetum* and *Carici elongatae-Alnetum* are characterised by *M. bifolium* individuals with a majority of younger shoots. In the populations of the transition zone between these associations polycormones may also be found with prevailing old shoots "non-renewal" (Table 3).

The age structure of *M. bifolium* populations as regards underground parts, like in the case of above-ground shoots, differs under various ecological conditions. In the populations of the phytocenoses of *Abietetum polonicum* — transition zone — *Dentario glandulosae-Fagetum* a marked increase is observed of the number of juvenile rhizomes and a decrease of the proportion of senile ones in the order from fir forest towards beech forest (Table 2, Fig. 6b). The participation of actively growing (juvenile) and "communicating" rhizomes (of the remaining age classes) described by the coefficient δ_2 are different in each of these three populations. In *Abietetum polonicum* there is a distinct tendency to a prevalence of rhizomes of older age classes. In the populations of the transition zone the range of variation is equally wide, but indicates an increase of noticeable participation of actively growing rhizomes. Polycormones

Table 4

Biomass of *Majanthemum bifolium* polycormones in various environmental conditions

Ecosystem	Biomass, g						Ratio a:b		
	above-ground parts (a)			underground parts (b)			in population	min.	max.
	$\bar{x} \pm s$	min.	max.	$\bar{x} \pm s$	min.	max.			
Abietetum polonicum	0.481 ± 0.33	0.158	1.061	1.263 ± 0.94	0.390	3.214	1:2.63	1:2.10	1:3.30
Ecotone	0.506 ± 0.22	0.273	0.848	1.398 ± 0.49	0.748	2.119	1:2.76	1:2.15	1:4.87
Dentario glandulosae--Fagetum	0.221 ± 0.12	0.043	0.387	0.485 ± 0.24	0.093	0.769	1:2.19	1:1.97	1:2.50
Querco-Piceetum	0.180 ± 0.14	0.023	0.547	0.430 ± 0.34	0.128	1.467	1:2.39	1:1.40	1:5.56
Ecotone	0.119 ± 0.06	0.029	0.198	0.251 ± 0.21	0.074	0.707	1:2.11	1:1.20	1:3.57
Carici elongatae-Alnetum	0.105 ± 0.06	0.031	0.212	0.204 ± 0.10	0.079	0.363	1:1.94	1:1.40	1:2.51

in the *Dentario glandulosae-Fagetum* phytocenosis show a greater stability of the proportion of young and old underground shoots (Table 3).

In the sequence of communities comprising moist mixed coniferous forest, the transition zone and alder forest, the percentual proportion of youngest rhizomes shows a diminishing tendency (Table 2, Fig. 7b). The highest participation of 2-year-old rhizomes is found in the alder forest, and the lowest in the above mentioned transition zone. In population of the moist mixed coniferous forest and alder forest about one half

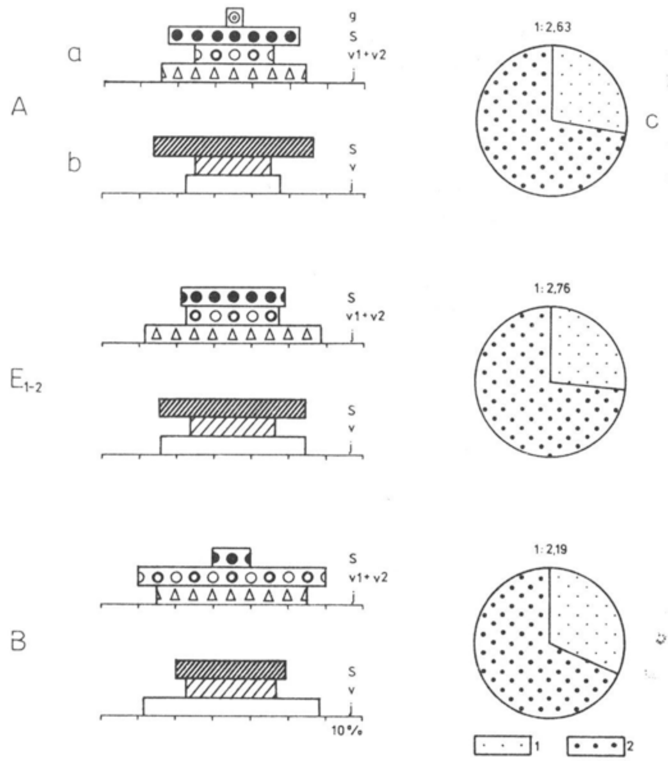

Fig. 6. Properties of *Majanthemum bifolium* polycormones in *Abietetum polonicum* (A), *Dentario glandulosae-Fagetum* (B) and their ecotone (E_{1-2}) populations; a — pyramids of age states of above-ground shoots, b — pyramids of age states of rhizomes, c — proportion of above-ground and underground parts in the polycormone biomass, 1 — biomass of above--ground parts, 2 — biomass of underground parts (remaining notations as in Fig. 4)

of the joint length falls to the oldest underground parts of the polycormones, and in the transition zone between these phytocenoses to even more than 60 per cent of the total rhizome length (Table 2, Fig. 7b). The coefficient δ_2 calculated for individuals of the *Querco-Piceetum* and *Carici elongatae-Alnetum* populations and the transition zone between them indicate an unfavourable proportion of "renewal" rhizomes and older "communicating" rhizomes in these three populations (Table 3).

