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THE ECOLOGY OF *LOBELIA DORTMANNA* L.
II. POPULATION STRUCTURE AND DYNAMICS WITHIN A CONSTANT DEPTH INTERVAL IN OLIGOTROPHIC LAKES

ABSTRACT: The subject of the study was *Lobelia dortmanna* population structure under various biotope and phytocoenose conditions of the same phytolittoral depth range (0.8 – 1.0 m) in two lakes in northern Poland. *L. dortmanna* populations were a priori subdivided into 9 smaller comparative units (subpopulations) on the basis of the following criteria: homogeneity of the biochore (i.e., area occupied by a phytocoenose) and the same plant community type. Within the subpopulations the following were determined: (1) density, (2) spatial organization, (3) age distribution, (4) proportion of seeds and vegetative diaspores. The method used was microscale underwater charting. The study was carried out in the period 1980 – 1984.

KEY WORDS: *Lobelia dortmanna,* isoetid, population structure, population demography, phytocoenose-biotope conditions, oligotrophic lakes.

1. INTRODUCTION

This paper is the second part of a series of studies dealing with the ecology of *Lobelia dortmanna.* The first paper of the series (Szmeja 1987a) has presented changes in individual size, habit and fecundity in relation to sediment type, plant community, population density and intensity of inter-species competition. The results presented in it have been obtained from investigations carried out over a depth range 0.8 – 1.0 m in the littoral of two lakes separated by some distance.

The aim of this, the second paper is to check: (1) whether population structure and dynamics vary with the phytocoenose-biotope conditions; (2) which of the factors are probably responsible for possible variations; (3) to what extent sediment and competition of other species contribute to them.

Here, phytocoenose conditions are treated as a complex of social factors resulting from the physiognomy, spatial structure, seasonal rhythm and diversity of the species making up a phytocoenose, while biotope conditions are identified with the kind of sediment, i.e., the degree of its granulation and organic matter content, as indicators of fertility and intensity of the biological and chemical processes that are going on in it. The following are features describing the population structure: density, spatial organization, age distribution, and number of diaspores per unit area.

The entities studied and used for comparing variation in population structure, and mechanisms of population functionning are subpopulations. Their location, selection criteria, and description of the habitat conditions under which they live have been presented in the first part of the series (Szmeja 1987a).

2. MATERIAL AND METHODS

The research was carried out in L. Dobrogoszcz in the period 1980–1984 and in L. Wielkie Oczko in the years 1980–1982, at nine sites situated in the phytolittoral at depths ranging from 0.8 to 1.0 m. Observation of the L. Wielkie Oczko population was terminated earlier because in 1983 all the sites marked permanently were totally destroyed. The lakes and the study sites laid out in them have been described in the first paper of the series (cf. Szmeja 1987a), some of the description has been repeated in this paper (Fig. 1, Table 1), mainly to make its contents more lucid.

The numbers, density and spatial organization of the subpopulations were determined on the basis of cartograms prepared once a year at the study sites in accordance with the topographic principles of distribution of individuals (cf. Kocimowski and Kwiatek 1976). Metal lattices, 1.0 × 1.0 m, each consisting of 100 squares, 0.1 × 0.1 m, were placed on those sites and connected so that they covered them completely. Density analysis was carried out on the basis of the number of individuals growing in a specified area (Kwiatkowska and Symonides 1978). The area of 0.1 m^2 was chosen because the variation coefficient, calculated for a series of variable-size samples, was in this case the lowest.

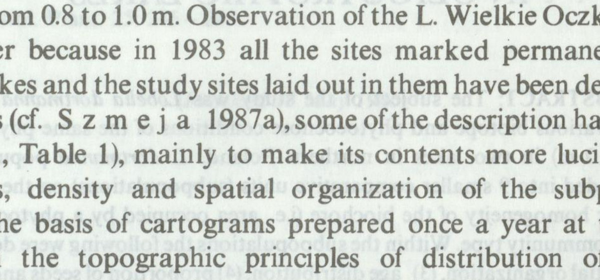

Fig. 1. Diagram presenting the subdivision of the populations under study
M-L – Myriophyllo-Littorelletum, I-L – Isoëto-Lobelietum, C.r. – Caricetum rostratae, R-J – Ranunculo-Juncetum bulbosi; sa – sand sediment, s-c – sand-clay sediment, sl – silt sediment

Table 1. A concise description of the study sites of the subpopulations
Kinds of sediment: sa – sand, sl – silt, s-c – sand-clay

Lake	Study site						Subpopulation
	No.	size (m^2)	organic matter content (per cent d. wt.)	plant dry weight ($g \cdot 0.1\ m^{-2}$)	kind of sediment	phytocoenose	symbol*
Dobrogoszcz	I	25	0.6 – 1.8	14.21	sa	Isoëto-Lobelietum	$I\text{-}L_{sa}$
	II	10	6.9 – 7.4	32.21	sl	Isoëto-Lobelietum	$I\text{-}L_{sl}$
	III	25	2.1 – 2.9	13.30	sa	Myriophyllo-Littorelletum	$M\text{-}L_{sa}$
	IV	10	5.2 – 8.7	20.16	s-c	Myriophyllo-Littorelletum	$M\text{-}L_{s-c}$
	V	10	5.8 – 13.1	49.78	sl	Myriophyllo-Littorelletum	$M\text{-}L_{sl}$
Wielkie Oczko	VI	10	1.8 – 2.4	12.46	sa	Isoëto-Lobelietum	$I\text{-}L_{sa}$
	VII	10	6.2 – 7.8	33.92	sl	Isoëto-Lobelietum	$I\text{-}L_{sl}$
	VIII	10	3.8 – 4.9	23.60	sa	Caricetum rostratae	$C.r_{sa}$
	IX	10	0.4 – 1.3	7.08	sa	Ranunculo-Juncetum bulbosi	$R\text{-}J_{sa}$

* The symbols are combinations of phytocoenose type and kind of sediment.

Production of seeds and vegetative diaspores, per unit area of a particular subpopulation, was estimated from the fecundity and density of the generative individuals (cf. Szmeja 1987a).

The stages of individual morphological development was assessed by the method suggested, e.g., by Gatsuk et al. (1980). The criteria for distinguishing these stages in *L. dortmanna* and their description were based on the paper by Szmeja (1987b).

Only the frequency of uneven-sized aggregations was examined outside the laid out sites. The length and breadth of each aggregation was measured by moving round the lake along the chosen depth range (0.8 – 1.0 m).

3. RESULTS

3.1. NUMBERS AND DENSITY OF SUBPOPULATIONS

Lake Dobrogoszcz. The number of mature and generative *L. dortmanna* individuals on the particular study sites varies widely, ranging from several tens in subpopulation M-L_{sl} to over a dozen thousand in I-L_{sa} (Table 2). Though not all the values are in this case comparable, because the study sites differ in size (10 or 25 m^2, cf. Table 1), they make the differences between the subpopulations sufficiently evident, approximately representing the range of their variation also in other parts of the phytolittoral.

Variation in numbers of particular subpopulations from year to year is not wide. The most stable in this respect is I-L_{sa}; here changes between years amount on the average to 2.1%, being six times lower than in I-L_{sl} (12.4%). Average fluctuation in numbers of aggregations consisting only of *L. dortmanna* is more than twice lower than that of aggregations including several species. In the former case, i.e., I-L_{sa} and I-L_{sl} the variations do not exceed 6%, and in the latter, i.e., M-L_{sa} and M-L_{s-c} without M-L_{sl} (subpopulations in Myriophyllo-Littorelletum) they amount to 15.6%.

