

<b>EKOLOGIA POLSKA</b> (Ekol. pol.)	<b>37</b>	<b>1 – 2</b>	<b>191 – 208</b>	<b>1989</b>
--	-----------	--------------	------------------	-------------

Bożenna CZARNECKA

Department of Ecology and Laboratory of Biology Didactics, Institute of Biology, M. Curie-Skłodowska University, Akademicka 19, 20-033 Lublin, Poland

## THE EFFECT OF MORPHOLOGICAL-DEVELOPMENT PROPERTIES OF INDIVIDUALS ON SPATIAL ORGANIZATION OF *MAIANTHEMUM BIFOLIUM* (L.) F. W. SCHMIDT POPULATIONS

**ABSTRACT:** Spatial structure of *Maianthemum bifolium* populations in forest phytocoenoses and transition zones (ecotones) is usually of an aggregated type. Such spatial organization of populations conditioned fundamentally by morphological-development properties of the species. These are: individual growth into polycormones, their internal spatial structure and dynamics of basic units, growing, regeneration and dying processes of permanent organs at an individual level and also dominance of vegetative reproduction.

**KEY WORDS:** *Maianthemum bifolium*, polycormone, forest ecosystems, ecotones, plant populations, spatial structure, vegetative reproduction.

### 1. INTRODUCTION

Aggregated type is the dominant one as regards spatial distribution of plants. An exception are only pioneer species settling on homogenous areas of seaside and inland dunes or salt pans. One of the three groups of factors conditioning such pattern of spatial distribution of vegetation are morphological properties of the species, the other being environmental and social (K e r s h a w 1978).

The aim here has been to show how such morphological-development properties of species as individual growth into polycormones, their own spatial structure and internal dynamics of basic units, including dominance of vegetative reproduction, influence the formation of spatial organization of population.

As an object of investigations *Maianthemum bifolium* has been chosen as a species having a broad ecological amplitude, representing perennial plants – the abundant group of plants in forest ecosystems. Individuals of May-flower in the biological sense



(polycormones) considerably develop permanent underground organs and multiply the number of aboveground shoots forming aggregations varying in size and durability (C z a r n e c k a 1986a). Under natural conditions this species reproduces practically only vegetatively, despite signs of generative reproduction (production of flowers, fruits and seeds) and preserved germination ability of seeds under laboratory conditions (B. Czarnecka – unpublished data).

## 2. OBJECT OF INVESTIGATIONS, MATERIAL AND METHODS

Between 1980 and 1983 several forest phytocoenoses in the Roztocze National Park were investigated: upland mixed fir forest [*Abietetum polonicum* (Dziub. 1928) Br. et Vlieg. 1939] and Carpathian beech forest [*Dentario glandulosae-Fagetum* (Klika 1927) em. Mat. 1964] with their transition zone, subboreal moist mixed coniferous forest [*Querco-Piceetum* (Mat. 1952) Mat. et Pol. 1955] and alder forest [*Carici elongatae-Alnetum* Koch. 1926] also with a transition zone. I z d e b s k i and P o p i o ł e k (1962) give the floristic, phytosociological and ecological characteristics of the first pair of associations. I z d e b s k i (1972) has described conditions in *Querco-Piceetum* and *Carici elongatae* – *Alnetum* phytocoenoses.

In these two systems of neighbouring phytocenoses research areas have been chosen (40 - 60 m long and 10 m wide) within which 2 m wide belt transects were determined. The transects were divided into squares of a side both 2 and 1 m. The fir forest had additionally 2 surface areas 20 × 10 m with short transects 10 × 2 m. Ecotones within all transect replications were determined on the basis of floristic composition of herb and moss layers and using degrees of floristic similarity between squares of transects. These coefficients were calculated both according to frequency and cover degree of species after Sørensen's formula (Č e š k a 1968). A detailed description of research transects can be found in the paper by C z a r n e c k a (1986b).

In three successive research seasons (1980, 1981, 1982) maps of all squares in transects were made in the scale of 1:10 indicating places of attachment of *Maianthemum bifolium*, considering as an individual each rooted aboveground shoot (R a b o t n o v 1969). On special forms the number of shoots, cover degree of species examined and of other remaining herb layer components, were recorded. This was repeated in 1983 but only in the case of squares, on which the density of *Maianthemum bifolium* shoots varied greatly in previous years.

The type of spatial distribution of May-flower population was estimated by means of aggregation coefficient, the so-called Leksis index (Steinhaus 1936, 1947 after K w i a t k o w s k a and S y m o n i d e s 1980). For mean population densities in phytocoenoses and ecotones, standard deviation and confidence intervals were determined (O k t a b a 1976).

The size of *M. bifolium* individual in the biological sense (polycormone) was determined on the basis of 54 units collected at the height of vegetation season (II half of



July) in 1982 in the close neighbourhood of research transects (C z a r n e c k a 1986a). The analysis of polycormones allowed to distinguish the following development stages of aboveground shoots: juvenile (j) — barren shoots without a trace of bygone year's shoot; virginal (v) — barren shoots with a trace of bygone year's shoot or bygone year's and older shoot; generative (g) — flowering (fruiting) shoots with a trace of older shoots; senile (s) — remnants of bygone year's and older shoots.

Knowing the number of shoots producing leaves, without taking into account senile shoots (s), one could determine population density expressed by the number of polycormones per 1 m<sup>2</sup>.

The plant material collected was used also to estimate vegetative reproduction of population under different ecological conditions. The measure of effectiveness of vegetative reproduction (without regeneration) was considered as: (1) The ratio of the number of "makings" of next year's above-ground shoots to the total of this year's shoots (i.e. in 1982) assuming that the "makings" of next year's shoots were only regenerative buds at the greatest distance from the oldest part of the polycormone. These buds have always in the nearest neighbourhood short branchings of rhizomes providing a new increment in the next season (Figs. 1, 2). Such rooted buds with their

