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THE ECOLOGY OF *LOBELIA DORTMANNA* L.
III. THE PLASTICITY OF INDIVIDUALS ALONG A GRADIENT OF INCREASING DEPTH IN OLIGOTROPHIC LAKES

ABSTRACT: *Lobelia dortmanna* size, habit and fecundity were assessed in phytolittoral fragments at gradually increasing depths in two lakes in northern Poland. The method used was random sampling of individuals from transects laid out between the upper and the lower population area limits on sand biochores of the phytocoenoses of two plant communities. The changes of all biometric characteristics were found to be directional. They depended among other things on the increasing organic matter content in the sediment, but were not related to the kind of lake or plant community.

KEY WORDS: *Lobelia dortmanna*, isoetid, gradient plastic reactions of organisms, biotope conditions, oligotrophic lakes.

1. INTRODUCTION

This paper is the third and at the same time the last part of a series of studies dealing with the ecology of *Lobelia dortmanna*. The first paper of the series (S z m e j a 1987a) contains a description of the modification of morphological features and fecundity of individuals, the second one (S z m e j a 1987b) describes variation in their population structure and dynamics under different phytocoenose and biotope conditions over the same phytolittoral depth range (0.8 – 1.0 m) in two oligotrophic lakes located in the Kashubian Lake District (northern Poland).

In this part of the series the following theses have been assumed: (1) with increasing depth *L. dortmanna* population area, limited by land and by the inaccessible bulk of deep water, becomes increasingly non-homogeneous in respect of biotope and biocoenose conditions; (2) the cause of the lack of homogeneity of this area is among other things directional changes of many physical parameters of the water bulk, e.g., light wave-length and intensity, temperature, sedimentation rate, turbulence rate and other factors (cf. H u t c h i n s o n 1957, G o l t e r m a n 1975); (3) biotope conditions determined by varying parameters of the aquatic environment are the cause of directional changes in individual size, habit and fecundity.

The aim of the study is to establish: (1) whether the size, habit and fecundity of individuals found in phytolittoral fragments vary with increasing depths, and if so, what is the effect of changes in individual size and fecundity; (2) which biotope and biocoenose factors are responsible for the plastic responses, and whether they agree with the direction of changes in some of the physical parameters of the water bulk; (3) what is the role of sediments, competitive actions of other species, and of the population structure which varies along the growing-depth gradient (cf. S z m e j a 1987c).

2. MATERIAL AND METHODS

The investigations were carried out in lakes Dobrogoszcz and Wielkie Oczko; their description, location and selection criteria have been presented in the first paper of the series (S z m e j a 1987a).

In each of the lakes a permanently marked transect was laid out consisting of five rows of plots 1.0 × 1.0 m in size (Fig. 1). They were situated between the upper (near-shore) and the lower (deepest-lying) limits of *L. dortmanna* populations on sand

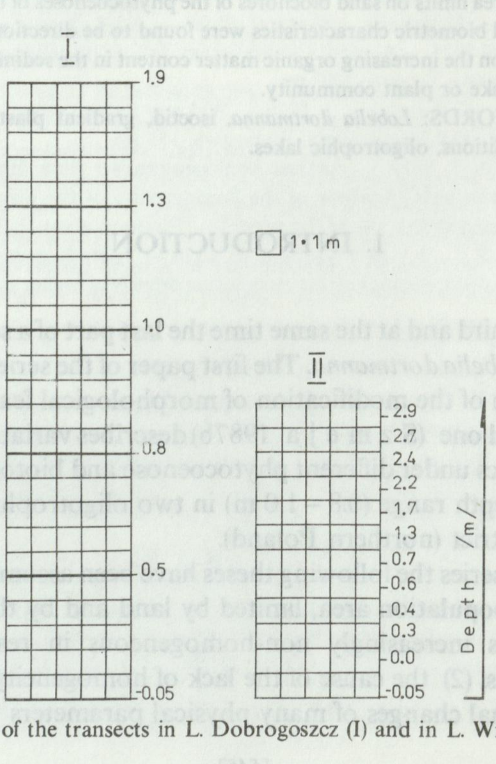

Fig. 1. Diagrams of the transects in L. Dobrogoszcz (I) and in L. Wielkie Oczko (II)

substrates occupied by the phytocoenoses of the following communities: in L. Dobrogoszcz – Myriophyllo-Littorelletum Jeschke 1959, in L. Wielkie Oczko – Isoëto-Lobelietum (W. Koch 1926) R. Tx. 1937. Each plot, 1.0 × 1.0 m, was divided into 100 squares 0.1 × 0.1 m in size. In the first transect (in L. Dobrogoszcz) there were 12500 of them, in the latter (in. L. Wielkie Oczko) – 6000.