Table 2. Number of mature (M) and generative (G) individuals in L. Dobrogoszcz subpopulations in the years 1980 – 1983

Sub-population *	1980		1981		1982		1983		Average for study years			
									subpopulation		coenopopulation	
	M	G	M	G	M	G	M	G	M	G	M	G
I-L_{sa}	11329	419	11017	684	11324	957	11403	783	11267.5	710.7	6536.1	450.7
I-L_{sl}	–	–	1973	155	1829	248	1612	171	1804.7	191.3		
M-L_{sa}	452	27	429	35	471	66	363	41	428.7	42.2	408.3	54.6
M-L_{s-c}	–	–	760	63	730	197	607	86	699.0	115.3		
M-L_{sl}	–	–	194	0	81	13	17	6	97.3	6.3		

*See Table 1.

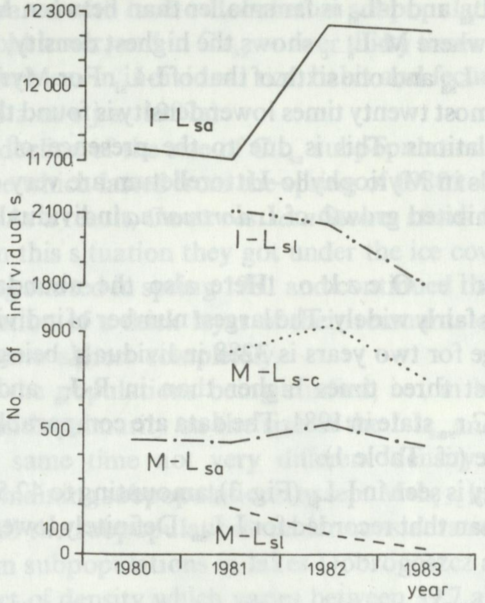

Fig. 2. Abundance dynamics of L. Dobrogoszcz subpopulations in the period 1980–1983
Subpopulation designations as in Figure 1; study site sizes as in Table 1

Each subpopulation has its own rhythm of abundance-variation between years, not synchronized with that of other subpopulations (Fig. 2). For example, from 1981 to 1982 the number of individuals increased in I-L_{sa}, M-L_{s-c}, and M-L_{sa}, and it decreased in I-L_{sl} and M-L_{sl}. A considerable reduction in numbers in M-L_{sl} in 1982 and 1983 was caused by a spontaneous detachment of several small but very dense aggregations from the muddy lake floor. Similar situations were seen in I-L_{sl} and M-L_{s-c}, but they occurred far less often and were less intensive.

Subpopulation I-L_{sa} is characterized by the highest density which amounts on an average to 56.7 individuals per 0.1 m^2, being nearly twice as high as that of I-L_{sl} (Table 3). The kind of phytocoenose and its structure are in either case the same, there are not in essence any competitors, and it is only the type of substratum that varies. Density

Table 3. *L. dortmanna* and *L. uniflora* density (individuals · 0.1 m^{-2}) in L. Dobrogoszcz study sites (I – V)

Species	Study site and subpopulation *				
	I	II	III	IV	V
	I-L_{sa}	I-L_{sl}	M-L_{sa}	M-L_{s-c}	M-L_{sl}
L. dortmanna	56.7	30.2	2.3	4.7	0.1
L. uniflora	0.2	0.1	276.5	198.4	48.7

*See Table 1.

difference between I-L_{sa} and I-L_{sl} is far smaller than between Myriophyllo-Littorelletum subpopulations, where M-L_{s-c} shows the highest density, but this density is only one twelfth of that of I-L_{sa} and one sixth of that of I-L_{sl}. For Myriophyllo-Littorelletum subpopulations an almost twenty times lower density is found than that seen in Isoëto-Lobelietum subpopulations. This is due to the presence of *Littorella uniflora* (L.) Aschers., whose stands in Myriophyllo-Littorelletum are very close and considerably limit the area of uninhibited growth of *L. dortmanna* individuals, mainly in M-L_{sa} and M-L_{s-c}.

Lake Wielkie Oczko. Here also the abundance of the particular subpopulations varies fairly widely. The largest number of individuals are found in I-L_{sl} (Table 4). The average for two years is 3288 individuals, being 33% higher than that found in I-L_{sa}, almost three times higher than in R-J_{sa} and four times higher in comparison with the C.r_{sa} state in 1981. The data are comparable because they relate to areas of the same size (cf. Table 1).

The highest density is seen in I-L_{sl} (Fig. 3), amounting to 42.5 individuals per 0.1 m^2, only slightly higher than that recorded for I-L_{sa}. Definitely lower values are recorded in

Table 4. Number of mature (M) and generative (G) individuals
in L. Wielkie Oczko subpopulations
in the period 1981 – 1982

Subpopulation *	1981		1982		$\bar{x}$
	M	G	M	G	
I-L_{sa}	2318	129	2170	146	2381.5
I-L_{sl}	3112	206	2985	273	3288.0
C.r_{sa}	719	41	8	0	760.0**
R-J_{sa}	1022	46	1219	77	1182.0

* See Table 1.
** As of 1981.

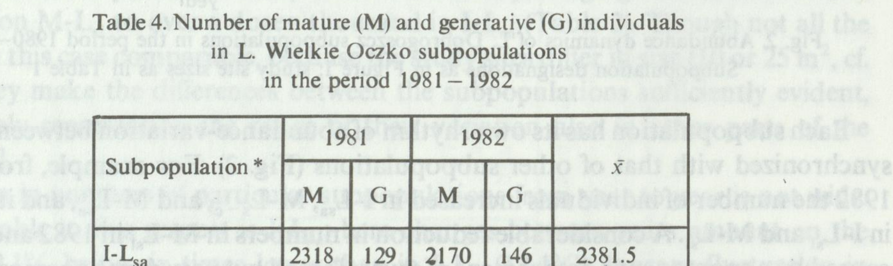

Fig. 3. Density (A) and frequency (B) of individuals in L. Wielkie Oczko subpopulations
Subpopulation designations as in Figure 1

C.r$_{sa}$ and R-J$_{sa}$. Compared with Isoëto-Lobelietum subpopulations, the density in R-J$_{sa}$ appears to be sevenfold lower, and in C.r$_{sa}$ – over thirty times lower. This is one of the causes of the big differences in individual size, habit and fecundity between I-L$_{sa}$ and C.r$_{sa}$ and R-J$_{sa}$ (cf. Szmeja 1987a).

In 1982, a rapid decline of the size of C.r$_{sa}$ subpopulations was caused by a high water level in the lake which lasted from the spring of 1980 to the summer of 1982 (cf. Szmeja 1987b). As a result, *Carex rostrata* Stokes stems were flooded during the spring in 1980 and in this situation they got under the ice cover in the winter of that year. Their slow dying started in spring 1981 and continued throughout the year. This resulted in the formation of a thick layer of their remnants on the lake floor, which eliminated *L. dortmanna* almost completely.

The size of both the populations being studied, i.e., in lakes Dobrogoszcz and Wielkie Oczko, depends primarily on the size of the I-L$_{sa}$ and I-L$_{sl}$ areas, where the highest, and at the same time not very different density levels are found. The contribution of the remaining subpopulations, except M-L$_{s-c}$ in L. Dobrogoszcz, to the overall numbers of all the subpopulations under consideration is small.

Isoëto-Lobelietum subpopulations in lakes Dobrogoszcz and Wielkie Oczko are very similar in respect of density which varies between 39.7 and 43.4 individuals per 0.1 m^2, the difference being as low as 8.5%. M-L$_{sa}$, M-L$_{sl}$, M-L$_{s-c}$, C.r$_{sa}$ and R-J$_{sa}$ are characterized by a much lower density than I-L$_{sa}$ and I-L$_{sl}$. It oscillates from 0.1 individual per 0.1 m^2 in M-L$_{sl}$ to 5.2 individuals per 0.1 m^2 in R-J$_{sa}$ (cf. Table 3, Fig. 3). Similar values have been recorded for: M-L$_{s-c}$ and R-J$_{sa}$, and M-L$_{sa}$ and C.r$_{sa}$.