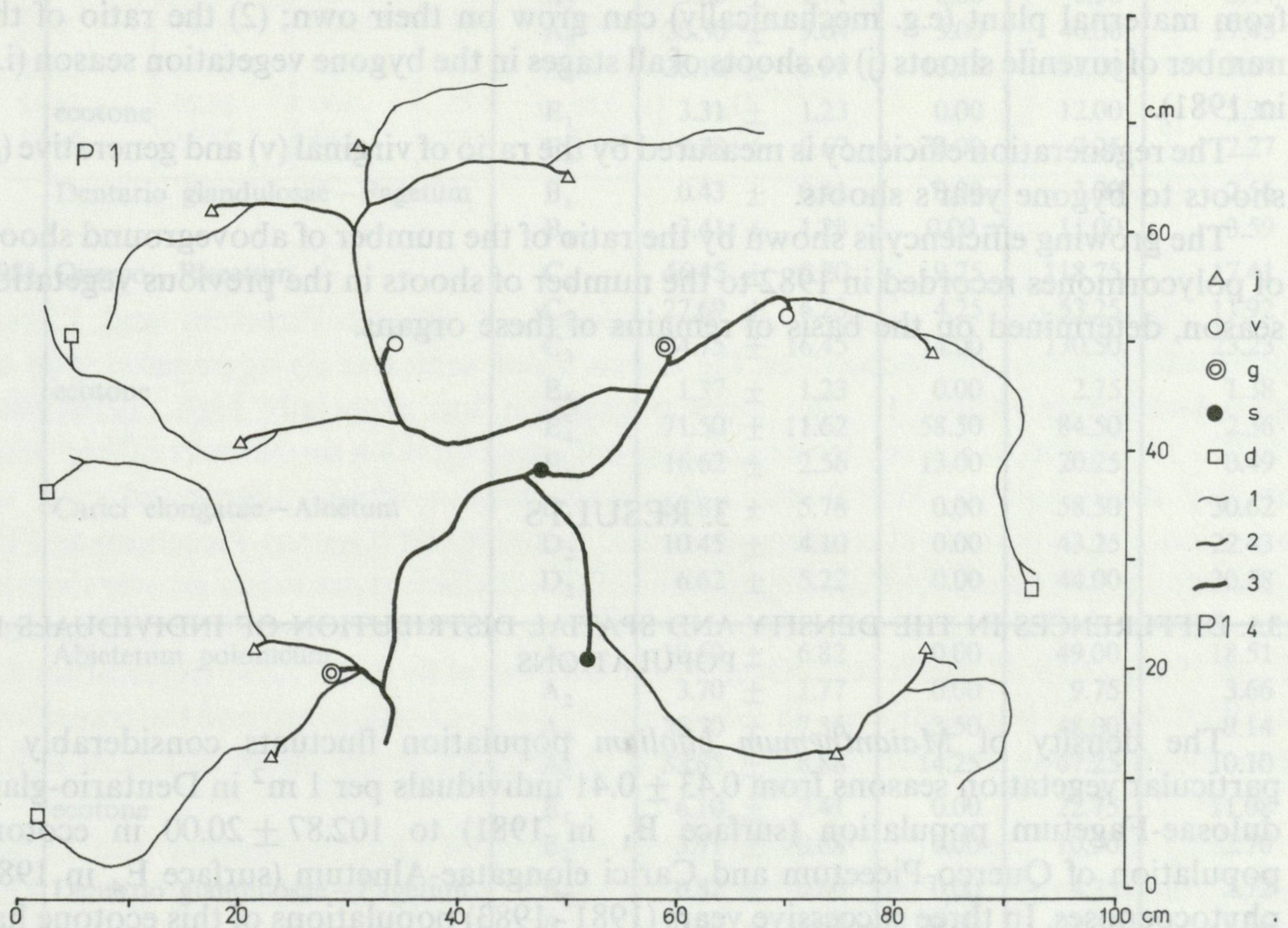


Fig. 1. *Maianthemum bifolium* individual in the biological sense (polycormone) from *Abietetum polonicum* phytocenosis

j — juvenile shoots, v — virginal shoots, g — generative shoots, s — senile shoots, d — regenerative buds playing the part of vegetative diaspores ("makings" of next year's aboveground shoots), 1 — juvenile rhizomes (1 year old), 2 — virginal rhizomes (2 years old), 3 — senile rhizomes (3 years and more), 4 — polycormone number



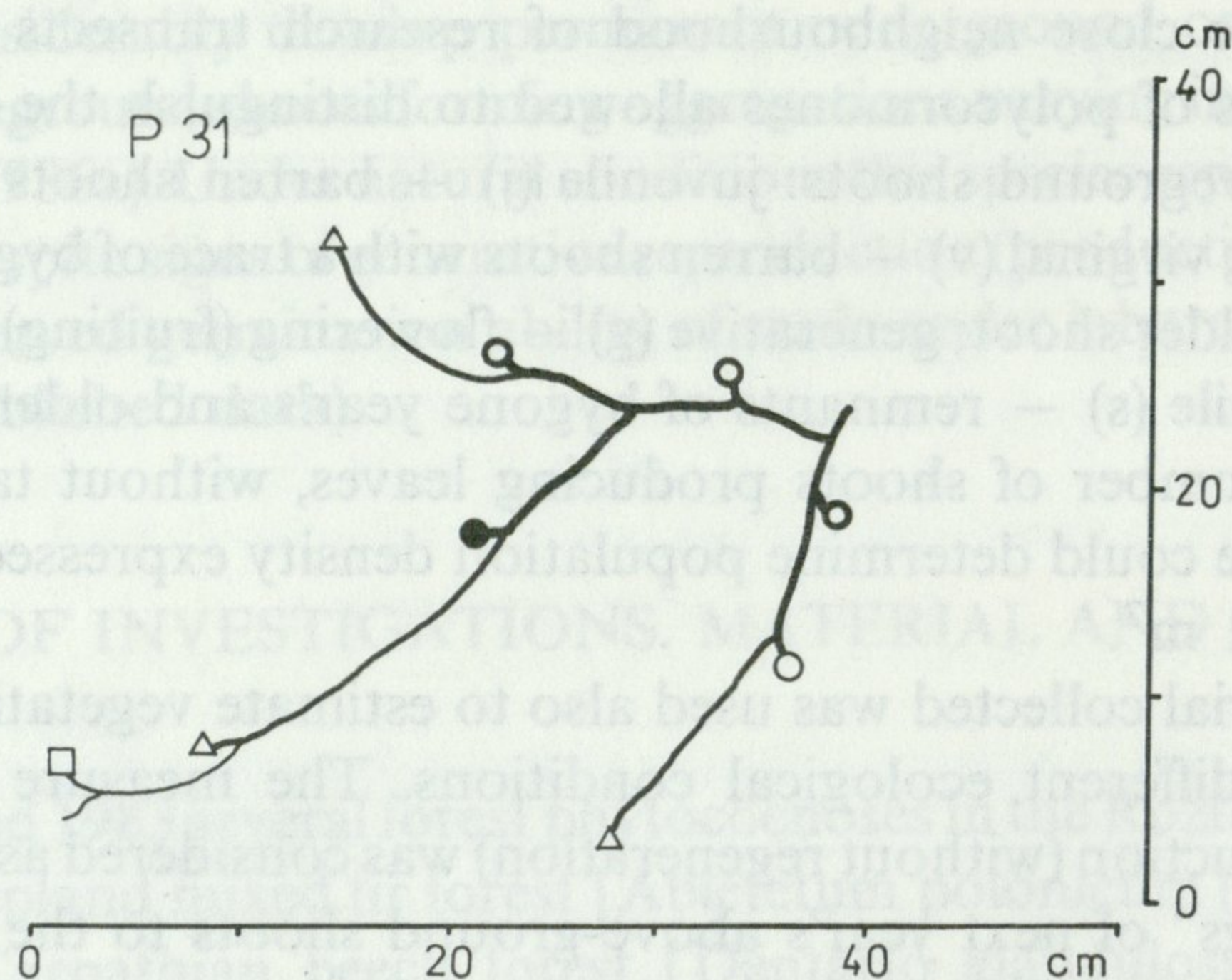


Fig. 2. *Maianthemum bifolium* polycormone from the Querco – Piceetum phytocoenosis. For symbols see Figure 1

rhizome parts can be treated as equivalents of vegetative diaspores, which disconnected from maternal plant (e.g. mechanically) can grow on their own; (2) the ratio of the number of juvenile shoots ( $j$ ) to shoots of all stages in the bygone vegetation season (i.e. in 1981).

The regeneration efficiency is measured by the ratio of virginal ( $v$ ) and generative ( $g$ ) shoots to bygone year's shoots.

The growing efficiency is shown by the ratio of the number of aboveground shoots of polycormones recorded in 1982 to the number of shoots in the previous vegetation season, determined on the basis of remains of these organs.

### 3. RESULTS

#### 3.1. DIFFERENCES IN THE DENSITY AND SPATIAL DISTRIBUTION OF INDIVIDUALS IN POPULATIONS

The density of *Maianthemum bifolium* population fluctuates considerably in particular vegetation seasons from  $0.43 \pm 0.41$  individuals per  $1 \text{ m}^2$  in Dentario-glandulosae-Fagetum population (surface  $B_1$  in 1981) to  $102.87 \pm 20.00$  in ecotone population of Querco-Piceetum and Carici elongatae-Alnetum (surface  $E_4$  in 1982) phytocoenoses. In three successive years (1981 - 1983) populations of this ecotone had the highest density ( $71.50 \pm 11.62$ ,  $102.87 \pm 20.00$  and  $90.87 \pm 26.93$  individual per  $1 \text{ m}^2$ ) and also that of alder forest ( $74.45 \pm 16.45$ ,  $85.71 \pm 12.39$  and  $58.82 \pm 9.52$  individuals per  $1 \text{ m}^2$ ). Whereas Dentario glandulosae-Fagetum and ecotone populations of beech and fir forests during the entire period of investigations did not exceed the density of 10 individuals per  $1 \text{ m}^2$  (Table 1, Fig. 3).