A feature common to both of the transects is their location in typologically similar lakes, on sand sediments, where organic matter content gradually increases towards deeper parts of the phytolittoral (Fig. 2). They differ, however, in the kind of plant community.

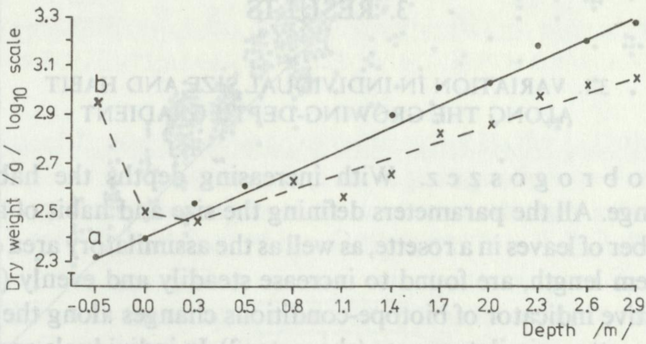

Fig. 2. Organic matter content in phytolittoral parts at increasing depths in L. Dobrogoszcz (a) and in L. Wielkie Oczko (b)

The content of organic matter in the sediment was calculated from 120 weight samples collected for each transect, 10 at each 0.30 m depth interval. The samples were dried at 105°C for 24 hrs., and incinerated in the muffle furnace at 550°C for 24 hrs. Organic matter has been presented as a percentage of sediment dry weight.

Samples to be used for biometric analyses were collected in the period 1980–1983, always at the turn of July during the flowering and fruiting phase of *L. dortmanna*. The sampling site (the number of a 0.1 × 0.1 m square) and plants to be measured in the field were selected at random. Only morphologically mature, i.e., mature and generative, individuals found within particular 0.30 m depth intervals were used; each interval was represented by 50–100 individuals.

In the study of *L. dortmanna* variation the following characters were taken into account: (1) leaf length (cm); (2) number of leaves; (3) assimilatory area of both rosette sides (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) inflorescence stem height (cm). The measurement methods used have been described in the first paper of the series (S z m e j a 1987a).

The fecundity of an individual was determined on the basis of the number of seeds found in its fruits (character 7), number of flowers and fruits in an inflorescence (6), and from the number of vegetative diaspores in the rhizome. Fruit length (character 4) and fruit breadth (5) were used as ancillary parameters. The remainder of characters (1, 2, 3 and 8) describe the habit and size of a plant examined.

The weight of mature individuals was estimated from root, rhizome and leaf dry weight, whereas that of generative individuals additionally from: flower, fruit, seed and vegetative diaspore dry weight.

A description of the statistical analysis methods used can be found in the first paper of the series (S z m e j a 1987a). All the processing has been done on an "Odra 204" computer at the Computing Centre of the Institute of Mathematics, University of Gdańsk.

3. RESULTS

3.1. VARIATION IN INDIVIDUAL SIZE AND HABIT ALONG THE GROWING-DEPTH GRADIENT

L a k e D o b r o g o s z c z. With increasing depths the habit and size of individuals change. All the parameters defining the size and habit of a plant, i.e., leaf length and number of leaves in a rosette, as well as the assimilatory area of a rosette, and inflorescence stem length, are found to increase steadily and evenly (Fig. 3).

A very sensitive indicator of biotope-conditions changes along the growing-depth gradient is the rosette assimilatory area (character 3). In individuals growing at a depth range of 1.41 – 1.70 m it appears to be almost six times as large as in those collected close to the lake edge, whereas the leaves are three times as long, and their number twice as large.

Extremely variable also is the inflorescence (character 8), whose height varies between about a dozen centimetres (on the shore) and almost one and a half metres at