3.2. SPATIAL ORGANIZATION OF THE SUBPOPULATIONS

Lake Dobrogoszcz. In all the subpopulations the frequency of individuals is directly proportional to their numbers; it is the highest in I-L$_{sa}$, only slightly lower in I-L$_{sl}$, and the lowest in M-L$_{sl}$ (Table 5). Its between-year variation is more or

Table 5. Frequency of mature (M) and generative (G) individuals in L. Dobrogoszcz subpopulations in the years 1980–1984

Subpopulation *	Frequency (in per cent)											
	1980		1981		1982		1983		1984		average	
	M	G	M	G	M	G	M	G	M	G	M	G
I-L$_{sa}$	90.7	9.6	87.1	12.4	88.0	22.2	84.3	18.7	82.2	11.8	86.5	14.9
I-L$_{sl}$	–	–	61.2	13.2	62.3	19.4	68.6	11.2	60.6	13.0	63.2	14.2
M-L$_{sa}$	11.3	1.7	9.9	2.9	10.0	6.8	6.7	2.1	8.2	3.2	9.2	3.3
M-L$_{s-c}$	–	–	14.3	4.0	14.8	8.8	16.4	2.6	17.5	5.6	15.7	5.2
M-L$_{sl}$	–	–	6.9	0.0	3.2	1.0	2.8	0.3	3.5	0.1	4.1	0.3

*See Table 1.

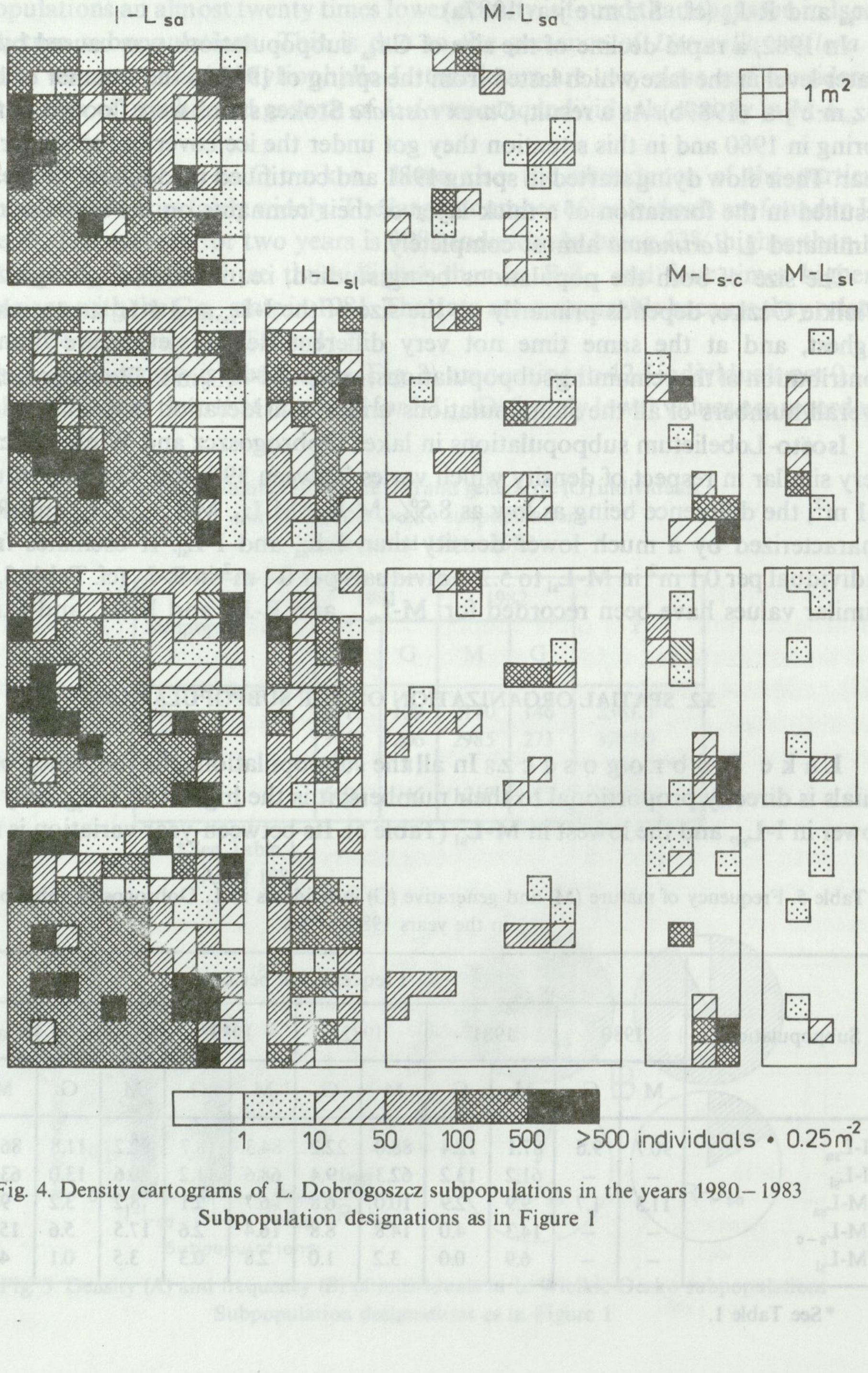

Fig. 4. Density cartograms of L. Dobrogoszcz subpopulations in the years 1980 – 1983
Subpopulation designations as in Figure 1

