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Józef SZMEJA

Department of Plant Ecology and Nature Protection,
University of Gdańsk, Czołgistów 46, 81–378 Gdynia, Poland

THE ECOLOGY OF *LOBELIA DORTMANNA* L.

I. THE PLASTICITY OF INDIVIDUALS WITHIN A CONSTANT DEPTH INTERVAL IN OLIGOTROPHIC LAKES

ABSTRACT: The condition and fecundity were studied of *Lobelia dortmanna* individuals growing within the same phytolittoral depth interval, 0.8–1.0 m, in two oligotrophic lakes in northern Poland (southern range of the species). The response was determined of this plant to: (1) kind of sediment and type of plant community, (2) varying population density, (3) competitive action of *Littorella uniflora* (L.) Aschers., *Myriophyllum alterniflorum* DC., *Carex rostrata* Stokes and *Juncus bulbosus* L. A considerable plasticity, among other things, has been demonstrated of individuals under identical phytocoenotic and biotope conditions, advantageous reactions of an oligophilous plant to increasing sediment fertility, and phenotypical plasticity.

KEY WORDS: *Lobelia dortmanna*, macrophyte, isoetid, fecundity, competition, overcrowding stress, phytocoenotic and biotope conditions, oligotrophic lakes.

1. INTRODUCTION

The reactions of isoetids to some conditions of the aquatic environment, e.g., temperature, light, depth, kind and chemical composition of sediments have many times been reported on in physiological and ecological papers. In those publications some interesting information can be found on the efficiency of photosynthesis (e.g., Sand-Jensen 1978, Sand-Jensen and Søndergaard 1979), habitat requirements, biomass production and reaction to the chemistry of the water (Iversen 1929, Seddon 1965, Toivonen and Lappalainen 1980), as well as on the resistance to the varying degrees of its pollution (Eloranta 1970, Kurimo 1970) and mortality at different depths (Rørslett 1985).

Lobelia dortmanna, an oligophilous plant, has so far been one of the best known isoetids. For instance, there have been studies of its biomass on various kinds of sediment (Kansanen and Niemi 1974), anatomic and morphologic structure of its leaves at different depths (Åberg 1943), course of photosynthesis (e.g., Raven 1970, Sand-Jensen and Borum 1984), habitat requirements (Lohammar 1938, Szmal and Szmal 1965) and phytocoenotic scale (e.g., Dąmbska 1965, Dierssen 1975, Pietsch 1977, Szmeja 1987a). It has been found (Wium-Andersen 1971) that at an extremely low nutrient concentration in water the occurrence of *L. dortmanna* depends, among other things, on its capability of absorbing carbon dioxide directly from the sediments, and on the presence of mycorrhizal vesicles on its roots. They facilitate the uptake of some nutrients from the sediments (Søndergaard and Laegaard 1977), which may to some extent compensate for their deficit in the water, and additionally strengthen the association of this plant with the substratum.

The results from previous studies of *L. dortmanna* and other isoetids permit the following hypotheses to be put forward:

(1) The size, habit and fecundity of a submerged plant, rooted in the floor of a water body and occurring over a constant depth interval should depend, among other things, on the kind of sediments and plant community.

(2) An increase in organic matter content in an infertile sandy sediment will create better nutrient conditions for an oligophilous plant.

(3) The responses of a plant to the heterogeneity of habitats in an isolated ecosystem (a lake), i.e., to their spatial and temporal variation are probably only unfixed changes in its phenotype.

(4) The range of variation of the morphological characters and fecundity of a plant depends on its inherited and acquired plasticity, as well as on the range of phytocoenotic and biotope conditions.

Verification of the above hypotheses was the main objective of the studies presented in this paper. They took into account *L. dortmanna* individuals growing on various sediment types and in phytocoenoses of different plant communities, formed in the phytolittoral over a depth range of 0.8 – 1.0 m.

It has been adopted that, as defined by Smirnova et al. (1976), an individual is a morphologically and physiologically continuous organism representing an ontogenetic unit. In the case of *L. dortmanna*, it is a reduced stem that consists of a rhizome and a rosette of leaves growing from it. In this paper, a population is an assemblage of conspecific individuals in an isolated lake. A population so defined consists of coenopopulations, that is, individuals from phytocoenoses of separate plant communities. Subcoenopopulations have also been distinguished. For simplicity these will be referred to as subpopulations. They are individuals found in a fragment, homogeneous in respect of habitat conditions, of a biochore, i.e., the space occupied by a phytocoenose.

This paper is the first of a series of publications dealing with the ecology of *L. dortmanna*, more precisely – individual variation, and population structure and dynamics within a constant littoral interval (0.8 – 1.0 m), and over a gradient of increasing depths (0.0 – 3.0 m).

2. STUDY AREA

The studies were carried out in lakes Dobrogoszcz and Wielkie Oczko, situated in the Kashubian Lake District (northern Poland), 13 km apart. The former is 5 km to the north-west, and the latter 8 km to the south of Kościerzyna (Fig. 1).

The selection of the lakes was based on the following criteria: (1) spatial separation, i.e., absence of natural or man-made connections between the lakes; (2) chemical composition of the water which should be of the commonest type found in *Lobelia* lakes in Poland; (3) presence of plant communities typical of this group of lakes in Poland; (4) varied substrate in the phytolittoral zone; (5) considerable water transparency; (6) occurrence of a sufficiently abundant *L. dortmanna* population.

Lake Dobrogoszcz, 53.3 ha in surface area, is characterized by a small maximum depth (6.6 m) and a fairly good transparency of the water (3.8 m) which is well

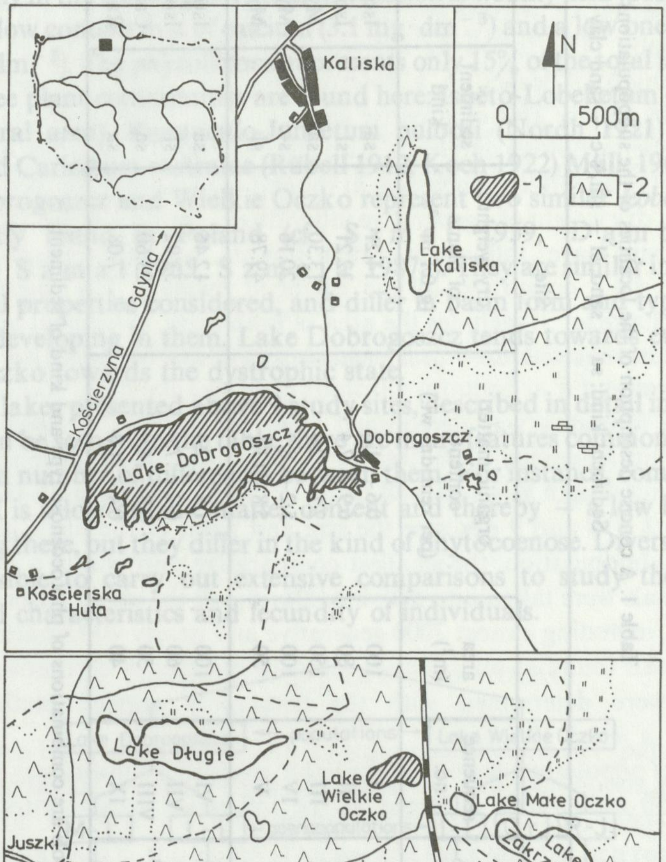

Fig. 1. Sketch map of the study lakes
1 — lakes, 2 — woods

Table 1. A concise description of the localities of the subpopulations under study

Sediment kind: sa – sand, sl – silt, s-c – sand clay

Lake	Site					Subpopulation	
	sequence no.	area (m^2)	organic matter content (per cent dry wt.)	dry weight of plants ($g \cdot 0.1\ m^{-2}$)	sediment kind	phytocoenose type	symbol *
Dobrogoszcz	I	100	0.6 – 1.8	14.21	sa	Isoëto-Lobelietum	I-L_{sa}
	II	80	6.9 – 7.4	32.21	sl	Isoëto-Lobelietum	I-L_{sl}
	III	150	2.1 – 2.9	13.30	sa	Myriophyllo-Littorelletum	M-L_{sa}
	IV	100	5.2 – 8.7	20.16	s-c	Myriophyllo-Littorelletum	M-L_{s-c}
	V	50	5.8 – 13.1	49.78	sl	Myriophyllo-Littorelletum	M-L_{sl}
Wielkie Oczko	VI	100	1.8 – 2.4	12.46	sa	Isoëto-Lobelietum	I-L_{sa}
	VII	60	6.2 – 7.8	33.92	sl	Isoëto-Lobelietum	I-L_{sl}
	VIII	50	3.8 – 4.9	23.60	sa	Caricetum rostratae	C.r_{sa}
	IX	40	0.4 – 1.3	7.08	sa	Ranunculo-Juncetum	R-J_{sa}