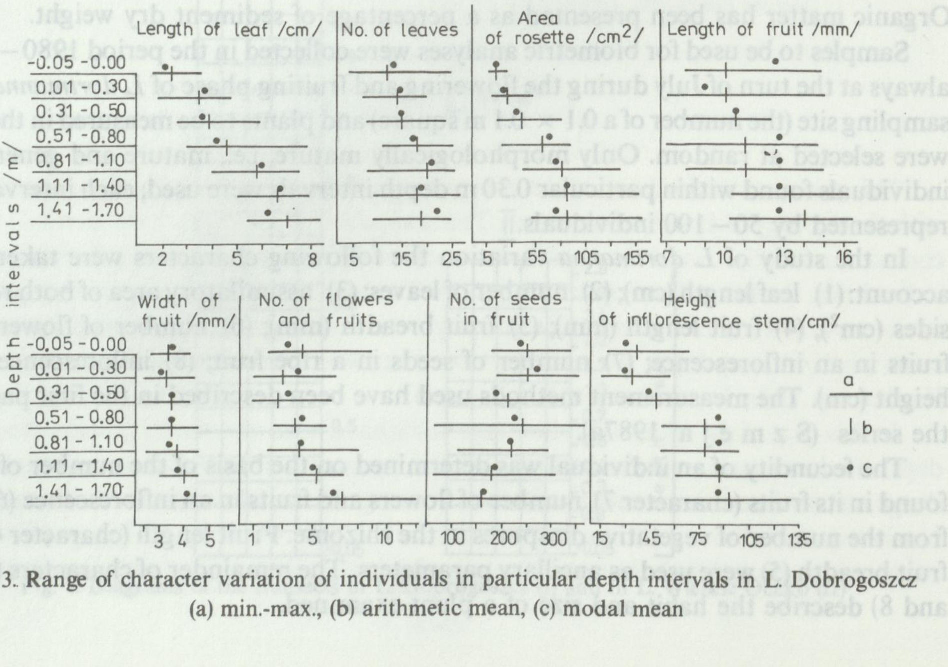

Fig. 3. Range of character variation of individuals in particular depth intervals in L. Dobrogoszcz (a) min.-max., (b) arithmetic mean, (c) modal mean

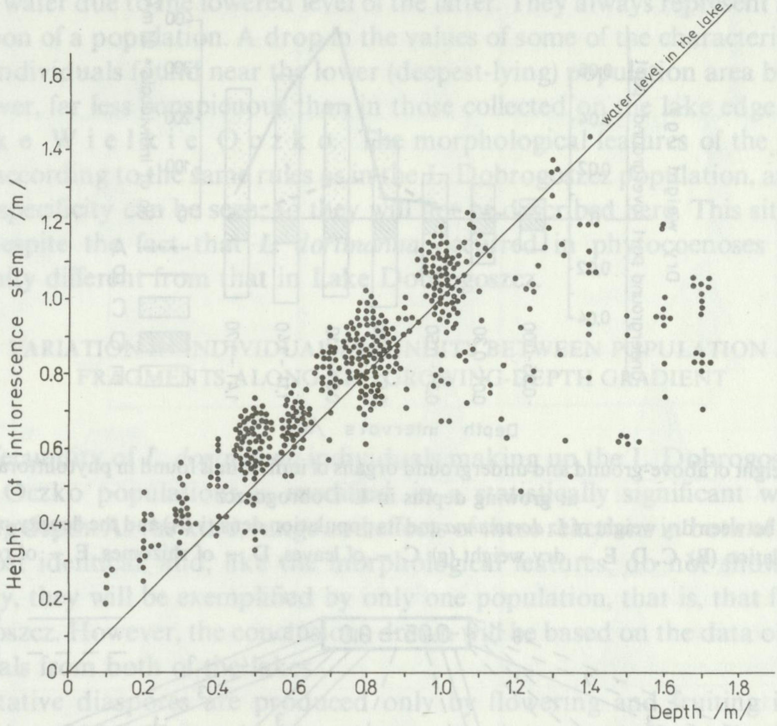

Fig. 4. Relationship between the depth of occurrence of *L. dortmanna* and inflorescence stem height

the depth of 1.40 m (Fig. 4). This is associated with a gradual, among other things, increase in individual size, as indicated by the constant ratio between leaf length and inflorescence stem height. Though there occur slight fluctuations, this proportion is in each depth interval 1 : 14. Apart from this, the gradual increase in depth is followed by a gradual decrease in the number of individuals flowering above the water.

The inflorescence stem height continues to be correlated with the direction of changes in the biotope with increasing depths, in spite of the growing population density of *Littorella uniflora* (L.) Aschers., which, as has been demonstrated (S z m e j a 1987a), is a stronger competitor than *L. dortmanna*.

A steady growth in the dry weight of an individual and its organs can be seen as one moves from the shore towards deeper and deeper fragments of the population area (Fig. 5). Here the weight increases, although the distribution of the density of *L. dortmanna* and *L. uniflora* varies. The most stable is the rhizome weight which depends primarily on the age of an individual.

Differences in the arithmetic means of characters, of the assimilatory area in particular, between successive depth intervals are statistically significant at the adopted 5% error risk level (Fig. 6).