STATE AND PROPORTIONS OF BIOMASS

The state of biomass and its proportion falling to above-ground and underground parts of *M. bifolium* individuals are an exponent of the area occupied, the number and calendar age of the above ground--shoots and the number and length of rhizome segments. The greater

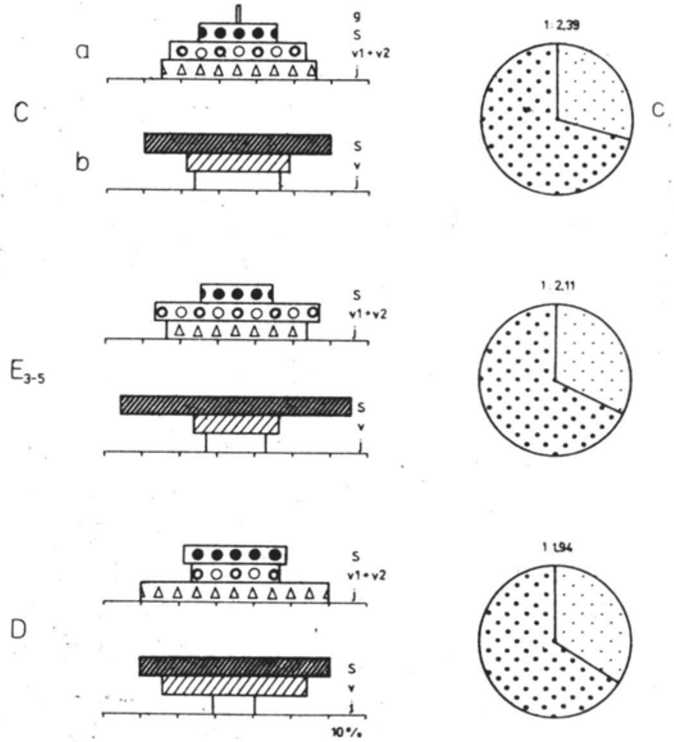

Fig. 7. Properties of *Majanthemum bifolium* polycormones in *Querco-Piceetum* (C), *Carici elongatae-Alnetum* (D) and their ecotone (E_{3-5}) populations; notations as in Figs. 4, 6

part of the polycormone biomass of *M. bifolium* polycormones is located in the permanent underground organs, but the ratio of the biomass of the underground parts to that of the above-ground ones varies both between individuals and whole populations.

For the selected polycormones from ecosystems of fir forest and moist mixed coniferous forest the proportion of the biomass of rhizomes in the particular development phases and calendar ages (Figs. 4b and 5b) is in general in agreement with the pyramids plotted on the basis of the sum of lengths of rhizome segments in the same phases (Figs. 4d and 5d). There is a distinct relation between the pyramid of developmental phases of above-ground shoots (Figs. 4c and 5c) and the proportion of the biomass of these parts to the underground parts of the polycormones (Figs. 4b and 5b). Younger polycormones exhibit a higher share of above ground parts in the total biomass as compared with individuals in which the process of shoot dying prevails over their renewal.

The highest mean biomass value of above-ground and under-ground parts and percentage of biomass falling to the underground organs is found in the polycormones of the transition zone between fir forest and Carpathian beech forest (Table 4). Mean values and biomass proportions for polycormone populations of *Abietetum polonicum* only slightly differ from those for the populations of the transition zone. The range of variability of biomass values of above-ground organs, and especially of the underground ones is here, however, much wider, with closer to equal proportions of biomass in the particular individuals, whereas the population of *M. bifolium* from the beech forest differs markedly as regards mean values of above--ground and underground parts weight from both the above mentioned populations. It is also characterised by a much higher biomass percentage in the above-ground shoots (Table 4, Fig. 6c).

In the phytocenose system moist mixed coniferous forest-transition zone--alder forest there is a distinct directional tendency of changes. The mean biomass value of above- and underground parts of individuals diminishes from the *Querco-Piceetum* towards the *Carici elongatae-Alnetum* population. The range of the compared variabilities is also much narrower in comparison with the previously discussed populations (Table 4). The participation of above-ground shoots in the total biomass of *M. bifolium* polycomones is highest in the alder forest population (Fig. 7c).

When comparing whole populations as in the case of individuals, the regularity is confirmed that, with increase of the percentual proportion of young age classes of shoots (juvenile, virginal 1 and virginal 2) more biomass falls to the above-ground parts of polycormones (Figs. 6 and 7).