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

oxygenated from surface (115.5%) to bottom (99.3%). The reaction of the water is neutral (pH 6.9 – 7.3), and there are low contents in it of calcium (6.8 $mg \cdot dm^{-3}$), phosphorus (0.3 $\mu mol \cdot dm^{-3}$), carbon dioxide (0.6 – 1.0 $mg \cdot dm^{-3}$), nitrites (trace amounts) and nitrates (0.6 $\mu mol \cdot dm^{-3}$). Dominant here are Myriophyllo-Littorelletum Jeschke 1959 phytocoenoses which cover about 3/4 of the phytolittoral area between isobaths 0.0 and 6.6 m, on all substrate types (sand, gravel, sandy silt and silt with clay). A large area is also covered by patches of Isoëto-Lobelietum (W. Koch 1926) R. Tx. 1937, although only in some lake parts between depths 0 and 4 m. In both of the phytocoenoses *L. dortmanna* occurs very abundantly, especially over the depth range 0.0 – 1.7 m; below this range *Isoëtes lacustris* L. is dominant.

Lake Wielkie Oczko in less than one tenth the size of L. Dobrogoszcz but twice as deep (11.4 m) as the latter, which fact significantly affects its limnological specificity. Here the littoral slopes rapidly, and the water is of a good transparency, well oxygenated only in the trophogenic zone, its reaction is weakly acid (pH 6.4 – 6.6), and there is a very low content in it of calcium (3.1 $mg \cdot dm^{-3}$) and a low one of carbonates (2.5 – 2.6 $mg \cdot dm^{-3}$). The phytolittoral represents only 15% of the total lake floor area. Patches of three plant communities are found here: Isoëto-Lobelietum (about 90% of the phytolittoral area), Ranunculo-Juncetum bulbosi (Nordh 1921) Oberd. 1957 (about 3%) and Caricetum rostratae (Rübell 1912, Koch 1922) Müll. 1961 (about 7%).

Lakes Dobrogoszcz and Wielkie Oczko represent two similar *Lobelia* lake types most frequently found in Poland (cf. Szmal 1959, Dąmbska 1965, Szmal and Szmal 1965, Szmeja 1987a). They are similar in respect of the water chemical properties considered, and differ in basin form and type of the plant communities developing in them. Lake Dobrogoszcz tends towards eutrophy, while L. Wielkie Oczko towards the dystrophic state.

In the two lakes presented above 9 study sites, described in detail in Table 1, were laid out. As can be seen from the table, there are many features common to all the sites and there are a number of differences between them. For instance, common to sites I, III, IV and IX is a low organic matter content and thereby – a low biomass of the plants growing there, but they differ in the kind of phytocoenose. Diversity of this type makes it possible to carry out extensive comparisons to study the variation of morphological characteristics and fecundity of individuals.

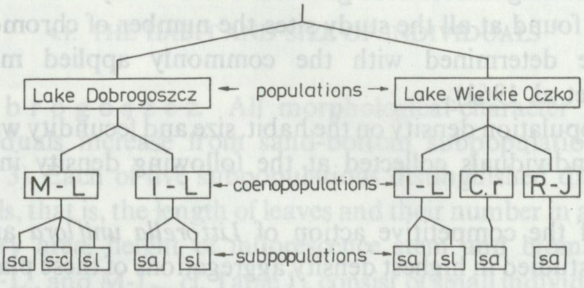

Fig. 2. Diagram showing the division of populations
M-L – Myriophyllo-Littorelletum, I-L – Isoëto-Lobelietum, C.r. – Caricetum rostratae, R-J – Ranunculo-Juncetum bulbosi; sediments: sa – sand, s-c – sand-clay, sl – silt

The main objects of the study are individuals and their subpopulations distinguished a priori. They come from two lakes, five coenopopulations and nine subpopulations (Fig. 2).

3. METHODS

3.1. FIELD OBSERVATIONS

Field investigation was carried out in the period 1980–1983, always in July and August, i.e., during the phases of flowering and fruiting of *L. dortmanna.*

Underwater samples, each of the size of 0.1 m^2, to be used for biometric analyses were collected with a specially made grab. Sampling sites were selected at random, and so were the plants to be measured directly in the field. Only morphologically mature forms were collected, i.e., mature and generative individuals which did not differ in size and rosette habit. The following individual characters were taken into account: (1) average length of leaves in a rosette (cm); (2) number of leaves in rosette; (3) assimilatory surface area of a rosette (cm^2); (4) fruit length (mm); (5) fruit breadth (mm); (6) number of flowers and fruits in an inflorescence; (7) number of seeds in a ripe fruit; (8) height of an inflorescence stem at the end of its growth, i.e., during the fruiting phase (cm); (9) dry weight of a generative individual – broken down into dry weight of the roots, rhizome, leaves, inflorescence stem, flowers, fruit and vegetative diaspores (g).

Characters 1–3 comprised all the leaves in rosettes. The rosette assimilatory surface area (character 3) includes the area of both sides, calculated according to the formula: $P = 2n(a \cdot b)$, where a – leaf length (cm), b – leaf breadth (cm), n – number of leaves in a rosette.

Individual fecundity was determined from the number of: seeds (character 7), flowers and fruits (character 6) and vegetative diaspores. The following were auxiliary parameters: fruit length (character 4), fruit breadth (character 5) and seed weight. Characters 1, 2, 3, 8 and 9 describe the size and habit of the plant under study.

For each subpopulation, the smallest comparative unit within a population, 100 – 200 individuals were taken into account. During all the study years a total of 6000 were collected, including almost 2000 generative and nearly 4000 mature individuals.

In individuals found at all the study sites the number of chromosomes and their morphology were determined with the commonly applied methods (cf., e.g., Skalińska et al. 1961).

The effect of population density on the habit, size and fecundity was assessed on the basis of 30–50 individuals collected at the following density intervals: < 10, 10 – 50, > 100.

The impact of the competitive action of *Littorella uniflora* and *Myriophyllum alterniflorum* was studied in highest density aggregations of these plants. From each of them 100 *L. dortmanna* individuals were taken. Their morphological characteristics and fecundity were subsequently compared with those that grew in maximum-density assemblages made up only of *L. dortmanna.*

3.2. STATISTICAL ANALYSES OF THE RESULTS

Prior to the statistical analyses the goodness of fit of the distribution of the characters considered with the Gaussian curve was verified by the chi^2 test (Greń 1974); the normal-distribution hypothesis was in most cases satisfied at a sufficient level of goodness of fit.

For the biometric features of individuals basic statistical characteristics have been established: extreme values (min.-max.), arithmetic mean and error of the mean ($\bar{x} \pm m$), modal mean (m_o), standard deviation (S) and variation coefficient (V).

In the comparisons of biometric characters histograms were used (cf. Perkal 1967). To determine the effect of habitat fertility, density and competitors on the characters of the plant species under consideration, correlation coefficients were calculated. Significance of differences between characters was verified with Student's *t*-test (Oktaba 1976). Statistical inferring was done at the 5% error risk.

For the grouping of individuals Ward's method was used (Chudzińska 1980). Each subpopulation was described with the arithmetic means of 9 standardized characters (cf. Perkal 1967). Euclidean distances from these quantities were subsequently determined, which in Ward's method are derived from the centre of gravity of the clusters that are analysed. The distances are obtained from the formula, given also by Chudzińska (1980):

$$d_{qr} = \sqrt{\frac{n_q \cdot n_r}{n_q + n_r}}\, d(\bar{x}_q, \bar{x}_r)$$

where n_q, n_r are the numbers of elements in clusters, d_{qr} – distance between clusters q, r. The subpopulations analysed can be graphically grouped in a hierarchical order to form dendrograms.

All the calculations were carried out on an Odra 1204 computer at the Computing Centre of the Institute of Mathematics of the University of Gdańsk.