Depth increase is followed by a slight decrease in the coefficients of variation of the characters defining rosette size and form, inflorescence stem height and the number of

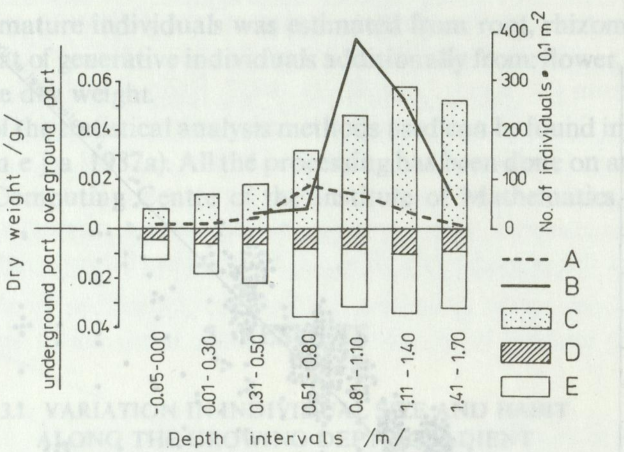

Fig. 5. Dry weight of above-ground and underground organs of individuals found in phytolittoral fragments at growing depths in L. Dobrogoszcz

Relationship between dry weight of *L. dortmanna* and its population density (A) and the density of *L. uniflora* population (B); C, D, E – dry weight (g): C – of leaves, D – of rhizomes, E – of roots

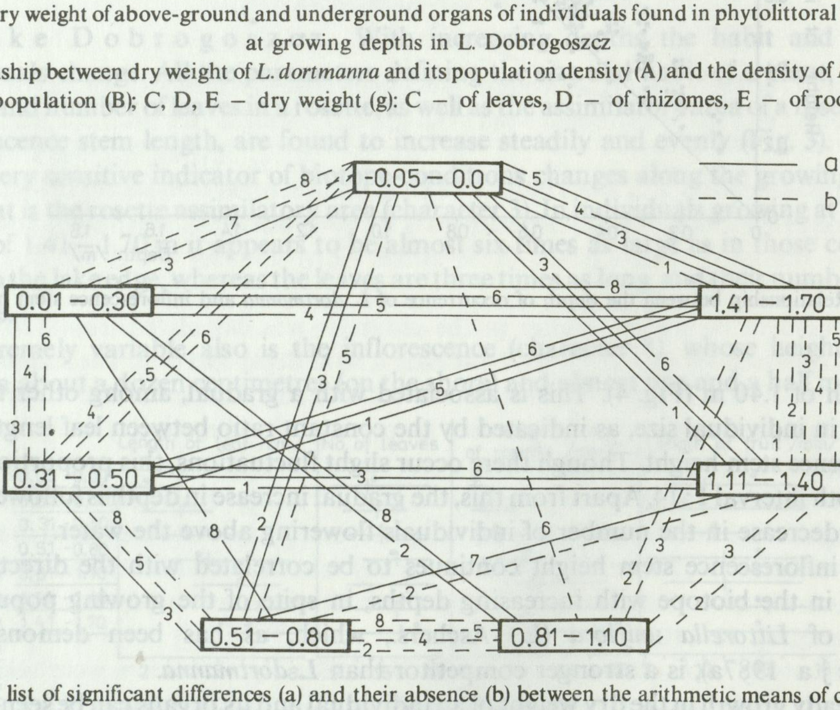

Fig. 6. A list of significant differences (a) and their absence (b) between the arithmetic means of characters (1 – 8) of individuals growing in successive depth intervals from –0.05 to 1.70 m in L. Dobrogoszcz
1 – leaf length, 2 – number of leaves, 3 – assimilatory area of a rosette, 4 – fruit length, 5 – fruit breadth, 6 – number of flowers and fruits in an inflorescence, 7 – number of seeds in a fruit, 8 – inflorescence stem height

flowers and fruits. Under the same conditions the coefficients of variation in the number of seeds and fruits appear to grow.

Plants growing on the lake shore, i.e., in the –0.05 – 0.00 m depth range, differ from other individuals in a population primarily in size and condition – being very small and weak. They are individuals which every spring or summer lose direct contact with the lake water due to the lowered level of the latter. They always represent a negligible proportion of a population. A drop in the values of some of the characteristics is also seen in individuals found near the lower (deepest-lying) population area boundary; it is, however, far less conspicuous than in those collected on the lake edge (cf. Fig. 3).