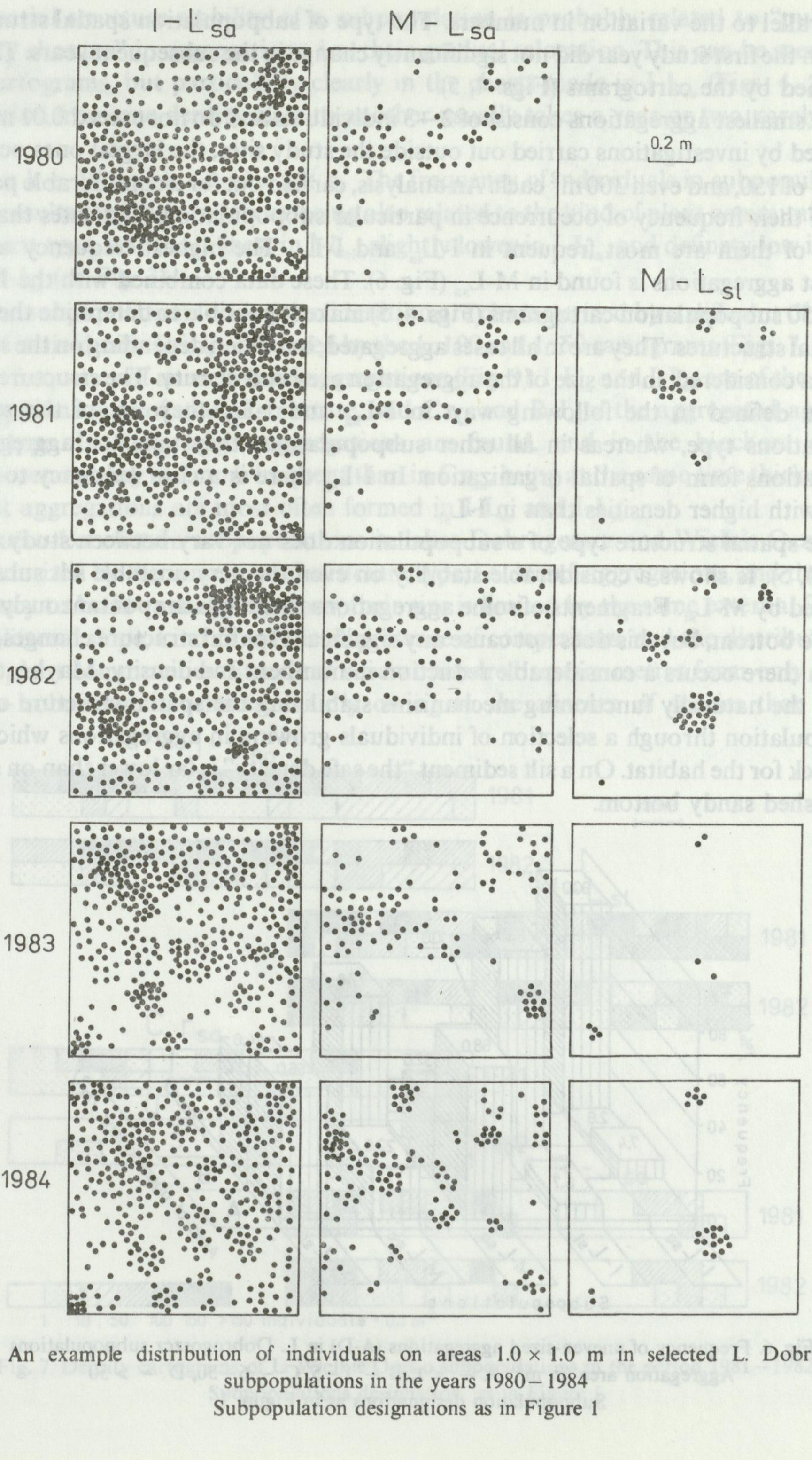

Fig. 5. An example distribution of individuals on areas 1.0 × 1.0 m in selected L. Dobrogoszcz subpopulations in the years 1980 – 1984
Subpopulation designations as in Figure 1

less parallel to the variation in numbers. The type of subpopulation spatial structure found in the first study year did not significantly change in the subsequent years. This is confirmed by the cartograms (Figs. 4, 5).

The smallest aggregations consist of 2–3 individuals and do not exceed 0.01 m^2; as indicated by investigations carried out outside the study sites, the largest ones occupy an area of 150, and even 300 m^2 each. An analysis, carried out for a considerable part of lake, of their frequency of occurrence in particular subpopulations, indicates that the largest of them are most frequent in I-L_{sa} and I-L_{sl}. The highest frequency of the smallest aggregations is found in M-L_{sa} (Fig. 6). These data combined with the 1 : 100 and 1 : 50 subpopulation cartograms (Figs. 4, 5) make it possible to determine the type of spatial structures. They are in all cases aggregated, but differ, depending on the size of the area considered, in the size of the aggregation area and density. The structures can thus be defined in the following way: in I-L_{sa} and I-L_{sl}, they are of the stand-aggregations type, whereas in all other subpopulations they take the aggregated-aggregations form of spatial organization. In I-L_{sa} there is a clear tendency to form zones with higher densities than in I-L_{sl}.

The spatial structure type of a subpopulation does not vary between study years (Figs. 4, 5). Is shows a considerable stability on even the very unstable silt substrate occupied by M-L_{sl}. Fragments of some aggregations there detach spontaneously from the lake bottom, but this does not cause any significant spatial structure changes, even though there occurs a considerable reduction in numbers and density. Maybe, this is one of the naturally functioning mechanisms stabilizing the spatial structure of this subpopulation through a selection of individuals growing in aggregations which are too thick for the habitat. On a silt sediment "the safe density" is far lower than on a well established sandy bottom.

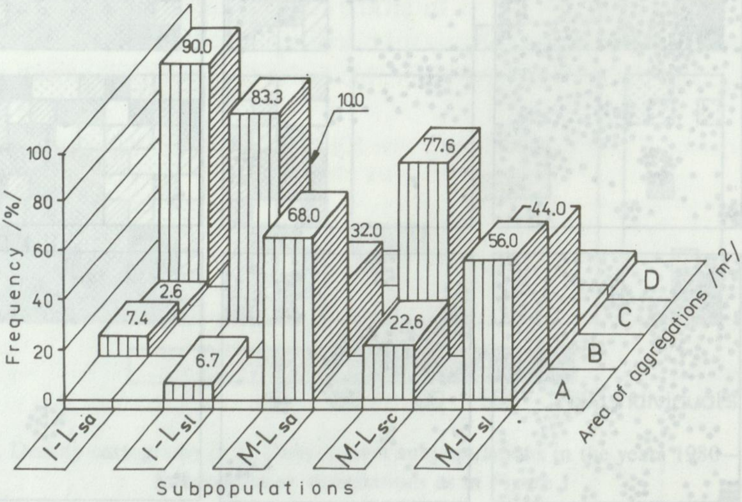

Fig. 6. Frequency of uneven-sized aggregations (A-D) in L. Dobrogoszcz subpopulations
Aggregation area (in m^2): A – < 1, B – 1–5, C – 6–50, D – > 50
Subpopulation designations as in Figure 1

Spatial structure stability of a subpopulation is probably related to "pulsating density changes" in aggregations, i.e., their gradual relocation. This can be seen in all the cartograms, but particularly clearly in the charts made in I-L_{sa} (Figs. 4, 5). The transition from one density class to another usually takes a year or two, rarely three years.

Lake Wielkie Oczko. The frequency of individuals in subpopulations is the resultant of their numbers, being also related to the kind of plant community and sediment type. It is the highest in I-L_{sl}, slightly lower in I-L_{sa}, and definety low in C.r_{sa} and R-J_{sa} (cf. Fig. 3).

The subpopulations under consideration are characterized by a different distribution of individuals. This is confirmed by the 1 : 100 and 1 : 50 cartograms (Figs. 7, 8), and by the frequency of uneven-sized aggregations (Fig. 9). I-L_{sa} and I-L_{sl} are of the stand-aggregations type of spatial structure, and C.r_{sa} and R-J_{sa} of the aggregated-aggregations type. In R-J_{sa} larger aggregations are found, and in the biochore of this phytocoenose they are more frequent than in C.r_{sa}, being at the same time thicker. The largest aggregations are most often formed in I-L_{sa} and I-L_{sl}.

Isoëto-Lobelietum subpopulations in lakes Dobrogoszcz and Wielkie Oczko are characterized by the same spatial structure type, i.e., stand-aggregations, and the same tendency to build vast aggregations; their size is limited by the same external factors: phytolittoral slope, kind of sediment, presence of competitors, and the distribution of other plant communities. Stands of several hundred square metres form only within Isoëto-Lobelietum biochores, mainly owing to the absence of species that would

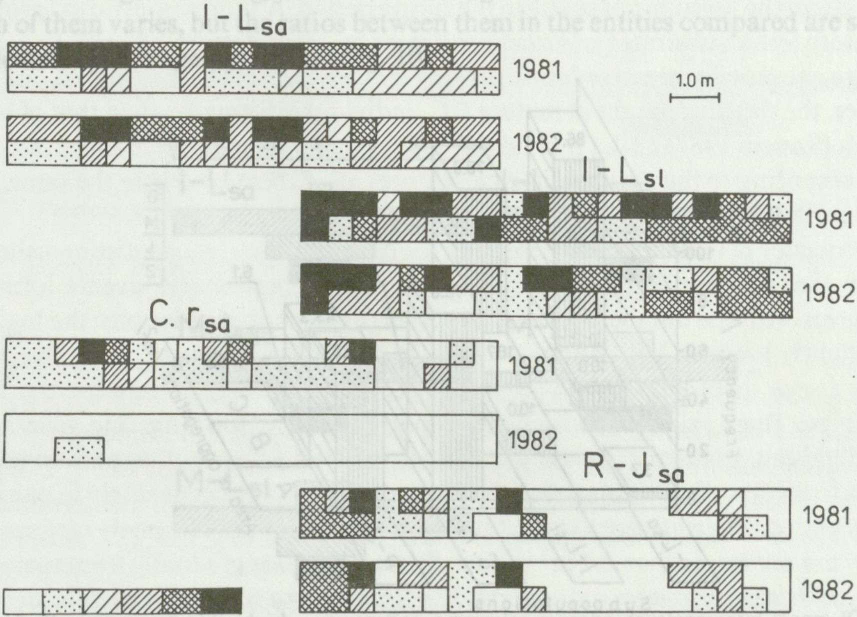

Fig. 7. Density cartograms of L. Wielkie Oczko subpopulations in the period 1981–1982
Subpopulations designation as in Figure 1