4. RESULTS

4.1. THE HABIT AND SIZE OF INDIVIDUALS

Lake Dobrogoszcz. All morphological-character parameters of *L. dortmanna* individuals increase from sand-bottom subpopulations to silt-bottom populations (Fig. 3). Each of five subpopulations distinguished differs in the size of mature individuals, that is, the length of leaves and their number in a rosette, as well as in the assimilatory area, height of inflorescence stem and biomass. Sand-bottom subpopulations (I-L_{sa} and M-L_{sa}, cf. Table 1), consist of small individuals, the variation of whose average weight and assimilation area is very narrow (Fig. 4). A rosette is made up of a few short leaves, and the inflorescence stem that grows out of it is thin, short, and

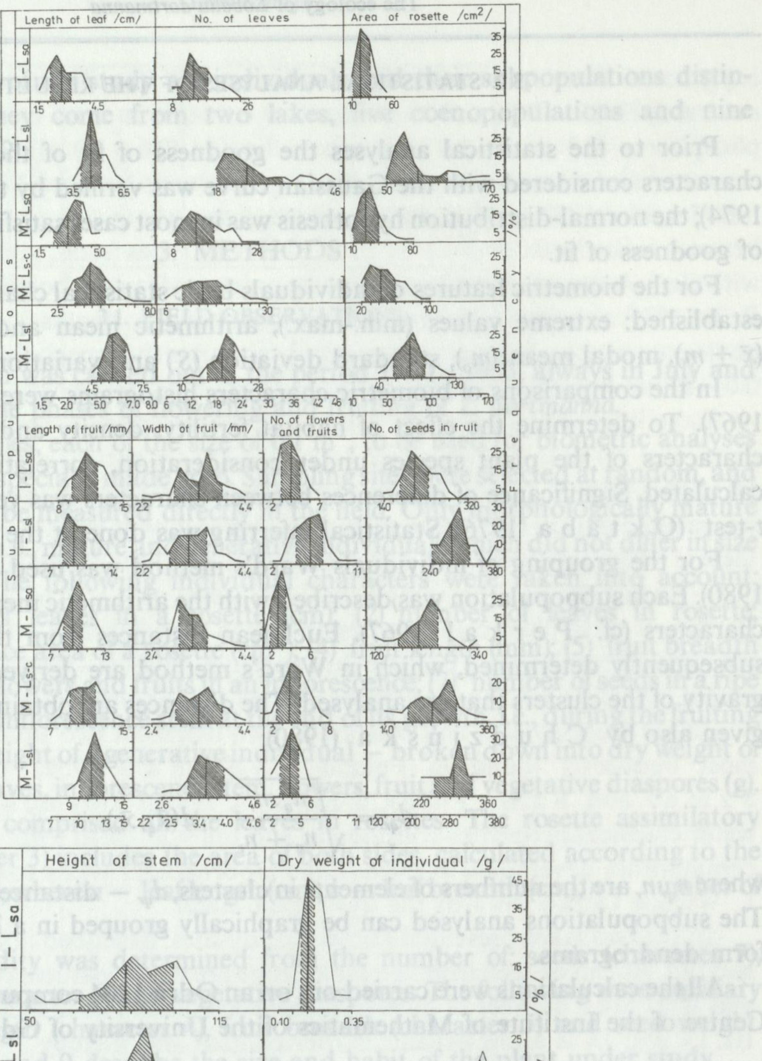

Fig. 3. Diagram of character frequencies of individuals in Dobrogoszcz subpopulations
Subpopulation designations as in Figure 2

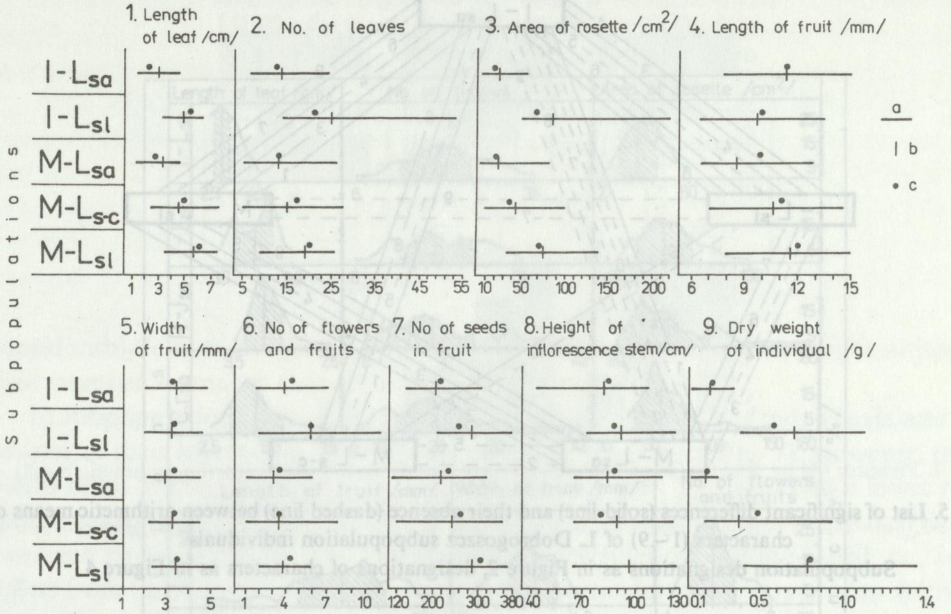

Fig. 4. Ranges of character variation in L. Dobrogoszcz subpopulations
a – min.-max., b – arithmetic mean, c – modal mean. Subpopulation designations as in Figure 2

it often fails to grow tall enough to reach the water surface. Relatively small, too, is the dispersion of the values of these characters.

The size and habit of individuals overgrowing a silt bottom clearly indicate that here they are bigger, shapelier and better nourished than those on a sand bottom. As a result, they are four times as heavy, have twice as meany leaves in rosettes, longer inflorescence stems and leaves.

The biggest differences between subpopulations are seen in the biomass (character 9), leaf length (1) and assimilatory area (3). These are the best diagnostic characteristics to describe the morphological responses of individuals. The least plastic feature is the inflorescence stem length (8, related to the constant depth interval) and the fruit length and breadth (4 and 5).

An “artificial grouping of subpopulations” derived from Isoëto-Lobelietum (i.e., I-L_{sa} + I-L_{sl}) and Myriophyllo-Littorelletum (i.e., M-L_{sa} + M-L_{s-c} + M-L_{sl}) phytocoenoses resulted in two *L. dortmanna* coenopopulations. The differences between the arithmetic means of their characteristics are statistically insignificant at the level of the adopted error risk (5%). This is in clear contrast to the results obtained for the subpopulations compared, for almost all (90%) of the 90 calculated differences are significant.

The largest number of statistically significant differences have been found between subpopulations from different types of bottom (Fig. 5). A synthetic picture of the inner diversity of the *L. dortmanna* population in Lake Dobrogoszcz is provided by the dendrogram (Fig. 6). It shows that the main factor modifying the size and habit of

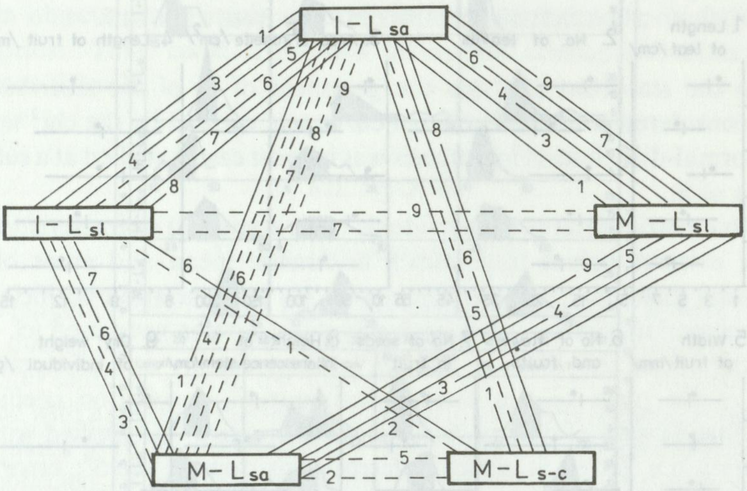

Fig. 5. List of significant differences (solid line) and their absence (dashed line) between arithmetic means of characters (1 – 9) of L. Dobrogoszcz subpopulation individuals
Subpopulation designations as in Figure 2, designations of characters as in Figure 4

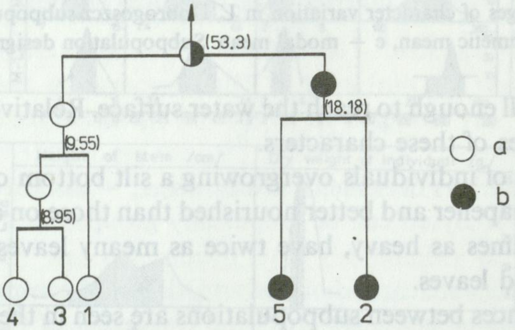

Fig. 6. Dendrogram of similarities between L. Dobrogoszcz subpopulations (1 – 5)
4 – M-L$_{s-c}$, 3 – M-L$_{sa}$, 1 – I-L$_{sa}$, 5 – M-L$_{sl}$, 2 – I-L$_{sl}$; a – sand-sediment subpopulations, b – silt-sediment subpopulations; Arabic numerals in brackets – Euclidean distances; subpopulation designations as in Figure 2

individuals in subpopulations is the substrate type, and to a lesser extent – the kind of the phytocoenose in which they are included.