Table 1. Density and distribution of individuals in *Maianthemum bifolium* populations under different ecological conditions and successive vegetation seasons

$\bar{x} \pm L$  — mean value and confidence intervals,  $I < 1$  tendency to uniform distribution,  $I = 1$  — random distribution,  $I > 1$  — aggregated distribution

Year	Ecosystem	Replica- tions	Number of individuals per 1 m <sup>2</sup>			Aggregation coefficient $I = \frac{s^2}{\bar{x}}$
			$\bar{x} \pm L$	min.	max.	
1	2	3	4	5	6	7
1980	Querco-Piceetum ecotone	C <sub>1</sub>	45.65 ± 8.83	3.50	109.25	16.31
		C <sub>3</sub>	61.89 ± 12.88	7.50	112.25	17.20
	Carici elongatae—Alnetum	E <sub>3</sub>	1.12 ± 0.78	0.25	2.00	0.69
		E <sub>5</sub>	13.50 ± 0.89	12.50	14.50	0.07
		D <sub>1</sub>	11.38 ± 4.79	0.00	49.00	25.54
		D <sub>3</sub>	4.12 ± 3.21	0.00	27.00	18.55
1981	Abietetum polonicum ecotone	A <sub>1</sub>	14.72 ± 5.58	0.00	39.75	15.76
		A <sub>2</sub>	3.60 ± 1.71	0.00	8.50	3.44
		A <sub>3</sub>	20.30 ± 9.04	3.00	40.00	17.45
		A <sub>4</sub>	28.10 ± 6.99	10.25	53.00	7.54
		E <sub>1</sub>	3.31 ± 1.23	0.00	12.00	5.30
		E <sub>2</sub>	2.78 ± 0.67	0.00	7.25	2.27
	Dentario glandulosae—Fagetum	B <sub>1</sub>	0.43 ± 0.41	0.00	3.00	2.56
		B <sub>2</sub>	3.41 ± 1.28	0.00	11.00	3.59
		Querco—Piceetum ecotone	C <sub>1</sub>	46.45 ± 9.20	9.75	118.75
	C <sub>2</sub>		27.69 ± 6.23	4.25	53.25	11.92
	C <sub>3</sub>		74.75 ± 16.45	14.00	130.50	23.23
	E <sub>3</sub>		1.37 ± 1.23	0.00	2.75	1.38
	E <sub>4</sub>		71.50 ± 11.62	58.50	84.50	2.36
	E <sub>5</sub>		16.62 ± 2.56	13.00	20.25	0.49
	Carici elongatae—Alnetum	D <sub>1</sub>	13.81 ± 5.78	0.00	58.50	30.62
D <sub>2</sub>		10.45 ± 4.10	0.00	43.25	22.43	
D <sub>3</sub>		6.62 ± 5.22	0.00	44.00	30.58	
1982	Abietetum polonicum ecotone	A <sub>1</sub>	18.69 ± 6.82	0.00	49.00	18.51
		A <sub>2</sub>	3.70 ± 1.77	0.00	9.75	3.66
		A <sub>3</sub>	25.70 ± 7.36	3.50	48.00	9.14
		A <sub>4</sub>	33.85 ± 8.88	14.25	67.25	10.10
		E <sub>1</sub>	6.10 ± 2.41	0.00	22.75	11.08
		E <sub>2</sub>	3.91 ± 0.88	0.00	10.50	2.70
	Dentario glandulosae—Fagetum	B <sub>1</sub>	0.82 ± 0.60	0.00	4.25	2.72
		B <sub>2</sub>	7.03 ± 3.02	0.00	21.75	9.66
	Querco—Piceetum ecotone	C <sub>1</sub>	59.89 ± 15.20	14.00	125.50	24.73
		C <sub>2</sub>	46.97 ± 10.66	6.00	94.25	20.54
		C <sub>3</sub>	85.71 ± 12.39	27.50	123.25	11.48
		E <sub>3</sub>	1.62 ± 1.14	0.00	3.25	1.01
E <sub>4</sub>		102.87 ± 20.00	80.50	125.25	4.87	
E <sub>5</sub>		24.25 ± 3.13	20.75	27.75	0.50	



Table 1, continued

1	2	3	4	5	6	7
	Carici elongatae – Alnetum	D <sub>1</sub>	17.10 ± 7.31	0.00	82.50	39.62
		D <sub>2</sub>	9.59 ± 2.60	0.00	45.75	18.50
		D <sub>3</sub>	7.66 ± 6.03	0.00	53.25	36.33
1983	Abietetum polonicum	A <sub>1</sub>	26.19 ± 8.98	0.00	62.00	22.92
		A <sub>2</sub>	2.40 ± 1.24	0.00	7.00	2.77
		A <sub>3</sub>	33.55 ± 9.45	5.00	58.50	11.55
		A <sub>4</sub>	47.10 ± 13.03	18.50	92.25	15.64
	ecotone	E <sub>1</sub>	5.54 ± 2.72	0.00	30.00	15.47
		E <sub>2</sub>	4.02 ± 0.94	0.00	10.0	3.01
	Dentario glandulosae – Fagetum	B <sub>1</sub>	0.68 ± 0.50	0.00	3.50	2.22
		B <sub>2</sub>	6.94 ± 2.93	0.00	20.25	9.19
	Querco-Piceetum	C <sub>1</sub>	33.57 ± 7.77	15.25	69.75	11.53
		C <sub>2</sub>	30.28 ± 7.18	1.25	69.25	14.47
		C <sub>3</sub>	58.82 ± 9.52	16.25	88.75	9.88
	ecotone	E <sub>3</sub>	1.12 ± 1.00	0.00	2.25	1.12
		E <sub>4</sub>	90.87 ± 26.93	60.75	121.00	9.99
		E <sub>5</sub>	22.00 ± 2.01	19.75	24.25	0.23
	Carici elongatae – Alnetum	D <sub>1</sub>	11.75 ± 4.96	0.00	56.50	26.48
		D <sub>2</sub>	6.86 ± 2.73	0.00	36.25	14.92
		D <sub>3</sub>	5.44 ± 4.57	0.00	38.25	28.53

In all populations, apart from the ecotone of Querco-Piceetum and Carici elongatae-Alnetum phytocoenoses, the Leksis index indicates an aggregated type of spatial structure (Table 1). The alder population has especially high coefficients (14.92 - 35.53) due to the occurrence of *Maianthemum bifolium* on hillocks rather than on dry small valleys. May-flower individuals have a highly aggregated type of occurrence in two kinds of coniferous forest: mixed moist (Querco-Piceetum) and fir (Abietetum polonicum) but the fluctuations of this coefficient are much greater than in the alder forest. In the case of moist mixed forest extreme values were 24.73 (replication C<sub>1</sub> in 1982) and 9.88 (replication C<sub>3</sub> in 1983), whereas of fir forest 22.92 (replication A<sub>1</sub> in 1983) and 2.77 (replication A<sub>2</sub> in 1983). Populations of beech forest and the transition zone between this association and fir forest show much lower values of Leksis index (Table 1).

Only in the population colonizing the ecotone of Querco-Piceetum and Carici elongatae-Alnetum the spatial structure tends to change in successive years. The distribution of shoots in a part of biochore is aggregated (replication E<sub>4</sub>) and in another one almost uniform (replication E<sub>5</sub>). Aggregation coefficient for replication E<sub>3</sub> in the vegetation season in 1980 showed a tendency for uniform distribution of May-flower individuals. In consecutive research season it was  $I > 1$ , proving the aggregated type of spatial structure. In 1982 the population discussed showed random type of dispersion of individuals, whereas in 1983 it was again an aggregated type (Table 1).