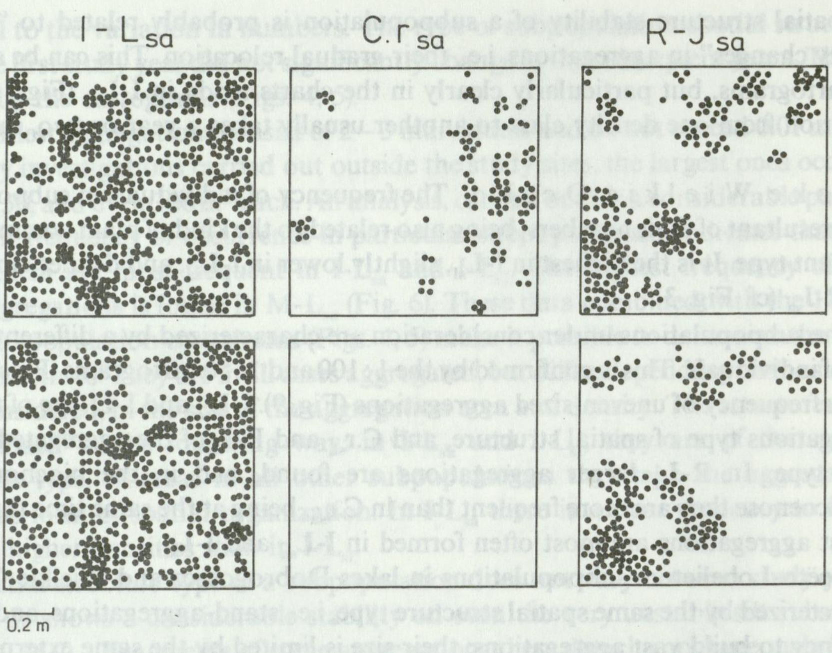

Fig. 8. An example distribution of individuals on 1.0 × 1.0 m areas in L. Wielkie Oczko subpopulations in the years 1981 – 1982
Subpopulation designations as in Figure 1

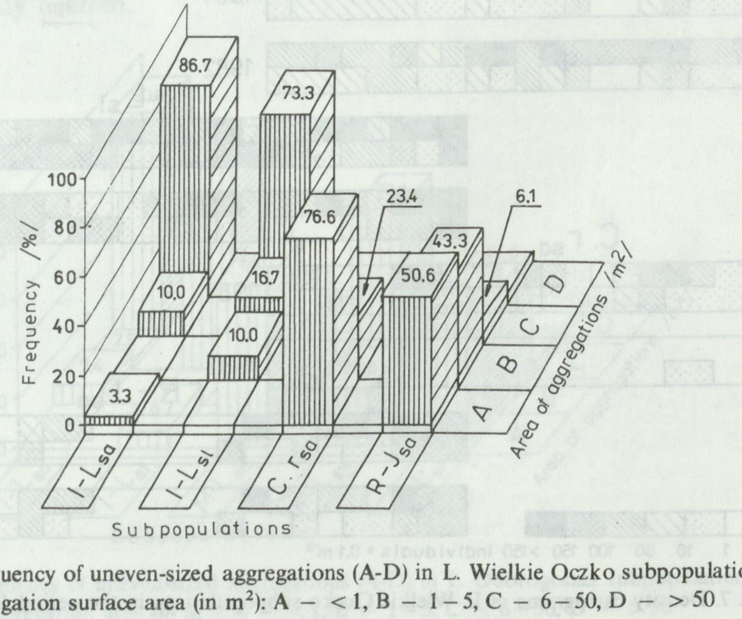

Fig. 9. Frequency of uneven-sized aggregations (A-D) in L. Wielkie Oczko subpopulations
Aggregation surface area (in m^2): A – < 1, B – 1 – 5, C – 6 – 50, D – > 50
Subpopulation denotations as in Figure 1

compete for the same space. The remaining units of comparisons, i.e., M-L_{sa}, M-L_{s-c}, M-L_{sl}, C.r_{sa} and R-J_{sa} are of a different spatial structure type. The following are found to be similar: M-L_{s-c} and R-J_{sa}, as well as M-L_{sa} and C.r_{sa}. Subpopulations of these pairs have many common features, although they belong to different phytocoenoses and lakes, and thereby also to different local populations. In spite of a fiftyfold density difference, found between M-L_{sl} and R-J_{sa}, they are, like M-L_{sa}, M-L_{s-c} and C.r_{sa}, of the same spatial structure, i.e., aggregated-aggregations type.

The proportion of small-sized aggregations and their frequency in the phytolittoral are determined by the intensity of competition between *L. dortmanna* and other species. Small aggregations form more often in M-L_{sa} and C.r_{sa} than in M-L_{s-c}, M-L_{sl} and R-J_{sa} (cf. Figs. 6, 9). In this respect the spatial organization of M-L_{sa} in L. Dobrogoszcz and C.r_{sa} in L. Wielkie Oczko show many common characteristics. These are manifested not only because these subpopulations occupy substrates of identical types, but also because they occur in the presence of a strong competitor; in the former case (M-L_{sa}) it is *L. uniflora,* in the latter (C.r_{sa}) – *C. rostrata.* There are a number of characteristics common to these units and R-J_{sa} where the growth of *L. dortmanna* individuals is limited by *Juncus bulbosus* L.

3.3. LIFE STAGES IN SUBPOPULATIONS

Lake Dobrogoszcz. Each subpopulation includes individuals representing all life stages: seedling, juvenile, mature, generative, subsenile. The contribution of each of them varies, but the ratios between them in the entities compared are similar, as indicated by the age pyramids (Fig. 10).

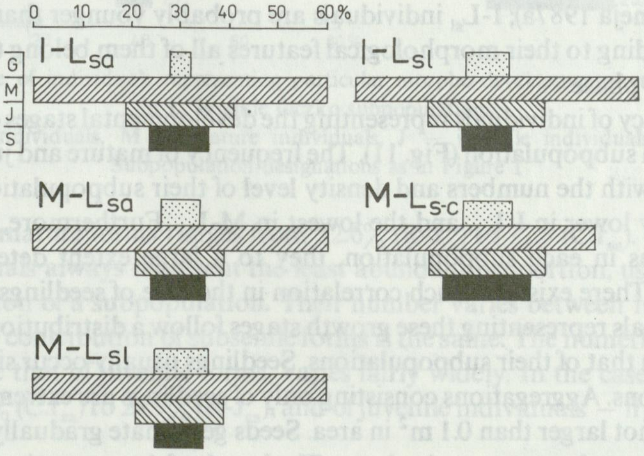

Fig. 10. Percentage of individuals representing particular morpho-developmental stages (G, M, J, S) in L. Dobrogoszcz subpopulations
G – generative individuals, M – mature individuals, J – juvenile individuals, S – seedlings. Subpopulation designations as in Figure 1

A feature common to, and at the same time characteristic of all the subpopulations is the numerical dominance of mature individuals over all the other developmental stages. Irrespective of the comparative entity, morphologically mature forms represent 47.5% (M-L_{s-c}) to 61.5% (M-L_{sa}). The proportion of seedlings is much lower, ranging from 10.5% (M-L_{sl}) to 18.2% (M-L_{s-c}), and of juveniles from 18.4% (M-L_{sl}) to 23.6% (M-L_{s-c}). Generative individuals always constitute the least numerous proportion. Their number varies between 4.2% (I-L_{sa}) and 10.7% (M-L_{s-c}). Subsenile forms represent the same proportion; they have not been placed in the age pyramids (Fig. 10) because all generative individuals pass into this stage, that is, on termination of the sexual reproduction this group is made up only of them (Szmeja 1987b). Their fully developed morphological structures then become disorganized: the leaf rosettes die, and the rhizomes after some time become subject to a gradual fragmentation. Parts of the rhizomes will continue to function the following spring only in the offspring produced through vegetative propagation. This mechanism of the individual developmental cycle functions in every subpopulation and is independent of the habitat conditions that are being considered. A mature plant in the subpopulation flowers and fructifies only once.