Lake Wielkie Oczko. Within a constant, and at the same time optimum for it, depth interval the *L. dortmanna* population is fairly strongly diversified in respect of the size of mature individuals (Fig. 7). The significance of differences between the arithmetic means of characters (Fig. 8) and the dendrogram (Fig. 9) indicate that in that lake, too, the main cause of individual morphological variation is the fertility of the sediments.

The diagnostic value of some of the characteristics is good, for they make individual populations distinct. These include: biomass (character 9), mean leaf length in rosettes (1) and the assimilatory area (3). A much worse indicator of habitat and phytocoenotic

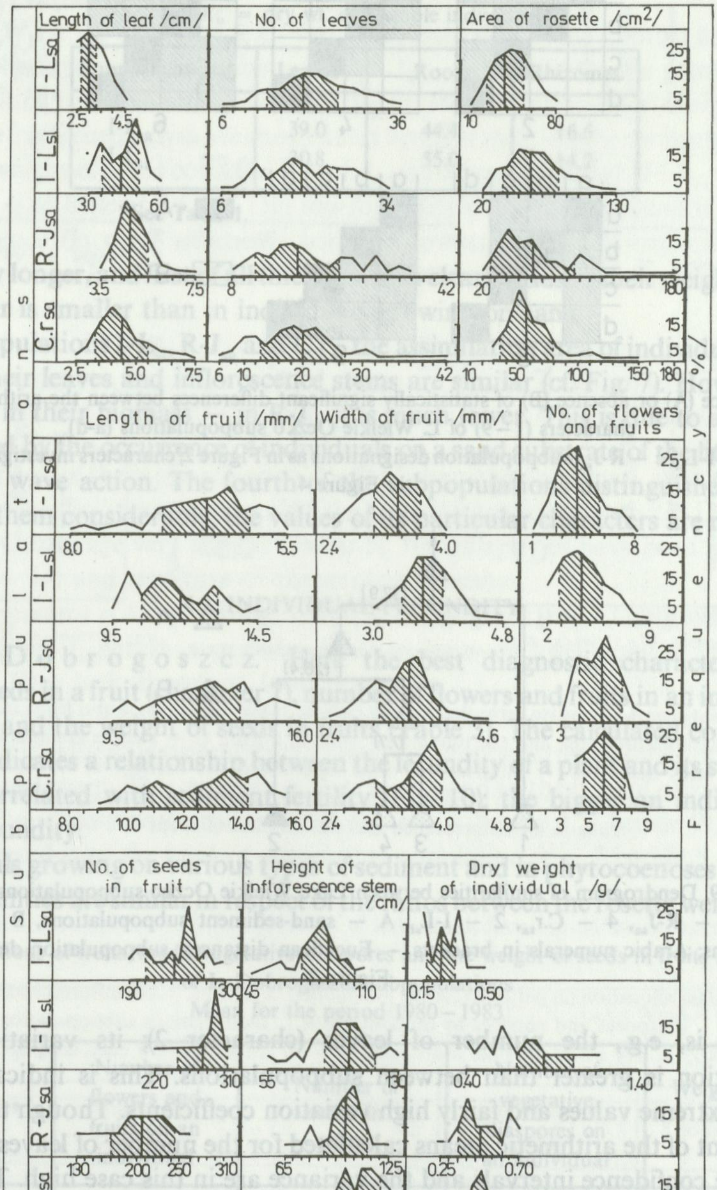

Fig. 7. Diagram character frequencies of L. Wielkie Oczko individuals
Subpopulation designations as in Figure 2

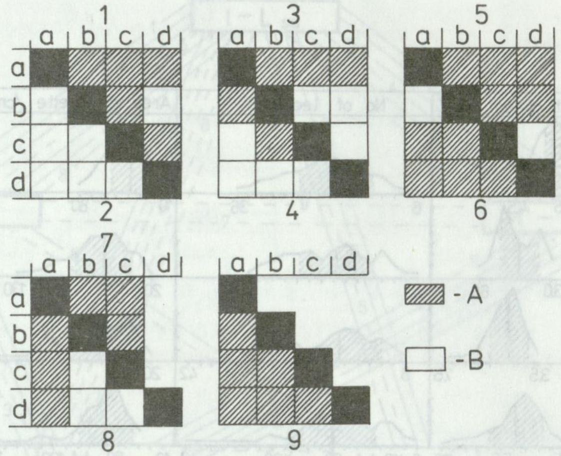

Fig. 8. Presence (A) or absence (B) of statistically significant differences between the arithmetic means of characters (1 – 9) of L. Wielkie Oczko subpopulations (a-d)
a – I-L$_{sa}$, b – I-L$_{sl}$, c – R-J$_{sa}$; subpopulation designations as in Figure 2; characters investigated (1 – 9) – as in Figure 4

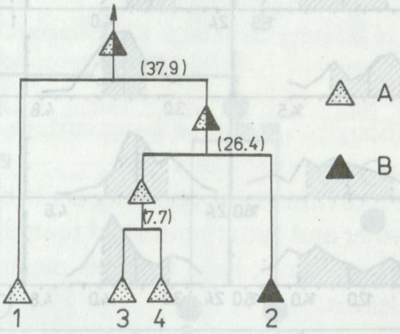

Fig. 9. Dendrogram of similarities between Lake Wielkie Oczko subpopulations (1 – 4)
1 – I-L$_{sa}$, 3 – R-J$_{sa}$, 4 – C.r$_{sa}$, 2 – I-L$_{sl}$; A – sand-sediment subpopulations, B – silt-sediment subpopulations; Arabic numerals in brackets – Euclidean distances; subpopulation designations as in Figure 2

conditions is, e.g., the number of leaves (character 2); its variation within a subpopulation is greater than between subpopulations. This is indicated by wide ranges of extreme values and fairly high variation coefficients. Though the histogram arrangement of the arithmetic means calculated for the number of leaves in rosettes is similar, the confidence intervals and the variance are in this case high. This ruins the diagnostic value of this character.

Individual dry weight is a global quantity, including the weight of leaves, rhizome and roots. The results obtained for I-L$_{sa}$ and I-L$_{sl}$ indicate that individuals growing on a silt bottom are heavier, and the distribution of the weight of particular plant parts differs from that found on sand (Table 2). On a substrate rich in organic matter the weight of leaves and rhizome decreases, whereas that of roots increases; they are

Table 2. Percentages of the dry weight of leaves, roots and rhizomes in mature individuals of I-L_{sa} and I-L_{sl} in L. Wielkie Oczko
100% = dry wt. of a whole individual

Subpopulation *	Leaves	Roots	Rhizomes
I-L_{sa}	39.0	44.4	16.6
I-L_{sl}	30.8	55.0	14.2

* See Table 1.

considerably longer, and first of all thicker, which clearly adds to their weight, although their number is smaller than in individuals growing on sand.

In subpopulations I-L_{sl}, R-J_{sa} and C.r_{sa} the assimilation area of individuals, and the lengths of their leaves and inflorescence stems are similar (cf. Fig. 7). However, these plants differ in their biomass – in R-J_{sa} it is much lower. This is due to a lower root weight caused by the occurrence of individuals on a sand substrate of the littoral that is damaged by wave action. The fourth of the subpopulations distinguished, i.e., I-L_{sa} differs from them considerably, the values of its particular characters are much lower.

4.2. INDIVIDUAL FECUNDITY

Lake Dobrogoszcz. Here the best diagnostic characteristics are: number of seeds in a fruit (character 7), number of flowers and fruits in an inflorescence (6, cf. Fig. 3) and the weight of seeds in fruits (Table 3). The calculated correlation of characters indicates a relationship between the fecundity of a plant and its size which is positively correlated with sediment fertility (Fig. 10); the bigger an individual, the higher its fecundity.