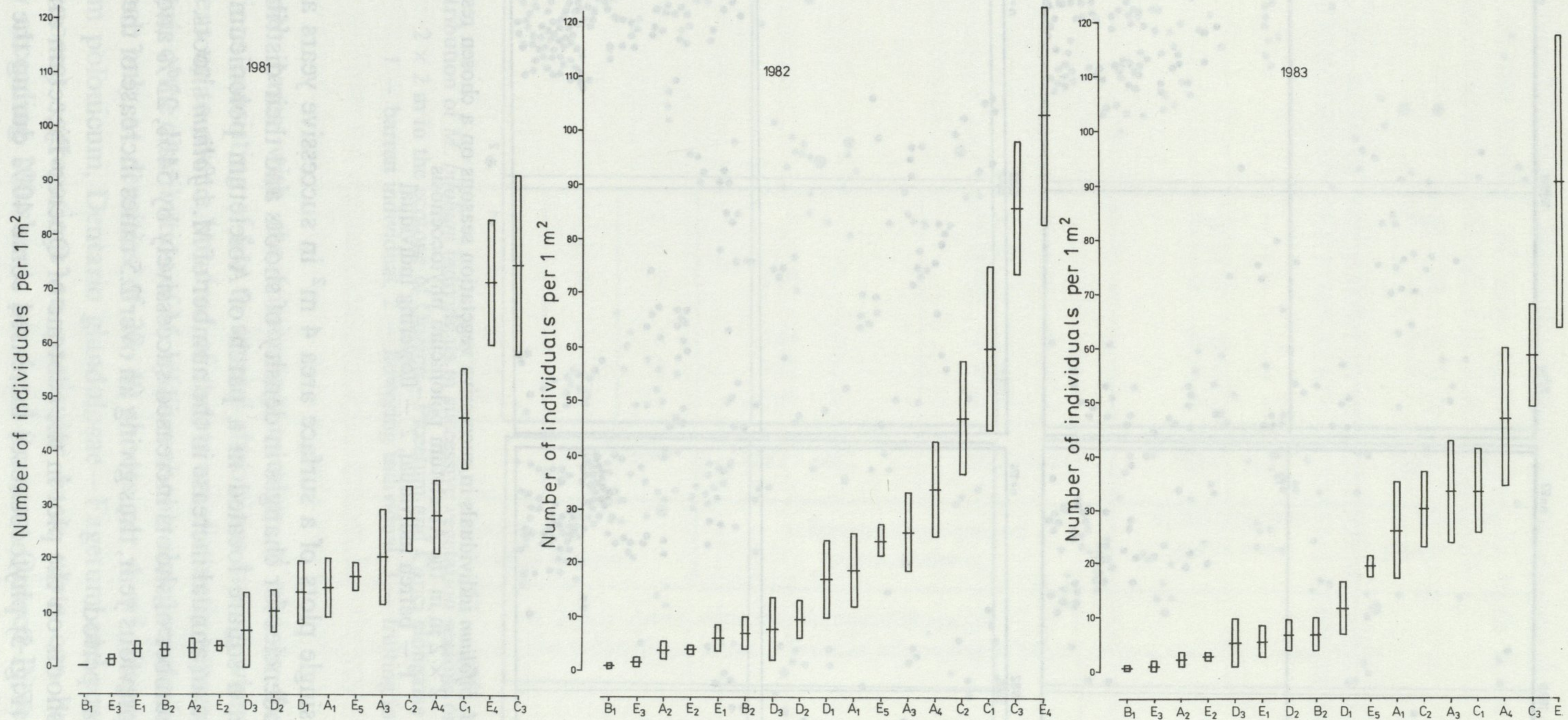


Fig. 3. Differences in the density of "conventional individuals" (shoots) of *M. bifolium* per 1 m<sup>2</sup> under various ecological conditions and in successive vegetation seasons (confidence levels for mean values at 5% level of risking an error)

Replication symbols: A<sub>1</sub>, A<sub>2</sub>, A<sub>3</sub>, A<sub>4</sub> — *Abietetum polonicum*, B<sub>1</sub>, B<sub>2</sub> — *Dentario glandulosae*—*Fagetum*, C<sub>1</sub>, C<sub>2</sub>, C<sub>3</sub> — *Querco*—*Piceetum*, D<sub>1</sub>, D<sub>2</sub>, D<sub>3</sub> — *Carici elongatae*—*Alnetum*, E<sub>1</sub>, E<sub>2</sub> — ecotone of *Abietetum polonicum* and *Dentario-glandulosae*-*Fagetum*, E<sub>3</sub>, E<sub>4</sub>, E<sub>5</sub> — ecotone of *Querco*—*Piceetum* and *Carici elongatae*—*Alnetum*



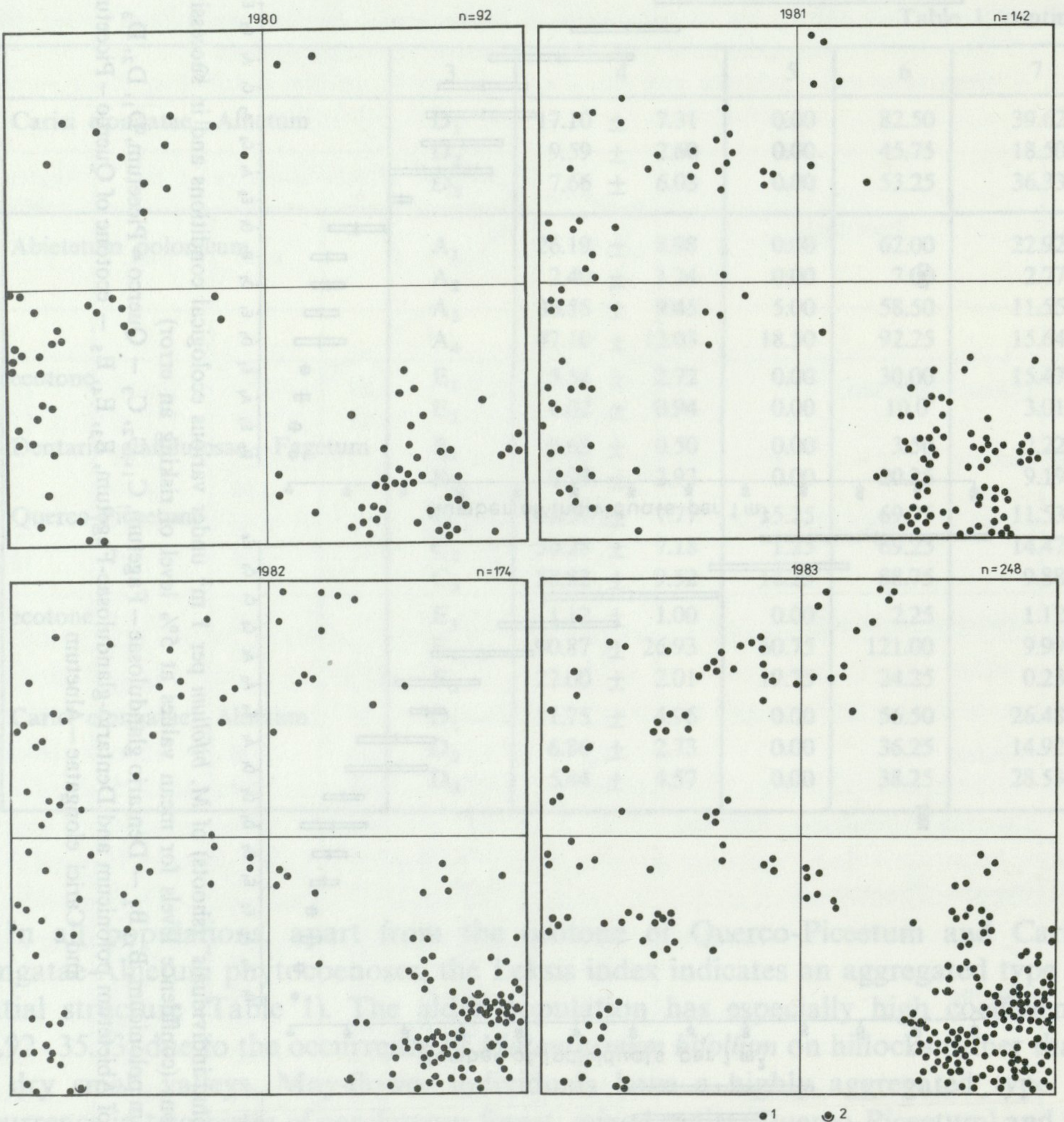


Fig. 4. Distribution of *M. bifolium* individuals in successive vegetation seasons on a chosen research plot  $2 \times 2$  m in the *Abietetum polonicum* phytocoenosis  
1 — barren individual, 2 — flowering individual

Observation of single plots of a surface area  $4 \text{ m}^2$  in successive years allows to observe different tendencies for changes in density of shoots and their distribution in space. For example, a square located in a patch of *Abietetum polonicum* (Fig. 4) phytocoenosis shows an annual increase in the number of *M. bifolium* shoots. Between 1980 and 1983 the number of shoots increased successively by 54%, 23% and 43% as compared with the previous year, thus giving an over 2.5 times increase of the number of shoots during that period.

The number of shoots on the plot in the ecotone of *Quercus-Piceetum* and *Carici elongatae-Alnetum* (Fig. 5) phytocoenoses increased some 40% during the two first years to decrease afterwards 13%.