L a k e W i e l k i e O c z k o. The morphological features of the individuals change according to the same rules as in the L. Dobrogoszcz population, and no signs of local specificity can be seen, so they will not be described here. This situation was found despite the fact that *L. dortmanna* occurred in phytocoenoses of a plant community different from that in Lake Dobrogoszcz.

3.2. VARIATION IN INDIVIDUAL FECUNDITY BETWEEN POPULATION AREA FRAGMENTS ALONG THE GROWING-DEPTH GRADIENT

The fecundity of *L. dortmanna* individuals making up the L. Dobrogoszcz and L. Wielkie Oczko populations is modified, in a statistically significant way, by the increasing depth. As the kind, range and effects of these reactions in both of these lakes are almost identical, and, like the morphological features, do not show any local specificity, they will be exemplified by only one population, that is, that found in L. Dobrogoszcz. However, the conclusions drawn will be based on the data obtained for individuals from both of the lakes.

Vegetative diaspores are produced only by flowering and fruiting individuals (S z m e j a 1987d). Thus, taking part in reproduction are only generative individuals which grow only in a part of the population area, forming a reproduction zone of variable width. In the period 1980–1983, it extended in L. Dobrogoszcz between depths –0.05 and 1.70 m, and in L. Wielkie Oczko, due to considerable water-level oscillations (S z m e j a 1987c), it was much narrower, occupying a depth range of 0.62–1.72 m. Flowering and fruiting individuals are randomly distributed, while their density in particular places of the reproduction zone is similar, on an average 1.35 individuals per 0.1 m^2 (S z m e j a 1987b, 1987c).

An increase in depth is accompanied by a steady increase in fruit length and breadth (cf. Fig. 3), and in the number of fruits in an inflorescence of a generative individual; simultaneously, the number of seeds in a fruit is gradually reduced (Fig. 7). For example, the arithmetic mean number of flowers and fruits calculated for individuals growing over the depth range of 0.01–0.30 m is 3.0, over 0.81–1.11 m – 4.2, and in the deepest part of the population area (1.41–1.70 m) – as high as 6.9. The average number of seeds in fruits here is of the level of: 249.6, 212.9 and 167.1, respectively.

In the phytolittoral of both lakes, from the edge to the deepest parts of the population area, individuals not only steadily increase in size, but also become more and more fecund; the change in the latter character is not as simple as the variation in size and habit. Though the actual number of seeds per fruit is reduced, the size of fruits and their number in an inflorescence grow gradually, and so do the size and weight of seeds in fruits. Thus, fecundity is the function of the size of a plant (Fig. 8) and depends