Individuals growing on various types of sediment and in phytocoenoses of different plant communities are similar in respect of the ratios between the rosette weight and the

Table 3. Proportions of fruits, seeds, vegetative diaspores and the weight of seeds in fruits in individuals of L. Dobrogoszcz subpopulations
Mean for the period 1980 – 1983

Subpopulation *	Number of flowers and fruits on an individual	Number of seeds in a fruit	Number of vegetative diaspores on an individual	Weight of seeds in a fruit (mg)
I-L_{sa}	3.9 ± 0.004	207.8 ± 1.2	1.7 ± 0.009	8.8 ± 0.07
I-L_{sl}	6.0 ± 0.005	287.8 ± 4.0	1.6 ± 0.012	13.2 ± 0.02
M-L_{sa}	3.1 ± 0.004	217.2 ± 1.3	1.5 ± 0.006	5.9 ± 0.04
M-L_{s-c}	3.5 ± 0.003	242.1 ± 0.6	1.9 ± 0.004	8.7 ± 0.02
M-L_{sl}	5.8 ± 0.010	287.0 ± 4.1	1.7 ± 0.010	9.3 ± 0.11

* See Table 1.

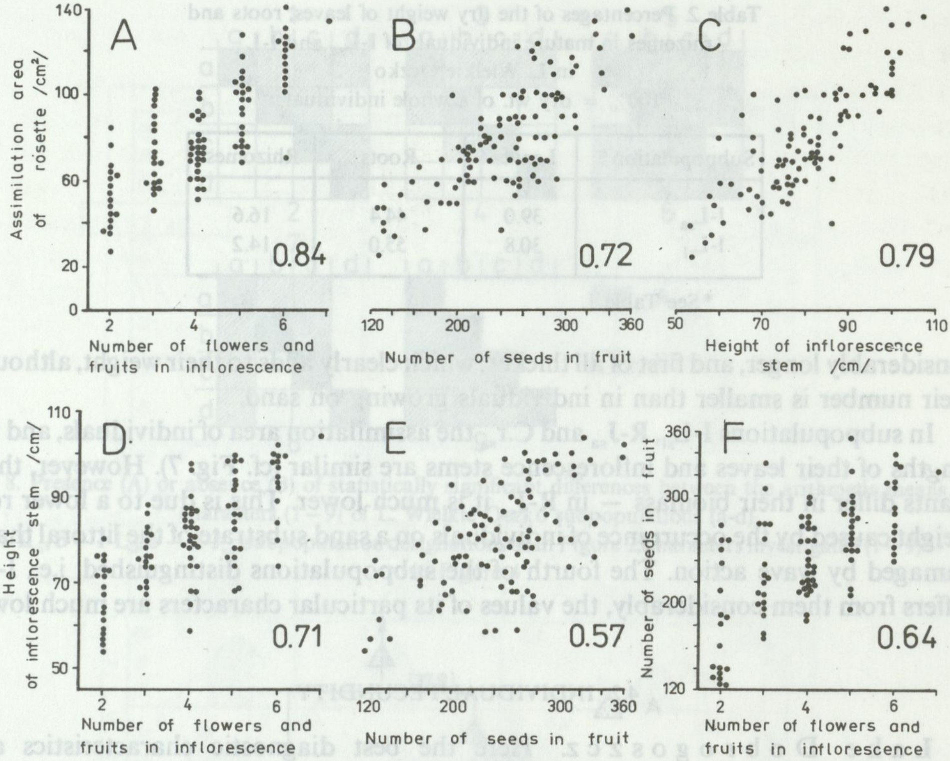

Fig. 10. Correlations: A – rosette assimilatory area and the number of flowers and fruits in an inflorescence; B – rosette assimilatory area and the number of seeds in a fruit; C – rosette assimilatory area and the inflorescence stem height; D – inflorescence stem height and the number of flowers and fruits in an inflorescence; E – inflorescence stem height and the number of seeds in a fruit; F – number of flowers and fruits in an inflorescence and the number of seeds in a fruit

Table 4. Biomass allocation (in per cent) for the production of flowers, fruits, inflorescence stems, vegetative diaspores and rosettes by individuals of L. Dobrogoszcz subpopulations
100% = dry wt. of a whole individual, $N = 50$ individuals for each subpopulation

Subpopulation *	Flowers and fruits	Inflorescence stem	Vegetative diaspores	Rosette of parent individual
I-L_{sa}	3.8	26.6	4.2	65.4
I-L_{sl}	4.2	34.5	3.1	58.2
M-L_{sa}	4.5	29.6	3.5	62.4
M-L_{s-c}	4.3	25.6	4.9	65.2
M-L_{sl}	3.3	32.7	3.5	60.5

* See Table 1.

weight of vegetative diaspores, inflorescence stem, flowers and fruits. These ratios are slightly affected by phytocoenotic and biotope conditions, and are most likely a feature of the taxon (Table 4).

Lake Wielkie Oczko. As can be judged from the number and quality of the potential offspring (seed), subpopulation I-L_{sl} grows under the most favourable conditions. Ripe fruits of its individuals contain the largest number of sizeable seeds, although the fruits themselves are shorter and broader than in other subpopulations (cf. Fig. 7). The weight of seeds collected from I-L_{sl} is 10.5 mg, and that of I-L_{sa} only 9.6 mg, and of R-J_{sa} – as little as 6.4 mg. This low fecundity of R-J_{sa} individuals is the result of their occurrence on sand sediments with the lowest content of organic matter (cf. Table 1). Important in this case is also the competitive action of other plants, especially *Juncus bulbosus*.

4.3. A COMPARISON OF THE MORPHOLOGICAL CHARACTERISTICS AND FECUNDITY OF INDIVIDUALS OF TWO ISOLATED POPULATIONS

A comparison of the range of variation of the characters analysed, arithmetic means and variation coefficients indicates that the populations found in lakes Dobrogoszcz and Wielkie Oczko are very similar (Table 5). No differences have been found in the number ($2n = 14$) and structure of chromosomes, either.

The arrangement of subpopulations in the dendrogram (Fig. 11) suggests that there is greater variation within a population than between two isolated geographical populations. They lack, therefore, local specificity.

The first (lowest) level of the above-mentioned dendrogram represents subpopulations; their arrangement is primarily the result of their occurrence on a specific (silt or sand) kind of sediment. This order does not correspond to the type of phytocoenose to which the subpopulations considered belong (e.g., 1 beside 3, 8 beside 9), and is not always connected with the kind of geographic population (e.g., 7 beside 5, 6 beside 4).

Table 5. Comparison of the characters of individuals found in the study lakes
$\bar{x}$ – arithmetic mean, V – variation coefficient

Character	Lake Dobrogoszcz			Lake Wielkie Oczko		
	min.-max.	$\bar{x}$	V	min.-max.	$\bar{x}$	V
Leaf length (cm)	1.3 – 7.7	4.2	0.28	2.1 – 7.8	4.0	0.28
Number of leaves	5.0 – 53.0	16.4	0.40	5.0 – 42.0	19.6	0.34
Rosette area (cm^2)	3.8 – 221.4	46.3	0.66	8.2 – 191.7	52.0	0.52
Fruit length (mm)	6.4 – 15.0	10.5	0.15	7.8 – 15.8	12.2	0.13
Fruit breadth (mm)	2.0 – 5.1	3.4	0.13	3.1 – 4.7	3.6	0.11
Number of flowers and fruits	1 – 11	4.1	0.38	1 – 9	4.9	0.34
Number of seeds in a fruit	107 – 337	236.3	0.22	119 – 320	229.2	0.22
Dry weight of an individual (g)	0.1 – 1.3	0.4	0.70	0.1 – 1.4	0.5	0.54
Inflorescence stem height (cm)	46.0 – 122.5	88.5	0.17	44.5 – 128.5	97.0	0.17