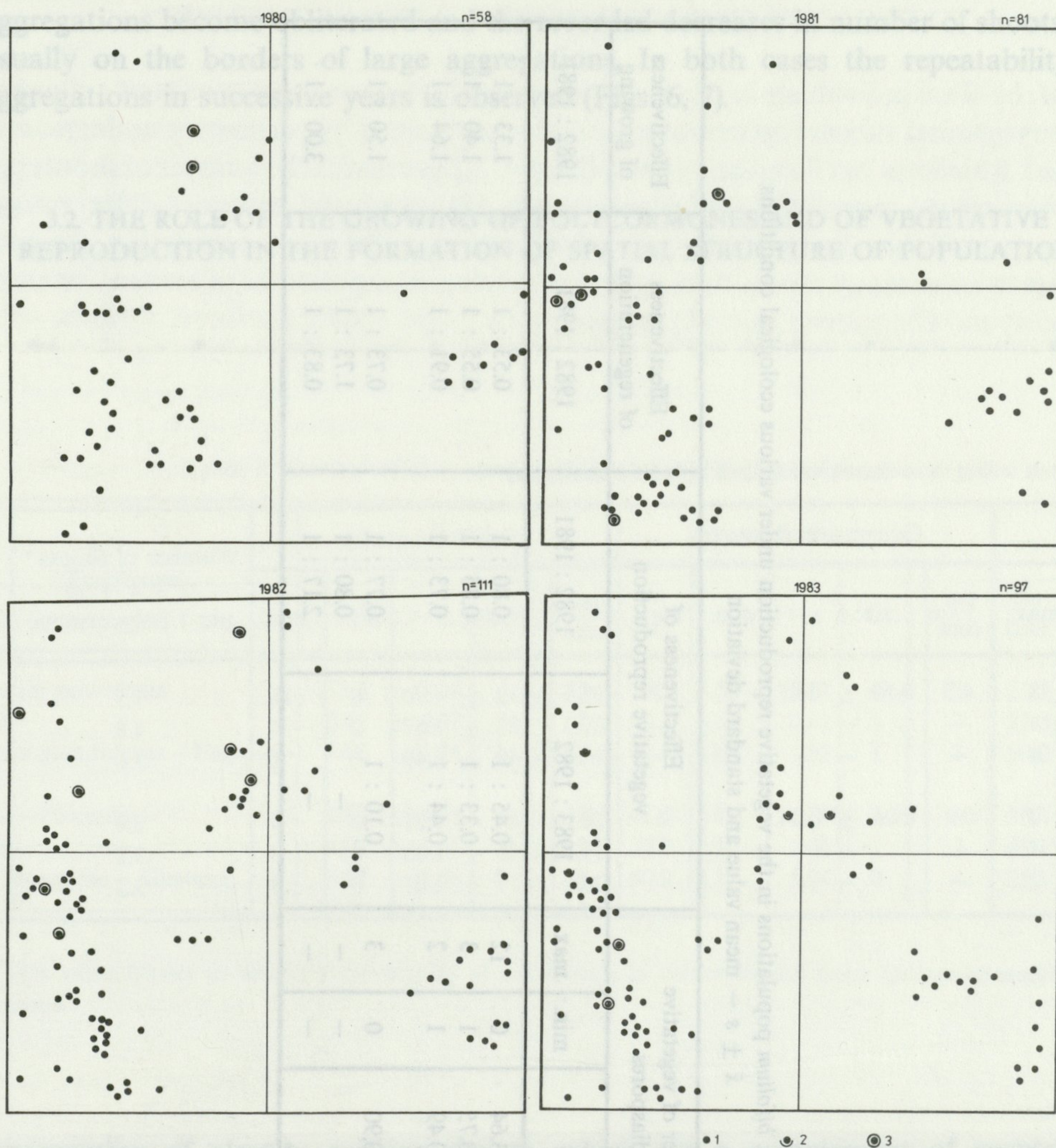


Fig. 5. Distribution of *M. bifolium* individuals in successive vegetation seasons on a chosen research plot 2 × 2 m in the ecotone of Querco – Piceetum and Carici elongatae – Alnetum  
 1 – barren individual, 2 – flowering individual, 3 – fruiting individual

In both cases with the increasing number of shoots the borders between aggregations consisting of few to several shoots are fading, whereas aggregations of several tens up to over a hundred of shoots are distinctly separate (Figs. 4, 5).

Analysis of the distribution of *M. bifolium* shoots along research transects (Figs. 6, 7) shows that only at densities of 20-40 shoots per 4 m<sup>2</sup> (fragment of biochore of Abietetum polonicum, Dentario glandulosae – Fagetum and ecotone between these phytocoenoses) aggregations on particular basic plots can be distinguished. At a density exceeding 100 shoots per 4 m<sup>2</sup> (transect Querco-Piceetum-Carici elongatae-Alnetum and fragment of Abietetum polonicum biochore) the borders of smaller



Table 2. Differences between *M. bifolium* populations in the vegetative reproduction under various ecological conditions  
 $\bar{x} \pm s$  — mean value and standard deviation

Ecosystem	Number of vegetative diaspores			Effectiveness of vegetative reproduction		Effectiveness of regeneration	Effectiveness of growing
	$\bar{x} \pm s$	min.	max.	1983 : 1982	1982 : 1981	1982 : 1981	1982 : 1981
Abietetum polonicum	3.37 $\pm$ 3.64	0	12	0.45 : 1	0.80 : 1	0.53 : 1	1.33 : 1
Ecotone	1.80 $\pm$ 0.75	1	3	0.33 : 1	0.85 : 1	0.55 : 1	1.40 : 1
Dentario glandulosae — Fagetum	1.60 $\pm$ 0.49	1	2	0.44 : 1	0.73 : 1	0.91 : 1	1.64 : 1
Querco — Piceetum	0.57 $\pm$ 0.90	0	3	0.10 : 1	0.77 : 1	0.73 : 1	1.50 : 1
Ecotone	—	—	—	—	0.80 : 1	1.73 : 1	—
Carici elongatae — Alnetum	—	—	—	—	2.17 : 1	0.83 : 1	3.00 : 1



Table 3. Number of aboveground shoots of *M. bifolium* polycormones under various ecological conditions  $\bar{x} \pm s$  — mean value and standard deviation

Ecosystem	Total				Juvenile shoots (j)			Virginal shoots (v)				Generative shoots (g)			Senile shoots (s)			Number of shoots* (j + v + g) per 1 polycormone		
	$\bar{x} \pm s$	min.	max.	per cent	$\bar{x} \pm s$	min.	max.	per cent	$\bar{x} \pm s$	min.	max.	per cent	$\bar{x} \pm s$	min.	max.	per cent	$\bar{x} \pm s$		min.	max.
Abietetum polonicum	11.62 ± 9.31	5	35	38.7	4.50 ± 3.27	1	11	21.5	2.50 ± 2.11	1	8	4.3	0.50 ± 0.87	0	2	35.5	4.12 ± 4.70	0	16	7.5
Ecotone	6.67 ± 4.37	2	13	47.5	3.17 ± 2.41	1	7	25.0	1.67 ± 1.32	0	4	—	—	—	—	27.5	1.83 ± 1.57	0	4	4.8
Dentario glandulosae — Fagetum	4.00 ± 1.26	1	6	40.0	1.60 ± 1.02	1	3	50.0	2.00 ± 1.41	0	4	—	—	—	—	10.0	0.40 ± 0.49	0	1	3.6
Querco — Piceetum	6.87 ± 4.01	2	16	41.8	2.87 ± 1.49	1	6	36.4	2.50 ± 1.69	0	7	0.9	0.06 ± 0.24	0	1	20.9	1.44 ± 1.27	0	4	5.4
Ecotone	4.00 ± 1.66	1	7	37.5	1.50 ± 1.00	0	3	43.7	1.75 ± 1.20	0	4	—	—	—	—	18.8	0.75 ± 1.00	0	3	3.2
Carici elongatae — Alnetum	4.33 ± 1.88	2	7	50.0	2.17 ± 1.34	0	4	23.1	1.00 ± 0.41	0	2	—	—	—	—	26.9	1.17 ± 1.07	0	3	3.2

\* This value allows to estimate the density of individuals in the biological sense (polycormones) per 1 m<sup>2</sup> in the *M. bifolium* populations.







aggregations become obliterated and the recorded decreases in number of shoots are usually on the borders of large aggregations. In both cases the repeatability of aggregations in successive years is observed (Figs. 6, 7).

### 3.2. THE ROLE OF THE GROWING OF POLYCORMONES AND OF VEGETATIVE REPRODUCTION IN THE FORMATION OF SPATIAL STRUCTURE OF POPULATION

The extent of vegetative reproduction depends on the number of regenerative buds acting as vegetative diaspores, which in turn depend on the size of polycormone (Figs. 1, 2) and can be different in particular populations (Table 2).

In the season of 1982 the number of equivalents of diaspores per 1 polycormone was  $0.57 \pm 0.90$  in population of moist mixed coniferous forest, to  $3.37 \pm 3.64$  in population of fir forest. Polycormones of populations of alder forest and ecotone between this association and moist mixed coniferous forest did not produce in the season discussed the “makings” of next year’s aboveground shoots (Table 2).

The efficiency of vegetative reproduction expressed by the ratio of the number of “makings” of next year’s to this year’s shoots (1982) is the highest in *Abietetum polonicum* (0.45:1) and *Dentario glandulosae* — *Fagetum* (0.44:1) populations. Very low is the efficiency of *Querco-Piceetum* population (0.10:1).