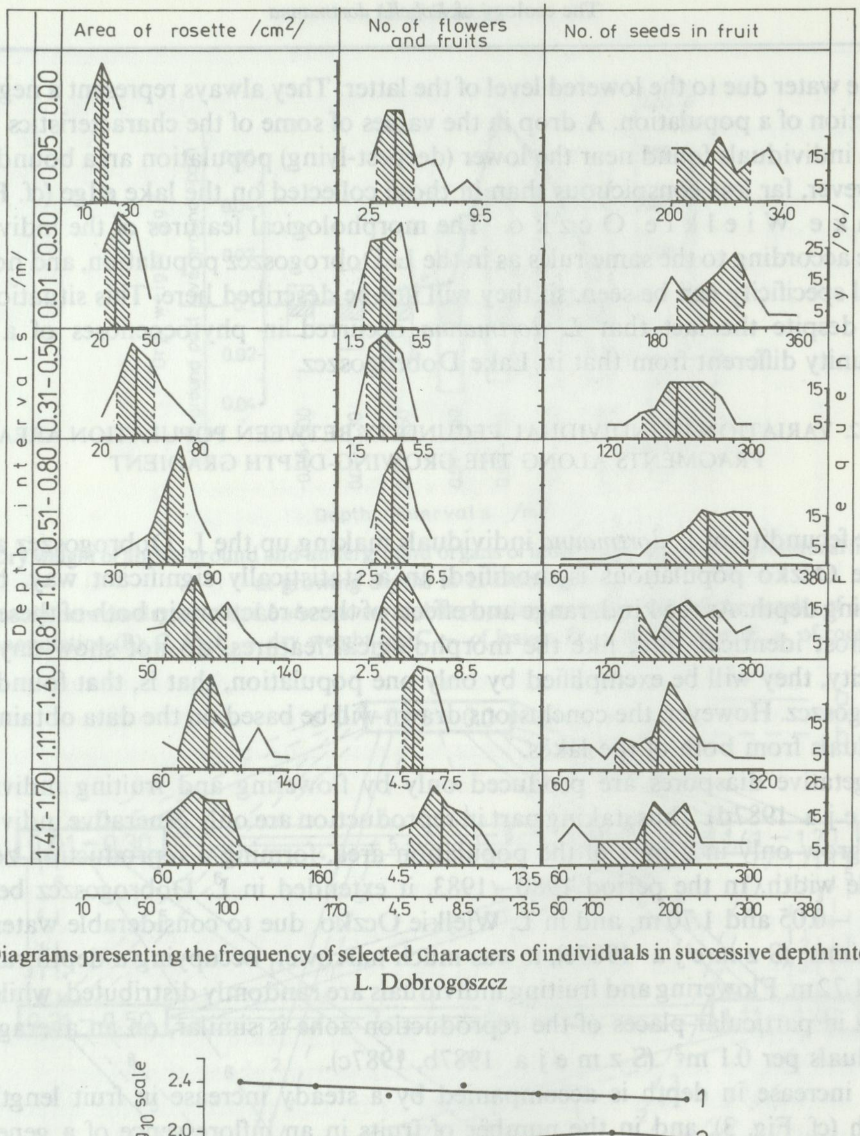

Fig. 7. Diagrams presenting the frequency of selected characters of individuals in successive depth intervals in L. Dobrogoszcz

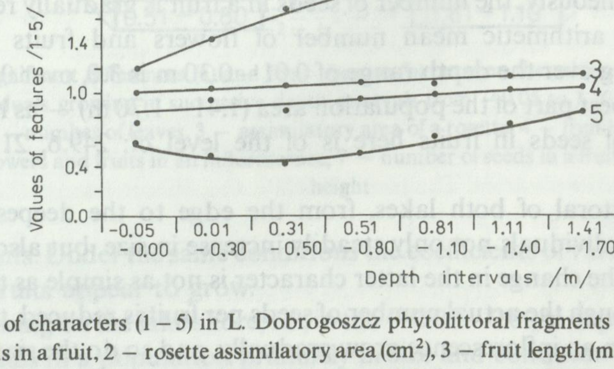

Fig. 8. Variation of characters (1 – 5) in L. Dobrogoszcz phytolittoral fragments at increasing depths
1 – number of seeds in a fruit, 2 – rosette assimilatory area (cm^2), 3 – fruit length (mm), 4 – weight of seeds in a fruit (g), 5 – number of flowers and fruits in an inflorescence

Table 1. Number and weight of seeds in the fruits of individuals found in L. Dobrogoszcz phytolittoral parts located at increasing depths

Depth (m)	Number of seeds	Seed weight (g)
−0.05 − 0.00	1068.5	0.0212
0.01 − 0.30	748.8	0.0286
0.31 − 0.50	601.1	0.0282
0.51 − 0.80	928.0	0.0327
0.81 − 1.10	894.2	0.0327
1.11 − 1.40	975.2	0.0551
1.41 − 1.70	1153.0	0.0704

among other things on the amount of available nutrients. The decrease in the number of seeds per fruit is compensated for, with some excees, by an increase in the number of fruits in an individual.

The total number of seeds produced by an individual is of the range of 750−1000, being more or less the same in every depth-interval of the reproduction zone (Table 1). The plant is able to produce this number of seeds owing to its reproduction strategy. According to its condition, it produces few fruits, each with a large number of small seeds or a larger number of fruits, each of which contains a smaller number of seeds which are, therefore, bigger. Slightly larger numbers of seeds are only found in individuals growing under less favourable habitat-topographic conditions, i.e., close to the upper (near-shore) and the lower (deepest-lying) limits of the reproduction zone. The differences found between individuals growing near the boundaries and other individuals in a population are smaller, but statistically significant.

The weight ratio between the parent individual and its vegetative diaspores and organs of generative reproduction, including seeds, is more or less the same in all the depth-intervals distinguished. Thus, with increasing depths it is only a sufficiently large individual that possesses enough energy to produce an appropriately long inflorescence stem with an increasingly large number of fruits.

Both of these methods of reproduction are subject to modification, the range of variation in the number and size of the vegetative offspring being far narrower. There usually form two, less often one or three, vegetative diaspores, depending on the condition of the parent individual. Furthermore, with increasing depths the onset of phenological growth phases is retarded, but the duration of the phases is prolonged.

3.3. CAUSES OF DIRECTIONAL CHANGES OF INDIVIDUALS ALONG THE DEPTH GRADIENT

Individuals found in population area fragments differing in depth show the same type of response, independent of the kind of lake, plant community and population density or spatial organization. All the biometric characteristics change in a directional way, which may suggest that they are modified by the same factor (or a complex of factors) of the underwater environment.