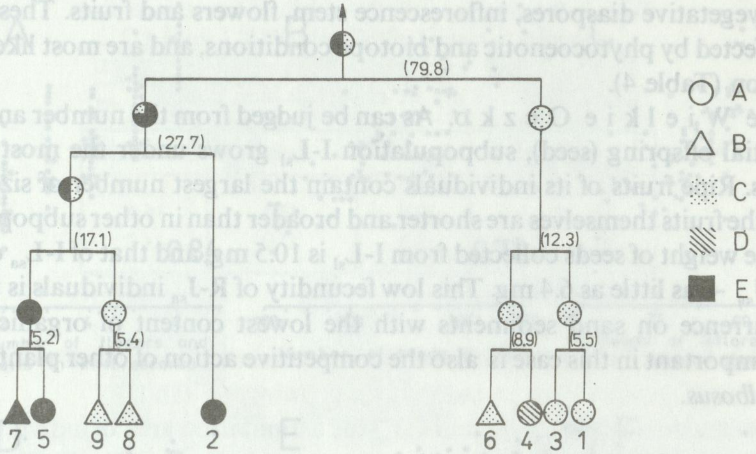

Fig. 11. Dendrogram of similarities between L. Dobrogoszcz (A) and L. Wielkie Oczko (B) subpopulations (1–9)

7 – I-L_{sl}, 5 – M-L_{sl}, 9 – C.r_{sa}, 8 – R-J_{sa}, 2 – I-L_{sa}, 6 – I-L_{sa}, 4 – M-L_{s-c}, 3 – M-L_{sa}, 1 – I-L_{sa}; C – sand sediments, D – sand-clay sediments, E – silt sediments; Arabic numerals in brackets – Euclidean distances; subpopulation designations as in Figure 2

The greatest similarity, expressed by the smallest Euclidean distance was found between subpopulations I-L_{sl} from L. Wielkie Oczko (7) and M-L_{sl} from L. Dobrogoszcz (5), derived from different lakes and plant communities, and connected only by the same type of lake floor. A similar situation is seen between I-L_{sa} (6) and M-L_{s-c} (4). Each of the two remaining pairs (9 and 8, 3 and 1) consists of subpopulations from the same lake, but from different phytocoenoses. It was expected that at least four subpopulations from Isoëto-Lobelietum phytocoenoses would be similar.

At the second level of the dendrogram (Fig. 11), the subpopulations under study are grouped into sets of two elements, which represent the role of similar ecological conditions. This level takes into account the whole physical space, over the depth range 0.8 – 1.0 m, of the populations studied. Thereby the cause of their inner diversity is here most fully manifested and at the same time provides an a posteriori criterion for the division of a population into real subpopulations. They comprise individuals living under the same biotope and social conditions. Such conditions arise not necessarily in phytocoenoses of the same plant community.

4.4. THE EFFECT OF POPULATION DENSITY ON INDIVIDUAL SIZE, HABIT AND FECUNDITY

The most suitable object for studies of this type is the I-L_{sa} subpopulation, in which *L. dortmanna* is not in essence accompanied by other species. In aggregations arranged in ascending order of density a systematic decrease is seen of the arithmetic means of all the characters analysed, and the distribution of size classes changes from a normal to a negatively skew one (Fig. 12). Individuals living under high-density conditions are on

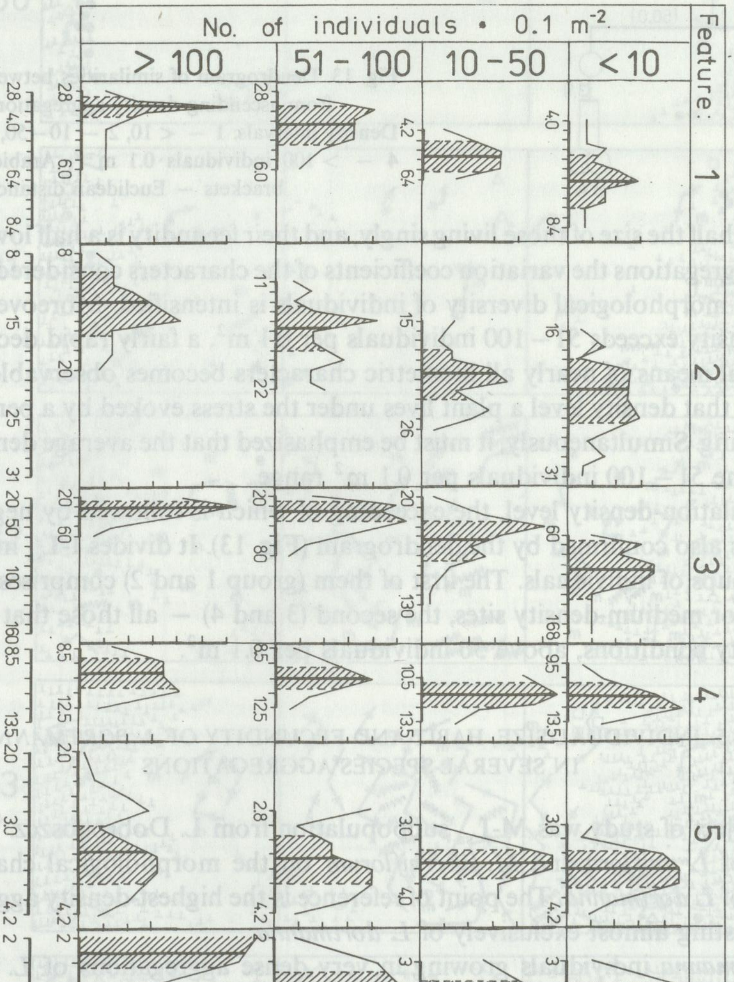

Fig. 12. Diagram of character (1 – 7) frequencies of *L. dortmanna* individuals in uneven-density aggregations
Designations as in Figure 4

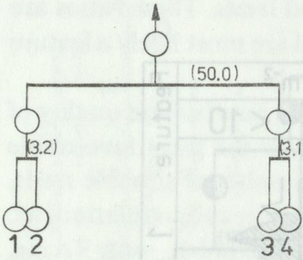

Fig. 13. Dendrogram of similarities between individuals from ascending-density aggregations (1, 4)
Density intervals: 1 – < 10, 2 – 10–50, 3 – 51–100, 4 – > 100 individuals·0.1 m^{-2}; Arabic numerals in brackets – Euclidean distances

an average half the size of those living singly, and their fecundity is a half lower. In high-density aggregations the variation coefficients of the characters considered are higher, that is, the morphological diversity of individuals is intensified. Moreover, when the level of density exceeds 51 – 100 individuals per 0.1 m^2, a fairly rapid decrease of the arithmetical means of nearly all biometric characters becomes observable. It follows that above that density level a plant lives under the stress evoked by a persisting high overcrowding. Simultaneously, it must be emphasized that the average density of I-L_{sa} is within the 51 – 100 individuals per 0.1 m^2 range.

A population-density level, the exceeding of which is followed by negative stress reactions is also confirmed by the dendrogram (Fig. 13). It divides I-L_{sa} into two very distant groups of individuals. The first of them (group 1 and 2) comprises individuals from low- or medium-density sites, the second (3 and 4) – all those that grew under high-density conditions, above 50 individuals per 0.1 m^2.

4.5. INDIVIDUAL SIZE, HABIT AND FECUNDITY OF *L. DORTMANNA* IN SEVERAL-SPECIES AGGREGATIONS

The object of study was M-L_{sa} subpopulation from L. Dobrogoszcz. The effect is analysed of *L. uniflora* and *M. alterniflorum* on the morphological characters and fecundity of *L. dortmanna*. The point of reference is the highest-density aggregations in I-L_{sa} consisting almost exclusively of *L. dortmanna*.

L. dortmanna individuals growing in very dense aggregations of *L. uniflora* are weaker, this condition being manifested by the reduction of the number of leaves by 25% and of seeds in fruits by about 10% in comparison with the highest-density aggregations of *L. dortmanna* alone (Table 6).

L. uniflora is an evergreen plant; it multiplies intensively by means of runners, and thereby colonizes an area at a faster rate and more efficiently, and increases the density of its own population (Fig. 14). Its food requirements are similar to those of *L. dortmanna*, and so is its individual size; its distribution range in the phytolittoral is almost the same as that of the latter species, but its mode of propagation is more efficient. This competition very strongly limits the numbers, density and "growing comfort" of *L. dortmanna*.