Differences in the morpho-developmental stage structure are small, and they result among other things from different growth rates of *L. dortmanna* in particular subpopulations. For example, in summer there are more seedlings per one generative individual in I-L_{sa} than in I-L_{sl} or M-L_{sl}. This is probably caused by a faster seedling growth in silt and sand-silt areas of the lake bed than on a sand substrate. Some of them probably attain the juvenile phase still in the spring period. A shorter individual growth cycle on more fertile substrates is further confirmed by other data: in I-L_{sl}, M-L_{s-c} and M-L_{sl} there are more generative forms per one mature individual than in I-L_{sa} or M-L_{sa}. Besides, the rhizome weight of mature I-L_{sl} individuals is smaller than that of I-L_{sa} individuals (Szmeja 1987a); I-L_{sl} individuals are probably younger than those of I-L_{sa}, although according to their morphological features all of them belong to the same, i.e., mature growth phase.

The frequency of individuals representing the developmental stages distinguished is different in each subpopulation (Fig. 11). The frequency of mature and juvenile forms in general agrees with the numbers and density level of their subpopulations: the highest in I-L_{sa}, slightly lower in I-L_{sl}, and the lowest in M-L_{sl}. Furthermore, being the most numerous forms in each subpopulation, they to a large extent determine the age-structure type. There exists no such correlation in the case of seedlings and generative forms. Individuals representing these growth stages follow a distribution pattern which is different from that of their subpopulations. Seedlings usually occur singly in uneven-aged aggregations. Aggregations consisting only of seedlings are extremely rare, and as a rule they are not larger than 0.1 m^2 in area. Seeds germinate gradually from spring to autumn, and do not form seasonal cohorts. The length of the generative cycle is more or less similar in all subpopulations.

Lake Wielkie Oczko. A feature common to I-L_{sa}, I-L_{sl}, C.r_{sa} and R-J_{sa} is the numerical dominance of mature individuals over other forms (Fig. 12). The

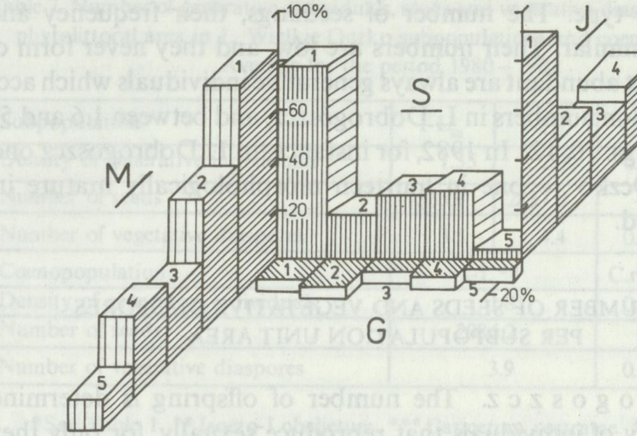

Fig. 11. Frequency of individuals representing particular morpho-developmental stages (M, S, G, J) in L. Dobrogoszcz subpopulations (1–5)
M – mature individuals, S – seedlings, G – generative individuals, J – juvenile forms; 1 – I-L_{sa}, 2 – I-L_{sl}, 3 – M-L_{sa}, 4 – M-L_{s-c}, 5 – M-L_{sl}. Subpopulation designations as in Figure 1

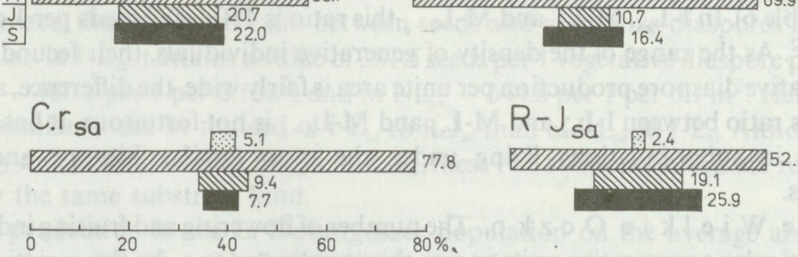

Fig. 12. Percentage of individuals representing particular morpho-developmental stages (G, M, J, S) in L. Wielkie Oczko subpopulations
G – generative individuals, M – mature individuals, J – juvenile individuals, S – seedlings. Subpopulation designations as in Figure 1

contribution of mature forms ranges from 52.6% (R-J_{sa}) to 77.8 (C.r_{sa}). Flowering and fruiting individuals always represent the least abundant proportion, usually up to 5% of the composition of a subpopulation. Their number varies between 1.6% (I-L_{sa}) and 5.1% (C.r_{sa}). The contribution of subsenile forms is the same. The numerical proportion of seedlings, like that of juvenile forms, varies fairly widely. In the case of seedlings it ranges from 7.7% (C.r_{sa}) to 25.9% (R-J_{sa}), and of juvenile individuals – from 9.4% (C.r_{sa}) to 20.7% (I-L_{sa}).

A common feature of both the populations under study, i.e., in Lake Dobrogoszcz and L. Wielkie Oczko, is a numerical dominance of mature forms over other developmental stages. Morphologically mature individuals, i.e., mature and generative, represent at least a half of the composition and determine the level of numbers, density and spatial structure type. The number of seedlings, their frequency and type of distribution are also similar. Their numbers are low, and they never form cohorts or aggregations. The least abundant are always generative individuals which account for 4 to 10% of the population numbers in L. Dobrogoszcz, and between 1.6 and 5% – in L. Wielkie Oczko (cf. Figs. 10, 12). In 1982, for instance, in L. Dobrogoszcz one in seven, and in L. Wielkie Oczko – one in fourteen morphologically mature individuals flowered and fructified.

3.4. NUMBER OF SEEDS AND VEGETATIVE DIASPORES PER SUBPOPULATION UNIT AREA

Lake Dobrogoszcz. The number of offspring is determined by the number and fecundity of individuals that reproduce sexually, for only they simultaneously produce seeds and vegetative diaspores. Regardless of the unit of comparison, there are on an average 500 to 1000 times more seeds than vegetative diaspores per 0.1 m^2 of its surface area (Table 6). In the terminal fruiting phase there fall over 3000 seeds per 0.1 m^2 I-L_{sl} area, whereas in I-L_{sa} about 2300, and in M-L_{s-c} only 1000. In the remaining two subpopulations, i.e., in M-L_{sa} and M-L_{sl}, the number of seeds produced is far lower. This is due to a low number of generative individuals.

Some of the subpopulations have similar seed to vegetative diaspores numerical ratios (Table 6). In I-L_{sa}, M-L_{sa} and M-L_{s-c} this ratio is 450–480 seeds per 1 diaspore per 0.1 m^2. As the range of the density of generative individuals, their fecundity, seed and vegetative diaspore production per unite area is fairly wide, the difference, as low as 6%, in this ratio between I-L_{sa} and M-L_{sa} and M-L_{s-c} is not fortuitous. It has become stabilized in subpopulations living under the most similar biotope and social conditions.