The intensification of vegetative reproduction may change in successive years. The production efficiency calculated as a ratio of the number of juvenile shoots, present in 1982, to that of bygone year’s was 0.73:1 in beech forest population to 0.85:1 in the ecotone of beech and fir forests. In *Carici elongatae* — *Alnetum* this ratio was much higher than under conditions of other phytocoenoses and was 0.17:1.

The efficiency of growing of *M. bifolium* polycormones, understood as a greater number of shoots as compared with the previous year, fluctuated between 1.33:1 in fir forest population to 3.00:1 in alder forest population. This means that the numbers of shoots in all populations increased 1.5-3 times. This increase was also due to regeneration of already existing shoots, which are a complement of vegetation reproduction during growing process. In populations of *Abietetum polonicum* and ecotone between this forest and Carpathian beech forest, vegetative reproduction prevails also over the regeneration of polycormones. It is the opposite in populations of *Dentario glandulosae* — *Fagetum* and ecotone between *Querco* — *Piceetum* and *Carici elongatae* — *Alnetum*. In the population of moist mixed coniferous forest both processes are equally strong, whereas polycormones from alder forest phytocenosis have a 3 times higher number of shoots due in 2/3 to vegetative reproduction (Table 2).

The growth of polycormones is accompanied in successive seasons by changes in spatial distribution of shoots due to dying of old shoots and production of new ones in some distance from the oldest part of the polycormone (Figs. 1, 2, 4, 5).



## 3.3 TWO LEVEL CHARACTER OF POPULATION ORGANIZATION

*M. bifolium* individuals in the biological sense (polycormones) consist of a number of aboveground shoots regenerating each year and joined by permanent underground organs. Rhizomes last 3 and more years (Figs. 1, 2). As regards the number of shoots per 1 polycormone, populations of phytocenoses examined and ecotones differ among themselves (Table 3). Polycormones of *Abietetum polonicum* population produce almost twice as many shoots than individuals living in populations of ecotone between fir forest and Carpathian beech forest and moist mixed coniferous forest (*Querco* – *Piceetum*) and almost 3 times as much as polycormones of 3 remaining populations: Carpathian beech forest, alder forest and ecotone between alder forest and mixed forest.

The number of aboveground shoots producing leaves, with the exception of senile ones, is a value for estimating population density expressed by the number of polycormones per surface area unit. This value fluctuates between 3.2 shoots per 1 polycormone in populations of alder forest and ecotone between alder and mixed

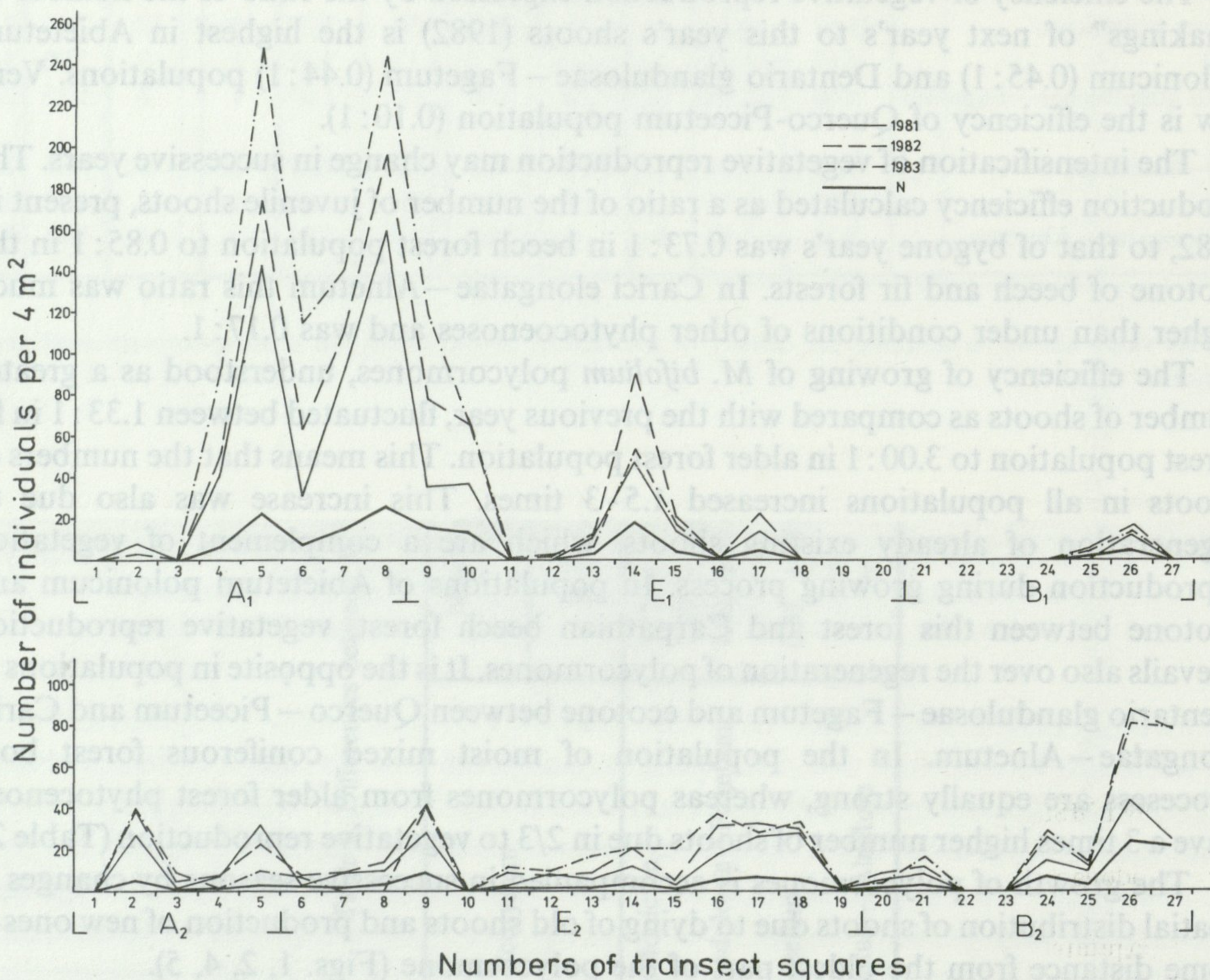


Fig. 6. Distribution of *M. bifolium* individuals along the transect *Abietetum polonicum*–*Dentario glandulosae*-*Fagetum* in successive vegetation seasons

Density values are given for the  $4 \text{ m}^2$  surface. Density of polycormones (N) according to the value given in Table 3. Replications as in Figure 3