M. alterniflorum is a much taller plant than *L. dortmanna*, so it shades the latter successfully. This causes the leaves of *L. dortmanna* to increase their length by 31%, and a growth in the number of seeds per fruit by 4.5%. Though the number of leaves per
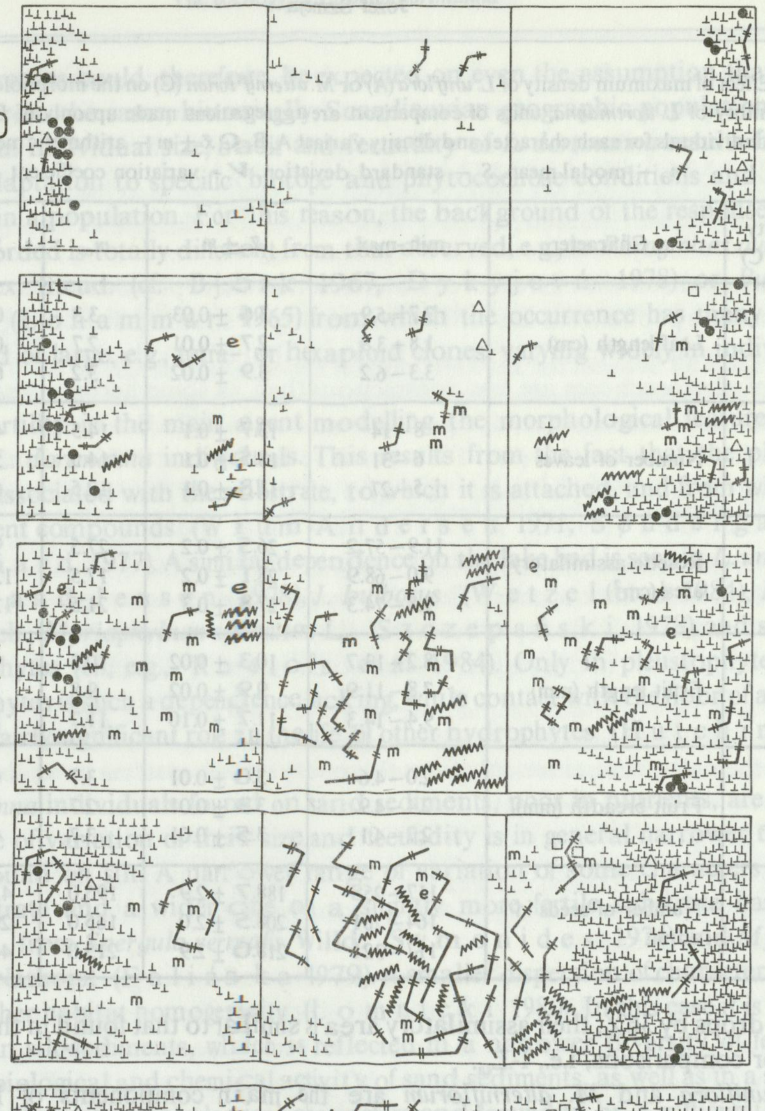
Fig. 14. Rate of plant encroachment upon sites where Myriophyllo-Littorelletum phytocoenoses were previously destroyed

1 — *L. uniflora*, 2 — *L. dortmanna*, 3 — *I. lacustris*, 4 — *M. alterniflorum*, 5 — *Drepanocladus vernicosus* (Lindb.) Warnst., 6 — *Luronium natans* (L.) Rafin, 7 — *E. canadensis*, 8 — *J. bulbosus*, 9 — *Polygonum amphibium* L. f. *natans*

Table 6. Effect of maximum density of *L. uniflora* (A) or *M. alterniflorum* (C) on the morphological characters and fecundity of *L. dortmanna*; units of comparison are aggregations made up only of *L. dortmanna* (B) $N = 100$ individuals for each character and density variant A, B, C; $\bar{x} \pm m$ – arithmetic mean and its error, m_o – modal mean, S – standard deviation, V – variation coefficient

Density (A, B, C)	Character	min.-max.	$\bar{x} \pm m$	m_o	S	V
A	Leaf length (cm)	2.7=5.9	3.6 ± 0.03	3.3	0.7	0.19
B		1.8 – 3.8	2.7 ± 0.01	2.7	0.4	0.15
C		3.3 – 6.2	3.9 ± 0.02	3.2	0.5	0.13
A	Number of leaves	8 – 14	13.7 ± 0.1	14.5	4.1	0.30
B		6 – 31	18.5 ± 0.1	14.5	5.8	0.31
C		5 – 27	11.8 ± 0.1	12.5	6.3	0.53
A	Rosette assimilatory area (cm^2)	11.9 – 57.2	26.5 ± 0.2	27.5	9.2	0.33
B		9.0 – 68.9	28.1 ± 0.2	17.5	13.6	0.48
C		9.8 – 74.3	27.8 ± 0.3	21.5	12.8	0.46
A	Fruit length (mm)	8.2 – 13.7	10.3 ± 0.02	10.3	1.1	0.11
B		7.8 – 11.9	9.9 ± 0.02	9.8	1.0	0.10
C		9.4 – 14.3	11.7 ± 0.10	11.7	1.4	0.12
A	Fruit breadth (mm)	2.0 – 4.6	3.0 ± 0.01	3.7	0.5	0.17
B		2.4 – 4.9	3.3 ± 0.01	2.7	0.4	0.12
C		2.7 – 4.1	3.5 ± 0.01	3.7	0.4	1.11
A	Number of seeds in a fruit	117 – 258	188.7 ± 2.9	195.0	43.7	0.23
B		164 – 261	208.5 ± 2.0	165.0	29.8	0.14
C		117 – 321	218.0 ± 2.9	215.0	44.4	0.20

rosette drops by 36%, their assimilatory area is similar to that found in the individuals used for comparisons, i.e., I-L_{sa}.

L. uniflora and *M. alterniflorum* are the main components of Myriophyllo-Littorelletum, for this reason the resultant of their action can to a large extent be identified with the effect of the whole phytocoenose.

5. DISCUSSION

The distance between the populations compared is 13 km. With the lack in *L. dortmanna* diaspores of clear predispositions to active (autogenic) or passive (e.g., zoogenic) migrations, this distance can be a sufficient cause of their complete isolation. Because of this, and of the fact that *L. dortmanna* is at present a self-pollinating plant (Szmeja 1987b and literature quot.), the probability of gene-pool mixing is extremely small. These populations have probably persisted in both lakes for several thousand years without any contact between them. Certain morphological and genetical differences could, therefore, be expected on even the assumption that they have derived from the same, historically, Scandinavian geographic population.

Variation in individual size, habit and fecundity of *L. dortmanna* results from a phenotypic adaptation to specific biotope and phytocoenose conditions and social relations within a population. For this reason, the background of the responses that have been recorded is totally different from that observed, e.g., in *Phragmites australis* (Cav.) Trin. ex. Steud. (cf. Björk 1967, Dykyjová 1978) or *Butomus umbellatus* L. (Lohammar 1965) from which the occurrence has many times been described of large, e.g., tetra- or hexaploid clones, varying widely in individual size and habit.

Habitat fertility is the main agent modelling the morphological features and fecundity of *L. dortmanna* individuals. This results from the fact that the plant is permanently associated with the substrate, to which it is attached, and from which it absorbs nutrient compounds (Wium-Andersen 1971, Søndergaard and Laegaard 1977). A similar dependence on the lake bed is seen in *L. uniflora, I. lacustris* (Sand-Jensen 1978), *J. bulbosus* (Wetzel et al. 1984), *Elodea canadensis* Rich., *Myriophyllum spicatum* L. (Szczepański 1978) and several other hydrophytes (cf., e.g., Roelofs et al. 1984). Only in pleustophytes and semipleustophytes is such a dependence lacking, while contact with the floor of a water body plays a fairly significant role in the life of other hydrophytes (Hutchinson 1975).

L. dortmanna individuals found on sand sediments, poor in nutrients, are small, and the range of variation of their size and fecundity is in general narrower than in individuals found on silt. A narrower range of variation of some characters on an infertile substrate and a wider one on a slightly more fertile substrate has been described, e.g., from *Spergula vernalis* Willd. (Symonides 1974) and *Myosotis palustris* (L.) Nathorst (Falińska 1979). A smaller dispersion of characters is the result of a higher habitat homogeneity (Łomnicki 1980). In this case it is higher for sand- than silt-sediments, which is reflected in a narrower diversity of fertility, granulation, biological and chemical activity of sand sediments, as well as in a similar range of modelling of morphological characters and fecundity by a sufficiently high (here usually high!) population density.

The most plastic characters are: individual biomass, individual assimilatory area and number of seeds in a fruit. They are parameters defining the size and fecundity. As the size of *L. dortmanna,* as well as of some other plants with narrow biotope and phytocoenose requirements, varies considerably (cf., e.g., Wilkoń-Michalska 1976), there is little justification in ascribing this character particularly to species with a wide ecological scale. A high plasticity of size and habit is probably peculiar to many plants, even those which, like *L. dortmanna* or *Salicornia patula* Duval-Jouve (Wilkoń-Michalska 1976), belong to species with a narrow ecological scale.