The kind and range of the observable variations here is the same as in habitats within the same depth interval, but forming a series from infertile to ones of the highest fertility (cf. S z m e j a 1987a). In the phytolittoral of both of the lakes studied, from the lake edge to the deepest-lying population-area parts, the content of organic matter grows steadily (cf. Fig. 2), due to which there arise better nutrient conditions for plants.

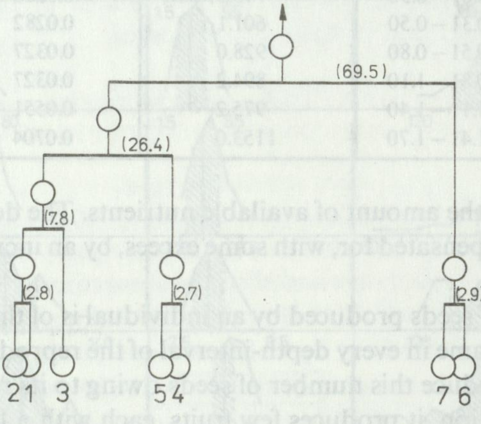

Fig. 9. A dendrogram showing similarity of individuals from different depth intervals (1 – 7) in L. Dobrogoszcz
1 – –0.05 – 0.00 m, 2 – 0.01 – 0.30 m, 3 – 0.31 – 0.50 m, 4 – 0.51 – 0.80 m, 5 – 0.81 – 1.10 m, 6 – 1.11 – 1.40 m, 7 – 1.41 – 1.70 m; Arabic numerals in brackets – Euclidean distances

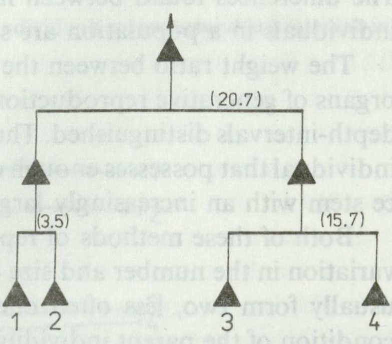

Fig. 10. A dendrogram to show similarity between individuals from different depth intervals (1 – 4) in L. Wielkie Oczko
1 – 0.50 – 0.80 m, 2 – 0.81 – 1.10 m, 3 – 1.11 – 1.40 m, 4 – 1.41 – 1.70 m; Arabic numerals in brackets – Euclidean distances

L. dortmanna is modelled primarily by increasing sediment fertility, as indicated by the grouping of individuals in the dendrograms (Figs. 9, 10). On the left of each of them are grouped individuals growing in shallow phytolittoral parts on infertile and intensively eroded sand. On the right side of each of the graphs are located individuals found in deeper parts, where the sand is more fertile owing to the organic residues accumulated during the sedimentation process.

Though individuals growing in L. Dobrogoszcz phytolittoral parts at increasing depths maintain a tendency towards increasing their biomass (cf. Fig. 5) and other parameters, the fluctuation of changes is clearly disturbed by inter-species competition. In this case it is the action of *L. unif lora* that causes a break-down of the population into two groups of individuals. In the dendrogram (Fig. 9) they are separated by a considerable Euclidean distance (69.5).

In the L. Wielkie Oczko (Fig. 10) population, included in Isoëto-Lobelietum phytocoenoses consisting almost solely of *L. dortmanna*, the regularity of individual variation along the depth gradient is far greater than that seen in the L. Dobrogoszcz population. This is indicated by the Euclidean distance, three times shorter (20.7), separating two most different (distant) groups of individuals in the population. In either of the populations compared the differences are, according to the set clustering rule of Ward's method, statistically significant at the adopted level (5%) of error risk.

4. DISCUSSION

Differentiation of the size, habit and fecundity of *L. dortmanna* individuals growing at increasing depths in the phytolittoral is the result of phenotype reaction to the action of many physical and chemical parameters of the aquatic environment, and of the phytocoenose and social conditions prevailing in a population. Most important are the biotope conditions which are subject to directional changes, primarily the increasing sediment fertility and its chemical and biological activity.