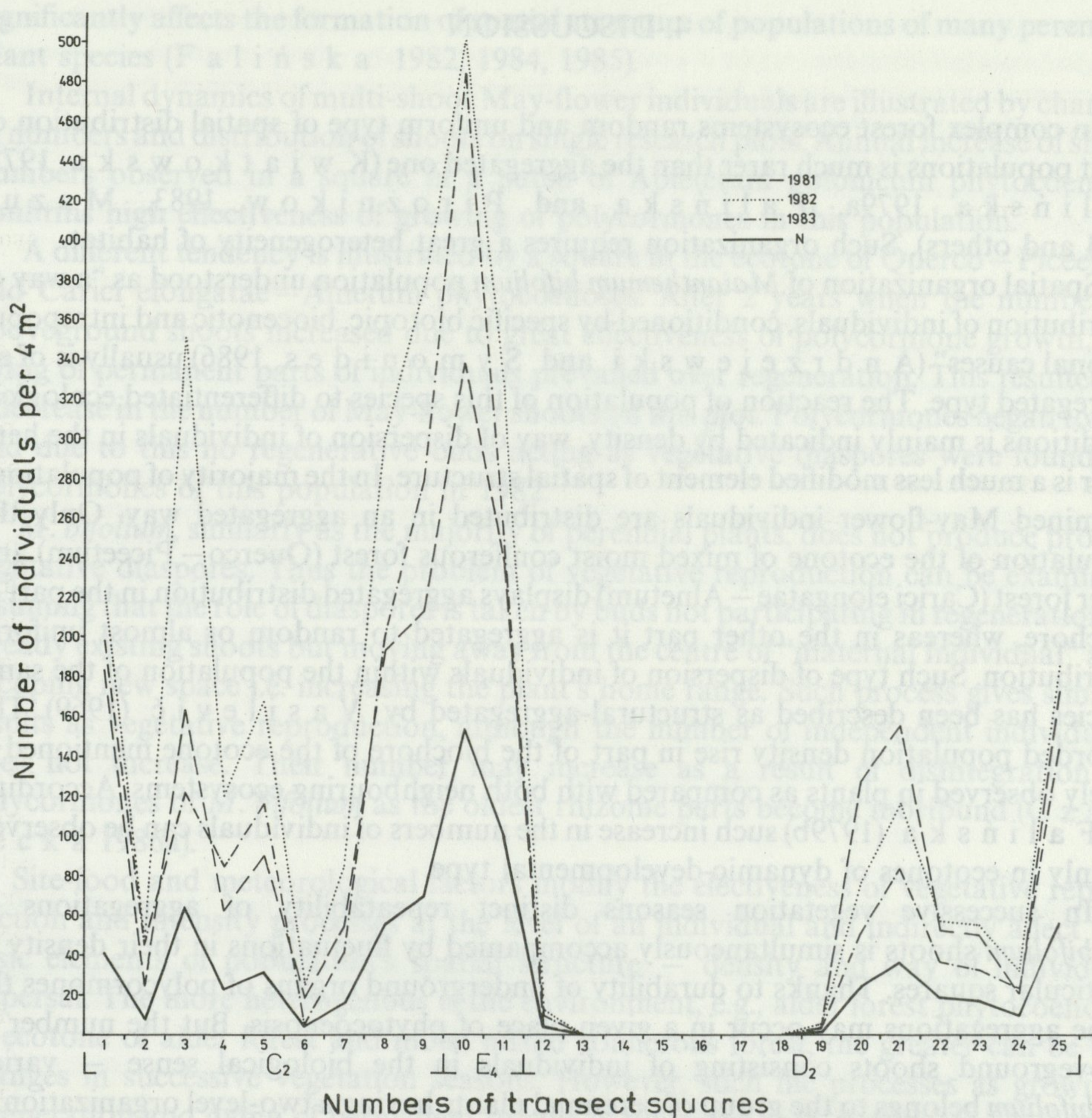


Fig. 7. Distribution of *M. bifolium* individuals along the transect *Querco-Piceetum* — *Carici elongatae*-*Alnetum* in successive vegetation seasons. For symbols see Figures 3, 6

forest to 7.5 shoots in fir forest (Table 3). Because of different proportions of shoots in particular development stages and especially the high percentage of the oldest (senile) shoots in individuals of *Abietetum polonicum* population, differences between this population and the remaining ones are less distinct than in the case of total shoots of all stages. This is also reflected by the course of curves illustrating the distribution of *M. bifolium* individuals along research transects (Figs. 6, 7). At the level of shoots neighbouring phytocoenoses differ several times as regards density, sometimes even upto several tens. At the level of individuals in the biological sense these differences decrease down to few times.



#### 4. DISCUSSION

In complex forest ecosystems random and uniform type of spatial distribution of plant populations is much rarer than the aggregated one (K w i a t k o w s k a 1972, F a l i ń s k a 1979a, F a l i ń s k a and P i r o ż n i k o w 1983, M a z u r 1984 and others). Such organization requires a great heterogeneity of habitat.

Spatial organization of *Maianthemum bifolium* population understood as “a way of distribution of individuals, conditioned by specific biotopic, biocenotic and intrapopulational causes” (A n d r z e j e w s k i and S y m o n i d e s 1986) usually is of an aggregated type. The reaction of population of this species to differentiated ecological conditions is mainly indicated by density, way of dispersion of individuals in the herb layer is a much less modified element of spatial structure. In the majority of populations examined May-flower individuals are distributed in an aggregated way. Only the population of the ecotone of mixed moist coniferous forest (Querco – Piceetum) and alder forest (Carici elongatae – Alnetum) displays aggregated distribution in the part of biochore, whereas in the other part it is aggregated to random or almost uniform distribution. Such type of dispersion of individuals within the population of the same species has been described as structural-aggregated by V a s i l e v i č (1969). The recorded population density rise in part of the biochore of the ecotone mentioned is rarely observed in plants as compared with both neighbouring ecosystems. According to F a l i ń s k a (1979b) such increase in the numbers of individuals can be observed mainly in ecotones of dynamic-developmental type.

In successive vegetation seasons distinct repeatability of aggregations of *M. bifolium* shoots is simultaneously accompanied by fluctuations in their density in particular squares. Thanks to durability of underground organs of polycormones the same aggregations may occur in a given place of phytocoenosis. But the number of aboveground shoots consisting of individuals in the biological sense – varies. *M. bifolium* belongs to the group of perennial plants having a two-level organization of population. Individuals of this species, being a “morphologically whole and physically uninterrupted organism being an ontogenetic unit which may be considered as an elementary source of phytogenic field” (S m i r n o v a et al. 1976) consist of a number of basic individuals – aboveground shoots with corresponding rhizome segments. Such basic individuals are considered by H a r p e r (1977) as modules, which can live on their own after separating from the host plant, but are not individuals in the genetic sense. R a b o t n o v (1969) has proposed to treat each rooted shoot as a “conventional-individual”, G a t s u k et al. (1980) consider such individuals as “partial shoots”.

Fluctuations in numbers rooted shoots are due to changes in the intensity of regeneration and decay. These processes are almost simultaneous, but their intensity varies in particular periods of developmental cycle of polycormones (Ł u k a s i e w i c z 1962, F a l i ń s k a 1984).

Changes in the distribution of aboveground shoots in successive years confirm the earlier reports that internal spatial structure of multi-sshoot and multi-root individuals



significantly affects the formation of spatial structure of populations of many perennial plant species (F a l i ń s k a 1982, 1984, 1985).

Internal dynamics of multi-shoot May-flower individuals are illustrated by changes in numbers and distribution of shoots on single research plots. Annual increase of shoot numbers observed in a square in a patch of *Abietetum polonicum* phytocoenosis confirms high effectiveness of growing of polycormones in this population.

A different tendency is illustrated by a square in the ecotone of *Querco* — *Piceetum* and *Carici elongatae* — *Alnetum* phytocoenoses. After 2 years when the number of aboveground shoots increased due to great effectiveness of polycormone growth, the dying of permanent parts of individuals prevailed over regeneration. This resulted in a decrease in the number of May-flower shoots on this plot. Polycormones began to age and due to this no regenerative buds acting as vegetative diaspores were found on polycormones of this population in 1982.

*M. bifolium*, similarly as the majority of perennial plants, does not produce proper vegetative diaspores. Thus the problem of vegetative reproduction can be examined assuming that the role of diaspores is taken by buds not participating in regeneration of already existing shoots but moving away from the centre of “maternal individual” and occupying new space i.e. increasing the plant’s home range. Such process gives similar results as vegetative reproduction, although the number of independent individuals does not increase. Their number may increase as a result of disintegration of polycormones of *M. bifolium* as the oldest rhizome parts become moribund (C z a r n e c k a 1986a).

Site-food and meteorological factors modify the effectiveness of vegetative reproduction and intensity processes at the level of an individual and indirectly affect the basic elements of population’s spatial structure — density and way of individual dispersal. The more heterogenous is the environment, e.g., alder forest phytocoenosis or ecotone of alder forest and moist mixed coniferous forest, the greater can be the changes in successive vegetation seasons. However, such life processes as growing, regeneration and dying of permanent organs of polycormones, their spatial structure and internal dynamics of basic individuals and dominance of vegetative reproduction are the morphological development properties of species fundamentally responsible for the spatial organization of its population.

**ACKNOWLEDGEMENTS:** The author wishes to acknowledge Ass. Prof. Dr K. Falińska for her valuable criticism thanks to which the present version of the paper has been written.

## 5. SUMMARY

Between 1980 and 1983 studies on *Maianthemum bifolium* populations were conducted in several forest phytocoenoses of the Roztocze National Park. These were: upland mixed fir forest (*Abietetum polonicum*) and Carpathian beech forest (*Dentario glandulosae* — *Fagetum*), subboreal moist mixed coniferous forest (*Querco* — *Piceetum*) and alder forest (*Carici elongatae* — *Alnetum*) with ecotones of these two pairs of associations.



The species examined has a two-level organization of population. May-flower individuals in the biological sense (polycormones) consist of a number of basic individuals — above-ground shoots connected by permanent underground organs (Figs. 1, 2). The number of shoots per 1 polycormone may vary under different ecological conditions (Table 3).

It is described how the spatial organization of population of *M. bifolium* is formed by individuals growing into polycormones, their internal spatial structure and dynamics of basic units, dominance of vegetative reproduction and different intensity of regeneration, growing and dying processes at an individual level.