Fecundity of generative individuals is positively correlated with their size. This relationship has many times been described from other plants (Harper and

Ogden 1970, Falińska 1979). In *L. dortmanna* a directly proportional relationship is found, e.g., between: (1) assimilatory area and the number of flowers and fruits in an inflorescence, as well as of seeds in a fruit; (2) inflorescence stem length and the number of flowers, fruits and seeds. This most likely is a genetically established mode of response of this plant to its own condition. Close correlation of characters may have a hereditary background.

In comparison with the effect of sediments, the role of phytocoenose as an agent is in *L. dortmanna* populations less reflected, seen only in stratified-structure patches, e.g., in a coenopopulation from Caricetum rostratae. Here individual reactions to different types of phytocoenoses are less conspicuous than in some herbaceous-layer components of forest communities (cf., e.g., Sulma et al. 1967, Falińska 1978, 1979), halophilous communities (Wilkoń-Michalska 1976), and of comparatively loose psammophyte sods (Symonides 1979a, 1979b). According to Symonides (1979a), Andrzejewska and Falińska (1983), such a situation arises when populations develop in very simple ecological systems of a weak social link with other species. The following phytocoenoses represent such systems: Isoëto-Lobelietum, Myriophyllo-Littorelletum and Ranunculo-Juncetum bulbosi; moreover, they are in this respect similar to the majority of aquatic plant communities (cf., e.g., Tomaszewicz 1979, Rejewski 1981). Since there are too few species that could compete in aquatic phytocoenoses, and thereby complicate and enrich their structure, there only form there very simple systems incapable of revealing their own ecological specificity. Such a situation may also result from the characteristics of an aquatic environment. Water is the carrier of almost all nutrients, at the same time manifesting a higher thermal capacity and thermal inertia than those of the air or soil, and can thus provide more stable living conditions for hydrophytes than can a terrestrial environment.

The low fecundity of *L. dortmanna* is the result of a strong pressure of other species and of its own individuals. Intra-population interactions are, however, less intensive than those exerted by species that compete with it for space and food (e.g., *L. uniflora*) or additionally for light (e.g., *C. rostrata, M. alterniflorum* and *J. bulbosus*). This inter-species competition leads on to, apart from, e.g., changes in the physical living conditions of one of them (Symonides 1979b), disturbances in ist structure proportions between its above- and underground parts. The results of such an impact are seen in *L. dortmanna* individuals shaded by *C. rostrata, M. alterniflorum* and *J. bulbosus*, e.g., in R-J$_{sa}$. In such a situation the growth of the assimilatory area is faster than the growth of the roots, which probably entails a reduction in the energetic capacity of the plant in the process of reproduction.

6. SUMMARY

The paper is the first part of a series of studies dealing with the ecology of *L. dortmanna*. The material of study included morphologically mature individuals from two isolated populations (Fig. 2) a priori subdivided into 9 smaller comparative units, i.e., subpopulations (cf. Table 1). Each of them consisted of

individuals growing under equal phytocoenose and biotope conditions, i.e., on sediments of similar degree of granulation and with a similar content of organic matter, and over the same depth range (0.8 – 1.0 m) and in the phytocoenose of an identical plant community.

Earlier studies (Wium-Andersen 1971, Søndergaard and Laegaard 1977) revealed that *L. dortmanna* takes up inorganic compounds of carbon and phosphorus and many other nutrients directly from the sediments, not from the water. It seemed, therefore, interesting to determine whether variation in, e.g., the content of organic matter in the sediments, and thereby their biological and chemical activity, affects the size, form and fecundity of this plant. Owing to the selection of suitable localities for study, it was possible to follow changes also in individuals of the phytocoenoses of different plant communities (Table 1).

Individuals found on sand sediments, poor in nutrients, are small, and their size, habit and fecundity usually demonstrate a narrower range of variation than that found for individuals collected from silt (Figs. 3, 4, 7). A narrower range of variation of some characters on an infertile sand substrate is the result, among other things, of its higher homogeneity in respect of the degree of fertility and granulation.

Individual fecundity is positively correlated with individual size, and the latter with sediment fertility (Fig. 10). Individual condition and fecundity are inversely proportional to population density (Fig. 12) and pressure from competing species (Table 6).

Populations found in two lakes, located 13 km apart, do not manifest any local specificity in individual size, habit or fecundity (Table 5). Differences between the populations, and between coenopopulations distinguished within them, that is, sets of individuals from phytocoenoses of different plant communities, irrespective of the type of their biochores, are statistically insignificant at the level of the adopted error risk (5%).

Statistically significant differences were only found between subpopulations (Figs. 3 – 5, 7, 8). The highest similarity was found among individuals living under similar biotope-social conditions which arise primarily on substrates of similar fertility and degree of granulation, but not necessarily in phytocoenoses of the same plant community (Fig. 11).

Fairly high individual variation has been found under even identical phytocoenose and biotope conditions. A situation of this kind was observed despite the predominance of vegetative reproduction in *L. dortmanna*. The role of the phytocoenose as a factor, compared with the influence of biotope conditions, was less markedly reflected in the populations, being seen only in aggregations of a stratified structure.

7. POLISH SUMMARY

Praca jest pierwszą częścią studiów poświęconych ekologii *L. dortmanna*. Obiektem badań były morfologicznie dojrzałe osobniki dwóch izolowanych populacji (rys. 2), w których a priori wyróżniono 9 mniejszych jednostek porównawczych (subpopulacji, por. tab. 1). Każdą z nich tworzyły osobniki występujące w wyrównanych warunkach fitocenotyczno-biotopowych, tzn. rosnące na osadzie o zbliżonej zawartości materii organicznej i o podobnym stopniu jego uziarnienia, a także w tym samym przedziale głębokości (0.8 – 1.0 m) i w fitocenozie identycznego zbiorowiska roślinnego.

Wcześniej stwierdzono (Wium-Andersen 1971, Søndergaard i Laegaard 1977), że nieorganiczne związki węgla, fosforu i wiele innych substancji pokarmowych *L. dortmanna* pobiera nie z wody, lecz wprost z osadu. Należało więc sprawdzić, czy zróżnicowanie osadu np. pod względem zawartości materii organicznej, a tym samym jego biologicznej i chemicznej aktywności, wpływa na wielkość, pokrój i płodność tej rośliny. Odpowiedni dobór miejsc do badań pozwolił na prześledzenie tych zmian również u osobników z fitocenoz różnych zbiorowisk roślinnych (tab. 1).

Okazy z osadu piaszczystego, ubogiego w składniki pokarmowe, są małe a ich dorodność i płodność waha się na ogół w mniejszym przedziale niż u pobieranych z mułu (rys. 3, 4, 7). Węższy zakres zmienności niektórych cech na jałowym podłożu piaszczystym jest rezultatem m. in. jego większej jednorodności pod względem stopnia żyzności i uziarnienia.

Płodność osobników jest dodatnio skorelowana z ich dorodnością, ta zaś – z żyznością osadu (rys. 10). Kondycja i płodność są odwrotnie proporcjonalne do zagęszczenia populacji (rys. 12) i presji gatunków konkurencyjnych (tab. 6).

Populacje z dwóch jezior, oddalonych od siebie o 13 km, nie wykazują własnej (lokalnej) specyficzności w zakresie wielkości, pokroju i płodności osobników (tab. 5). Różnice między populacjami, a także między wyróżnionymi w nich cenopopulacjami, czyli zbiorami osobników z fitocenoz odrębnych zbiorowisk roślinnych niezależnie od rodzaju ich biochor, są statystycznie nieistotne na poziomie przyjętego ryzyka błędu (5%).

Statystycznie istotne różnice zanotowano dopiero między subpopulacjami (rys. 3 – 5, 7, 8). Największe podobieństwo wykazują osobniki żyjące w zbliżonych warunkach biotopowo-socjalnych, które tworzą się przede wszystkim na podłożach o zbliżonym stopniu żyzności i uziarnienia, lecz niekoniecznie w fitocenozach tego samego zbiorowiska roślinnego (rys. 11).

Stwierdzono dość dużą zmienność osobników nawet w identycznych warunkach fitocenotyczno-biotopowych. Sytuację taką obserwowano pomimo przewagi pomnażania wegetatywnego u *L. dortmanna*. Rola czynnika fitocenotycznego, w porównaniu z wpływem warunków biotopowych, jest w populacji słabiej zarysowana, widoczna tylko w skupiskach o warstwowej strukturze.

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