DISCUSSION

Perennial herbaceous plants are characterised by a two-level organisation of their populations. Individuals in the biological sense (polycormones) consist of a number of basic units — above-ground shoots with rhizome segments corresponding to them. Determination of the number, size and age of these units serves as basis for establishing the role of the individual in the population and in the plant community. The area occupied and nutritional requirements of individuals, in turn, depend on their size and biomass as do also their chances of servival and participation in reproduction (Falińska 1981, 1984).

M. bifolium polycormones have their own individual structure even within the same population and structure of the development phases of above-ground and underground parts. Pyramids of age states of the population illustrate not only the current age structure but also its perspectives of further population development. Prognoses for the future are, however, much more reliable on the basis of coefficients δ_1 and δ_2. They indicate the intensity of the renewal and dying processes occurring at the level of multi-shoot individuals. They occur almost simultaneously, but with varying intensity in the particular periods of the polycormone developmental cycle (Falińska 1984). A favourable proportion of actively growing rhizomes to the "communicating" ones indicates, moreover, the formation of "markings" of new above-ground shoots which will participate in the increase of the individual area. On the other hand, prevalence of older age classes of rhizomes points to a greater probability of polycormone disintegration leading to an increase of the number of independent units in the population. Disintegration of the polycormone stimulates, in turn, development of regenerative buds from which new rhizome segments arise. As results from the investigations of Łukasiewicz (1962) on rhizomic plants, the underground shoots still transmit for some time nutrient components to younger rhizome segments after the death of the corresponding above-ground shoots. In *M. bifolium* polycormones segments ending in remains of above-ground shoots constitute often a considerable percentual participation in the total length and biomass of the underground parts. In this light the process of gradual dying of permanent polycormone organs, and, as consequence, their disintegration are favourable events for the further fate of the population.

In the case of *M. bifolium* the disintegration process is observed usually in 3- to 4-year-old polycentric individuals which are in the phase of vegetative (virginal) or generative maturity. In comparison *Mercurialis perennis* polycormones start dying back of the oldest parts in the 5-6th year of life (Falińska 1982, 1985), while *Aegopodium podagraria* ones at the age of 5–7 years (Gatsuk et al. 1980). Polycormone disintegration in *M. bifolium* occurs much more frequently in *Abietetum polonicum* and *Querco-Piceetum* populations than in those of other phytocenoses. This is probably a reaction to the stress of the environment, especially to phosphorus and nitrogen deficit, or to the light conditions (Grime 1979).

The supply of nutrient compounds, mainly nitrogen, in the habitat influences the development of biomass, its state and proportion. In poorer habitats it is mainly the underground parts that multiply, decisive for the durability and role of the organism in the given phytocenosis. Richer habitats make possible a greater biomass increment in above-ground parts. The ratio of biomass of shoots to the biomass of the underground parts is much more favourable in the *Dentario glandulosae-Fagetum* and *Carici elongatae-Alnetum* populations, where nitrogen is present in nitrate form (Czarnecka 1985).

The number of above-ground shoots per one individual finds also its reflection in the biomass proportion. In *M. bifolium*, the plagiotropic segments of the rhizomes connect the single above-ground shoots distributed at large distances from one another. In another caulophyte, *Mercurialis perennis* which forms agglomerations of above-ground shoots, the percentual participation of these parts in the biomass of even-aged polycormones may be 1.5–2 times higher (Falińska 1982). On the other hand, results similar to those obtained for *M. bifolium* were reported by Noble et al. (1979) for the *Carex arenaria* population.

The size and durability in time and space of the underground organs of *M. bifolium* polycormones modified by the environmental conditions decide of the structural and functional properties of the population, contribute to the stabilisation of the population and determine the participation of this species in forest phytocenoses. In this way the relations and links at several levels of biological organisation: the individual — the population — the phytocenosis — the ecosystem, are realised.

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Właściwości biologiczne polikormonów Majanthemum bifolium (L.) F. W. Schm. w różnych warunkach ekologicznych

Streszczenie

Badano właściwości osobników *Majanthemum bifolium* (L.) F. W. Schm. w sensie biologicznym (polikormonów) w populacjach kilku fitocenoz leśnych: wyżynnego jodłowego boru mieszanego (*Abietetum polonicum*) i buczyny karpackiej (*Dentario glandulosae-Fagetum*) ze strefą przejścia między nimi oraz subborealnego wilgotnego boru mieszanego (*Querco-Piceetum*) i olsu (*Carici elongatae-Alnetum*), również ze strefą przejścia między tymi asocjacjami. Stwierdzono, że polikormony w populacjach tych fitocenoz różnią się liczbą pędów nadziemnych i długością kłączy oraz arealem osobniczym, który jest wykładnikiem liczby wytworzonych organów. Osobniki konwalijki wykazują odmienną strukturę faz rozwojowych części nadziemnych i podziemnych, a poszczególne populacje różnią się strukturą stanów wiekowych. Przeważająca większość biomasy przypada na organy podziemne, przy czym zarówno pojedyncze polikormony, jak i całe populacje różnią się proporcjami biomasy pędów nadziemnych i kłączy. W miarę wzrostu udziału młodszych klas wiekowych pędów, więcej ogólnej biomasy przypada na części nadziemne.