Lake Wielkie Oczko. The number of flowering and fruiting individuals in the particular comparative units varies; this is indicated, e.g., by the variation in the

Table 6. Number of generative individuals, seeds and vegetative diaspores per 0.1 m^2 phytolittoral area in L. Dobrogoszcz subpopulations and coenopopulations
Average for the period 1980–1983

Subpopulation *	I-L_{sa}	I-L_{sl}	M-L_{sa}	M-L_{s-c}	M-L_{sl}
Density of generative individuals	2.80	1.90	0.20	1.15	0.05
Number of seeds	2301.6	3298.2	114.5	974.4	65.4
Number of vegetative diaspores	4.8	3.0	0.3	2.2	0.1
Coenopopulation	I-L**		M-L***		
Density of generative individuals	2.35		0.46		
Number of seeds	2799.9		348.8		
Number of vegetative diaspores	3.9		0.9		

* See Table 1. ** Isoëto-Lobelietum. *** Myriophyllo-Littorelletum.

Table 7. Number of generative individuals, seeds and vegetative diaspores per 0.1 m^2 phytolittoral area in L. Wielkie Oczko subpopulations and coenopopulations Average for the period 1980 – 1982

Subpopulation *	$I\text{-}L_{sa}$	$I\text{-}L_{sl}$	$C.r_{sa}$	$R\text{-}J_{sa}$
Density of generative individuals	1.35	2.40	0.15	0.55
Number of seeds	1335.4	2837.0	–	598.1
Number of vegetative diaspores	3.5	4.4	0.4	1.3
Coenopopulation	I-L **		C.r ***	R-J ****
Density of generative individuals	1.87		0.15	0.55
Number of seeds	2086.2		–	598.1
Number of vegetative diaspores	3.9		0.4	1.3

* See Table 1. ** Isoëto-Lobelietum. *** Caricetum rostratae. **** Ranunculo-Juncetum bulbosi.

density of generative individuals (Table 7), which is the highest in $I\text{-}L_{sl}$ (2.40 generative individuals per 0.1 m^2), much lower in $I\text{-}L_{sa}$ (1.35 per 0.1 m^2) and the lowest in $C.r_{sa}$ (0.15 per 0.1 m^2). The density in $R\text{-}J_{sa}$ is 3.5 times lower than the arithmetic mean calculated for $I\text{-}L_{sa}$ and $I\text{-}L_{sl}$.

The data contained in Table 7 indicate that in the L. Wielkie Oczko population there are over 700 times more seeds than vegetative diaspores per 0.1 m^2. As in L. Dobrogoszcz, the numerical ratio between seeds and vegetative diaspores is more or less similar. In $I\text{-}L_{sa}$ it attains a value of 381.5 seeds per 1 vegetative diaspore per 0.1 m^2, in $R\text{-}J_{sa}$ – 460.1 per 1 per 0.1 m^2, and in $I\text{-}L_{sa}$ – 644.8 per 1 per 0.1 m^2. Here a much greater similarity can be noticed of $I\text{-}L_{sa}$ to $R\text{-}J_{sa}$ than of $I\text{-}L_{sa}$ to $I\text{-}L_{sl}$. Although there are many differences between $I\text{-}L_{sa}$ and $R\text{-}J_{sa}$, these two subpopulations are related first of all by the same substrate kind.

Seed production in the L. Dobrogoszcz population on the average amounts to 1574.3 seeds per 0.1 m^2, and in L. Wielkie Oczko it is lower by 15% (cf. Tables 6, 7). The cause of this difference is primarily a smaller number of generative individuals in the L. Wielkie Oczko population. It affects the total number of offspring resulting from sexual and vegetative reproduction. At the end of the fruiting phase there are on an average 656 times more seeds than vegetative diaspores per 0.1 m^2 of the phytolittoral. In L. Wielkie Oczko this ratio is 718 : 1. The difference between the populations compared is as small as 9%.

4. DISCUSSION

Over the depth range of 0.8 – 1.0 m in the phytolittoral *L. dortmanna* population structure is modelled by diversified biotope and phytocoenose conditions such as the degree of sediment fertility, granulation and establishment, spatial heterogeneity and the intensity of inter-species and intra-population competition. The way in which the influence of these factors is exerted varies, and so do the kind and extent of the changes caused by them. These responses can only be compared with terrestrial plants because existing hydrobotanical publications lack data on the population structure of the macrophytes in relation to the kind of phytocoenoses and their biochores.

The populations of most terrestrial plants have an aggregated spatial organization, often irrespective of the mode of reproduction of individuals (Kwiatkowska 1972, Falińska 1976, 1979). An aggregated structure is also seen in the *L. dortmanna* population. The distribution of its individuals is the result among other things of the vegetative propagation, seed hydrobarochory and a more frequent seed germination near the rosettes of individuals that are already growing (Szmeja 1987a, 1987b). Important, too, is its strong association with the sediment; CO_2 concentration in the root system of *L. dortmanna* is 100 – 400 times higher than outside it (Wium-Andersen 1971). Apart from this, the uptake of some nutrients, especially phosphorus, is aided by mycorrhizal vesicles (Søndergaard and Laegaard 1977). Thus, the formation of aggregations is an expression of a competitive struggle for food and space (Zarzycki 1965, Harper 1977), and it at the same time ensures a more efficient adjustment of the habitat to their needs. Within the interlaced root systems of the already formed aggregations there probably is a higher nutrient concentration and faster cycles of nutrients, including phosphorus and carbon, as well as a greater probability of encountering a mycorrhizal fungus than outside them.

The above-mentioned ecological situation may initiate reversible mechanisms: beneath the very close, and as a rule one-species aggregations the selectivity with regard to the same nutrients will be more intensive. This can to some extent be identified with so-called "soil fatigue" (cf. Zarzycki 1965) which probably is in this case efficiently alleviated through a relocation of densities and thinnings within the population area. This could be observed in all the units compared, being most conspicuous in those subpopulations where there were very dense aggregations, e.g., in I-L_{sa}. Moreover, water is capable of dissolving and transporting almost all nutrients (Golterman 1975, Hutchinson 1975), thus being able to efficiently offset "soil fatigue" processes.

L. dortmanna is a competitively weak species: (1) it is not expansive – and does not extend its range or increase the number of habitats in Poland (Szmeja 1987c); (2) it can only live in a small number of ecosystems – in Poland only in 1.4% of all lakes (Szmeja 1987c); (3) it mainly inhabits sand habitats which are at the same time infertile; (4) it colonizes the phytolittoral area, accessible to it, more slowly and less efficiently than some other species which cooccur with it (Szmeja 1987a). In this situation the formation of aggregations is for *L. dortmanna,* as well as for many competitively weak species, the most advantageous adaptive option, justifiable both from the point of view of defensive responses to the pressure of competitors (Zarzycki 1965), severity of living conditions (Symonides 1979), and of the course of the main physiological processes.

Irrespective of the pattern of distribution of individuals within the subpopulations studied, their density is subject to a continual "pulsating", as a result of which individual aggregations and the spatial structure of these subpopulations bear features of a greater durability. Similar reactions take place in the populations of some forest herb layer species (Pirożnikow 1983). In the case of *L. dortmanna,* the size of aggregations and their density are inversely proportional to the intensity of the pressure of competitor species and habitat fertility. These are the main factors determining the spatial organization of the population and the social status of the individuals living in it.

Differences in the age, size and numbers of the individuals in aggregations (Mazur 1984), as well as the functioning of the mechanisms controlling their persistence and nutrient cycling rate agree with the statement put forward by Symonides (1983) that they form independent ecological systems. A competitive partitioning of nutrients and space takes place in them, and thereby diversification of the social position of individuals (Łomnicki 1980), which considerably affects their condition and fecundity.