Density of shoots is the element of population spatial structure modified the most by ecological conditions (Table 1, Fig. 3). But in the majority of populations dispersion has an aggregated character. Only the population of ecotone of *Quercus*—*Piceetum* and *Carici elongatae*—*Alnetum* phytocoenoses has an aggregated distribution in part of biochore and in the other an aggregated up to random type or almost uniform (Table 1). A repeatability of shoot aggregations in successive research seasons due to considerable permanence of underground organs of May-flower polycormones has been observed. Simultaneously there are great fluctuations in numbers of shoots within aggregations (Figs. 4-7). Such spatial organization of *M. bifolium* population reflects largely the different effectiveness of vegetative reproduction, regeneration and growing of polycormones (Table 2). Particular populations show different tendencies of changes due to internal dynamics of multi-shoot individuals (Figs. 4, 5) and also under the influence of external factors: site-food and meteorological.

## 6. POLISH SUMMARY

Badania nad populacjami *Maianthemum bifolium* prowadzono w latach 1980-1983 w kilku fitocenozach leśnych Roztoczańskiego Parku Narodowego. Były to: wyżynny jodłowy bór mieszany (*Abietetum polonicum*) i buczyna karpacka (*Dentario glandulosae*—*Fagetum*) oraz subborealny wilgotny bór mieszany (*Quercus*—*Piceetum*) i ols (*Carici elongatae*—*Alnetum*) wraz ze strefami przejścia w obrębie obu par zespołów.

Badany gatunek wykazuje dwupoziomową organizację populacji. Osobniki konwalijki w sensie biologicznym (polikormony) składają się z szeregu jednostek podstawowych — pędów nadziemnych, które połączone są trwałymi organami podziemnymi (rys. 1, 2). Liczba pędów przypadających na 1 polikormon może być różna w różnych warunkach ekologicznych (tab. 3).

Określono w jaki sposób rozrastanie się osobników w polikormony, ich wewnętrzna struktura przestrzenna i dynamika jednostek podstawowych, dominacja reprodukcji wegetatywnej oraz różne nasilenie procesów odnawiania, rozrastania i obumierania zachodzących na poziomie osobniczym kształtują organizację przestrzenną populacji *M. bifolium*.

Najbardziej modyfikowanym przez warunki ekologiczne elementem struktury przestrzennej populacji jest zagęszczenie pędów (tab. 1, rys. 3), natomiast sposób dyspersji osobników jest w większości populacji skupiskowy. Jedynie populacja zasiedlająca strefę przejścia fitocenozy *Quercus*—*Piceetum* i *Carici elongatae*—*Alnetum* wykazuje w części biochory rozkład skupiskowy, w części zaś od skupiskowego po losowy lub prawie równomierny (tab. 1). Stwierdzono powtarzalność skupień pędów w kolejnych sezonach badawczych, uwarunkowaną znaczną trwałością organów podziemnych polikormonów konwalijki. Jednocześnie obserwuje się wahania liczebności pędów w obrębie skupień (rys. 4-7). Taka organizacja przestrzenna populacji *M. bifolium* jest w znacznym stopniu odzwierciedleniem różnej efektywności reprodukcji wegetatywnej, odnawiania i rozrastania polikormonów (tab. 2). Poszczególne populacje wykazują odmienne tendencje zmian spowodowane wewnętrzną dynamiką wielopędowych osobników (rys. 4, 5), jak również wpływem warunków zewnętrznych: siedliskowo-pokarmowych i meteorologicznych.



## 7. REFERENCES

1. Andrzejewski R., Symonides E. 1986 – Organizacja przestrzenna populacji [Spatial structure of populations] (In: Populacje roślin i zwierząt. Ekologiczne studium porównawcze [Plant and animal populations. Comparative ecological study], Eds. R. Andrzejewski, K. Falińska) – Państwowe Wydawnictwo Naukowe, Warszawa, 442 pp.
2. Češká A. 1968 – Application of association coefficients for estimating the mean similarity between sets of vegetational relevés – Folia Geobot. Phytotax., Praga, 3: 57-65.
3. Czarnicka B. 1986a – Biological properties of *Maianthemum bifolium* (L.) F. W. Schm. polycormones under various ecological conditions – Acta Soc. Bot. Pol. 55: 659-678.
4. Czarnicka B. 1986b – Zmienność składu florystycznego i struktury przestrzennej runa fitocenozy leśnych i stref przejścia w Roztoczańskim Parku Narodowym [Variability of floristic composition and spatial structure of the herb layer of some forest phytocoenoses and transition zones in the Roztocze National Park] – Ann. UMCS, C, 41: 55-72.
5. Falińska K. 1979a – Modification of plant populations in forest ecosystems and their ecotones – Pol. ecol. Stud. 5: 89-150.
6. Falińska K. 1979b – Populacje roślin w ekotonie [Plant populations in an ecotone] – Wiad. ekol. 25: 3-21.
7. Falińska K. 1982 – The biology of *Mercurialis perennis* L. polycormones – Acta Soc. Bot. Pol. 51: 127-148.
8. Falińska K. 1984 – Demografia roślin [Plant demography] – Wiad. bot. 28: 105-130.
9. Falińska K. 1985 – The demography of coenopopulations of forest herbs (In: The population structure of vegetations, Ed. J. White) – Dr. Junk Publishers, Dordrecht, 241-264.
10. Falińska K., Pirożnikow E. 1983 – Ecological structure of *Geranium robertianum* L. populations under natural conditions and in the garden – Ekol. pol. 31: 93-121.
11. Gatsuk L. E., Smirnova O. V., Vorontzova L. I., Zaugolnova L. B., Zhukova L. A. 1980 – Age states of plants of various growth forms: a review – J. Ecol. 68: 675-696.
12. Harper J. L. 1977 – Population biology of plants – Academic Press, London-New-York San-Francisco, 896 pp.
13. Izdebski K. 1972 – Zbiorowiska roślinne projektowanego rezerwatu leśnego „Zwierzyniec” [Plant communities of the future forest reserve „Zwierzyniec”] – Ann. UMCS, C, 27: 207-231.
14. Izdebski K., Popiołek Z. 1969 – Charakterystyka geobotaniczna projektowanego rezerwatu leśnego im. Z. Czubińskiego na Roztoczu Środkowym [A geobotanical characteristics of the future Czubiński reserve in Central Roztocze] – Ann. UMCS, C, 24: 135-162.
15. Kershaw K. A. 1978 – Ilościowa i dynamiczna ekologia roślin [Quantitative and dynamic plant ecology] – Państwowe Wydawnictwo Naukowe, Warszawa, 384 pp.
16. Kwiatkowska A. J. 1972 – Analiza homogeniczności runa fitocenozy przy zastosowaniu nieparametrycznego testu serii [Analysis of the homogeneity of the phytocoenosis herb layer with application of the non-parametric test of the series] – Phytocoenosis, 1: 37-77.
17. Kwiatkowska A. J., Symonides E. 1980 – Przegląd metod oceny typu rozkładu przestrzennego populacji roślinnych [Review of methods for estimating the spatial distribution of plant populations] – Wiad. ekol. 26: 25-56.
18. Łukasiewicz A. 1962 – Morfologiczno-rozwojowe typy bylin [Morpho-developmental types of perennial plants] – Pr. Komis. Biol. PTPN 27, Poznań, 398 pp.
19. Mazur M. 1984 – Internal structure of the new growth and up-growth of silver fir (*Abies alba* Mill.) in forest communities – Ekol. pol. 32: 61-77.
20. Oktaba W. 1976 – Elementy statystyki matematycznej i metodyka doświadczalnictwa [Elements of mathematical statistics and methodology of experimentation] – Państwowe Wydawnictwo Naukowe, Warszawa, 310 pp.



21. R a b o t n o v T. A. 1969 — On coenopopulations of perennial herbaceous plants in natural coenoses — *Vegetatio*, 19: 87-95.
22. S m i r n o v a O. V., Z a u g o l n o v a L. B., E r m a k o v a I. M. 1976 — Cenopopuljacji rasteń — Nauka, Moskva, 217 pp.
23. V a s i l e v i č V. I. 1969 — Statističeskie metody v geobotanike — Akad. Nauk SSSR, Leningrad, 230 pp.

(Received 19 May 1987)

Państwowe Wydawnictwo Naukowe  
Oddział w Łodzi 1990

Wydanie I. Nakład 1222—98 egz. Ark. wyd. 17,25. Ark. druk. 13,00 +3 str. abst. +1 wkl.

Papier offset. kl. III, 80 g. 70×100. Oddano do składania w lipcu 1989 r.

Podpisano do druku w maju 1990 r. Druk ukończono w czerwcu 1990 r. Zam. 579/89

Zakład Graficzny Wydawnictw Naukowych  
Łódź, ul. Żwirki 2