Most numerous in a *L. dortmanna* population are mature individuals, i.e., those that are morphologically fully mature and potentially able to reproduce. Here the proportion of seedlings or generative individuals is small, usually not greater than 10% of the total abundance. Such a distribution of the morpho-developmental phases is typical of a number of perennials, mainly monocarpic, to which *L. dortmanna* also belongs (Szmeja 1987b).

The numerical ratio between seeds and vegetative diaspores per phytolittoral unit area is similar only in those subpopulations which live under the most similar biotope and social conditions. As has been demonstrated (Szmeja 1987a), this is the main factor that causes individuals of a population to become similar to one another.

Viewed statically, the morpho-developmental stage structure does not show any clear relationship to the kind of a local population, its density, spatial organization and type of the phytocoenose to which it belongs. It probably depends primarily on the reproduction strategy of the species, rate of generation rotation within the population, and on the temporal and spatial durability of the phytocoenose.

5. SUMMARY

The paper presents the results from studies of *L. dortmanna* population structure and dynamics under diverse phytocoenose and biotope conditions over the same depth (0.8 – 1.0 m) interval of the phytolittoral of two lakes in the period 1980 – 1984. Two populations (in lakes Dobrogoszcz and Wielkie Oczko) were a priori divided into 9 comparative units (subpopulations, cf. Table 1, Fig. 1). Their density, spatial organization, morpho-developmental stage structure and diaspore production were studied once a year. The criteria used for identifying subpopulations included: biochore homogeneity and the same type of plant community.

Nearly all the population structure parameters, and probably the numbers-controlling mechanisms as well, change significantly in relationship to the specific system of biotope and biocoenose conditions. Subject to variation is, for example, the spatial structure type, as well as the number of seeds and vegetative diaspores per unit of population area.

Variation in the number of individuals between subpopulations from year to year is not wide (Table 2). Abundance fluctuation in aggregations made up only of *L. dortmanna* is on the average more than a half lower than in several-species aggregations. In the former case (subpopulations I-L_{sa} and I-L_{sl}) these variations are not greater than 6%, in the latter (M-L_{sa} and M-L_{s-c}), where there is a strong competitor (*L. uniflora*) they come up to 15.6%. The particular subpopulations have their own rhythm, not synchronized with that of other subpopulations, of abundance variation from year to year (Fig. 2).

The distribution of individuals in the phytolittoral of both lakes is aggregated, regardless of the kind of phytocoenoses and their biochores (Figs. 4, 5, 7, 8). The size and frequency of *L. dortmanna* aggregations is negatively correlated with habitat fertility and intensity of pressure of rival species competing with it for space and food (Figs. 6, 9). In the study years the distribution of individuals showed a high stability, on even a poorly established silt substrate and in the presence of strong competitors (Figs. 5, 8).

The subpopulations include individuals representing all morpho-developmental stages (Figs. 10, 12). Features common to all the entities compared are: the dominance of mature forms (47.5 – 77.8%), low percentage of seedlings (7.7 – 25.9%) and generative individuals (1.6 – 10.7%). There are on an average several hundred to a thousand times more seeds than vegetative diaspores per 0.1 m^2 phytolittoral area (Tables 6, 7); vegetative diaspores to a large extent determine the population size. Subpopulations occurring under similar biotope and social conditions are found to be most similar in respect of the numerical seed to vegetative diaspore ratio (Table 6).

The frequency of mature and juvenile forms generally agrees with the numbers and density of subpopulations (Fig. 11). Apart from this, being the most numerous stages present in each subpopulation, they considerably contribute to the type of spatial organization and age structure. There exists no such correlation between seedlings and generative forms. Individuals representing these morpho-developmental stages follow a different distribution pattern. Seedlings as a rule occur singly in uneven-aged aggregations, and do not form seasonal cohorts.

6. POLISH SUMMARY

W pracy przedstawiono wyniki badań struktury i dynamiki populacji *L. dortmanna* w różnych warunkach fitocenotyczno-biotopowych stałego przedziału fitolitoralu (0,8 – 1,0 m głębokości) dwóch jezior w latach 1980 – 1984. Dwie populacje (w jez. Dobrogoszcz i jez. Wielkie Oczko) podzielono a priori na 9 jednostek porównawczych (subpopulacji, por. tab. 1, rys. 1). Raz w roku badano ich zagęszczenie, organizację przestrzenną, strukturę stanów morfologiczno-rozwojowych i produkcję diaspor. Kryteriami do wydzielenia subpopulacji były: jednorodność biochory i ten sam typ zbiorowiska roślinnego.

Zależnie od konkretnego układu czynników biotopowych i biocenotycznych zmieniają się istotnie niemal wszystkie parametry struktury populacji, a przypuszczalnie także mechanizmy regulujące liczebność. Odmienne jest np. zagęszczenie, typ organizacji przestrzennej, a także liczba nasion i diaspor wegetatywnych przypadających na jednostkę powierzchni zajmowanej przez populację.

Wahania liczby osobników w poszczególnych subpopulacjach z roku na rok nie są duże (tab. 2). Przeciętna fluktuacja liczebności w skupiskach utworzonych wyłącznie z *L. dortmanna* jest o połowę mniejsza niż w kilkugatunkowych. W pierwszym przypadku, a dotyczy on subpopulacji I-L_{sa} i I-L_{sl}, zmiany te nie przekraczają 6%. W drugim – tj. w M-L_{sa} i M-L_{s-c}, gdzie obecny jest silny konkurent (*L. uniflora*), wynoszą 15,6%. Poszczególne subpopulacje mają własną, między sobą nie zsynchronizowaną rytmikę zmian liczebności (rys. 2).

Rozmieszczenie osobników w fitolitoralu obu jezior jest skupiskowe, niezależnie od rodzaju fitocenoz i ich biochor (rys. 4, 5, 7, 8). Wielkość i frekwencja skupisk *L. dortmanna* są ujemnie skorelowane ze stanem zasobności siedlisk i z natężeniem presji gatunków konkurujących z nią o przestrzeń i pokarm (rys. 6, 9). W latach badań sposób rozmieszczenia osobników wykazywał dużą trwałość, nawet na słabo utrwalonym podłożu mulistym i obecności silnych konkurentów (rys. 5, 8).

W skład każdej subpopulacji wchodzą osobniki z wszystkich stanów morfologiczno-rozwojowych (rys. 10, 12). Cechą wspólną badanych jednostek porównawczych jest: dominowanie form maturalnych

(47,5 – 77,8%), niewielki udział siewek (7,7 – 25,9%) i osobników generatywnych (1,6 – 10,7%). Na 0,1 m^2 fitolitoralu przypada przeciętnie od kilkuset do tysiąca razy więcej nasion niż diaspor wegetatywnych (tab. 6, 7); te ostatnie w dużej mierze kształtują liczebność populacji. Najbardziej zbliżoną proporcję liczby nasion do liczby diaspor wegetatywnych na jednostkę powierzchni mają subpopulacje występujące w zbliżonych warunkach biotopowo-socjalnych (tab. 6).

Frekwencja form maturalnych i juwenilnych jest na ogół zgodna z liczebnością i stanem zagęszczenia subpopulacji (rys. 11). Ponadto, jako stadia najliczniej reprezentowane w każdej subpopulacji, w dużej mierze tworzą typ organizacji przestrzennej i struktury wieku. W przypadku siewek i form generatywnych nie ma takiej korelacji. Osobniki z tych stanów morfologiczno-rozwojowych mają inny wzorzec rozmieszczenia. Siewki występują przeważnie pojedynczo w różnowiekowych skupiskach i nie tworzą sezonowych kohort.

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