Many of the processes going on in the sediment result first of all from bacterial activity, due to which CO_2 concentrations are one up to several magnitude classes higher than in the water (G o l t e r m a n 1975, W e t z e l et al. 1985). This high CO_2 level is brought about by an aerobic and anaerobic bacterial metabolism in the substratum and immediately above it, where the concentrations of labile substrates and inorganic nutrients are much higher than in the water (W e t z e l and G r a c e 1983). This is important for *L. dortmanna* which is in permanent contact with the sediments from which it takes inorganic carbon and a number of nutrient compounds (W i u m - A n d e r s e n 1971, S ø n d e r g a a r d and L a e g a a r d 1977). A similar dependence on the substratum is found for other vascular underwater plants (S a n d - J e n s e n 1978, W e t z e l et al. 1984, 1985). In accordance with the depth-increase direction, the content of organic matter, and thereby of mineral nutrient substrates in the substratum, grows steadily. As a result, even under the very similar social conditions prevailing in the Isoëto-Lobelietum population of *L. dortmanna* there occur considerable directional changes in individual size and habit. This in turn causes variation in the fecundity of individuals, which is positively correlated with individual size (S z m e j a 1987a), as has many times been reported on also from other plant species (H a r p e r and O g d e n 1970, F a l i ń s k a 1979).

The very steady and even growth, along the growing-depth gradient, of the assimilatory area and height of the inflorescence stem, raising flowers towards the sun, is the result of stimulation not only by the ever-increasing sediment fertility, but by the steadily deteriorating light conditions as well. This interpretation is based on the commonly known physiological regularity that light and available CO_2 sources act as a photosynthesis-controlling agent (W e t z e l et al. 1985). The effect of these factors, mainly light, has been studied most often to explain the way of plant distribution in the littoral (S c u l t h o r p e 1967, S p e n c e and C h r y s t a l 1970a, 1970b, R ø r s l e t t 1984, 1985), as well as to determine the course of photosynthesis, e.g., in *L. dortmanna* (S ø n d e r g a a r d 1979, S a n d - J e n s e n and P r a h l 1982, S a n d - J e n s e n and B o r u m 1984) and in other isoetids (S a n d - J e n s e n and S ø n d e r g a a r d 1979).

Biomass allocation for generative and vegetative reproduction varies with the depth. This results from the fact that the plants destine increasing amounts of biomass, and thereby energy, primarily to produce a sufficiently high inflorescence stem with a larger number of flowers. Growth in depth across the phytolittoral is also followed by an increase in size of the parent individual, due to which the ratio of its biomass to the biomass of vegetative diaspores and organs of generative reproduction, including seeds, is more or less constant. If this ratio in *L. dortmanna* depended on biotope conditions, as it does in, e.g., *L. uniflora* or *Ranunculus reptans* L., then with the high adaptive plasticity of this species there would occur at least one case of elimination of either method of reproduction. Such a situation has not been seen in *L. dortmanna*, but is common in *L. uniflora* and *R. reptans*. In *L. dortmanna* the proportion of biomass allocated for both modes of reproduction is not modified by plant communities; a different type of response is seen in, e.g., *Caltha palustris* L. (F a l i ń s k a 1979).

In *L. dortmanna* phenotype variation is to a larger extent related to the kind of sediment and its fertility than to the physical parameters of the water bulk at a particular depth. A similar suggestion, although referring to other species, has been put forward by P e a r s a l l (1920).

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5. SUMMARY

The present paper is the third and at the same time the last part of a series dealing with the ecology of *Lobelia dortmanna*. The material studied included morphologically mature individuals found at increasing depths in the phytolittoral of two lakes (Fig. 1), on sand substrates of two plant communities.

The size, habit and fecundity of *L. dortmanna* were found to be modified along the growing-depth gradient (Figs. 3 – 5, 7, 8). The assimilatory area appears to be a very sensitive indicator of changes in biotope conditions. In individuals collected at the depth range of 1.41 – 1.70 m it is nearly six times as large as in those found close to the lake edge, whereas the leaves are three times as long, and their number twice as large (Fig. 3). Very plastic, too, is the inflorescence stem (Fig. 4). Its height varies between over a dozen centimetres (on shore) and almost one and a half metres (at the depth of 1.40 m). Individual weight continues to increase in spite of the varying distribution of *L. dortmanna* and *Littorella uniflora* populations (Fig. 5). The most stable is the weight of the rhizome, the mass of which depends mainly on the age of a plant.

Increasing submergence of generative individuals is accompanied by a gradual growth in length and breadth of their fruits (Fig. 3) and an increase in the number of flowers and fruits in an inflorescence, and a reduction in the number of seeds in a fruit (Fig. 7). Fecundity is directly proportional to the size of a plant

(Fig. 8), and depends among other things on the amount of available food. Both ways of reproduction are subject to modification, but variation in number and size of the vegetative offspring is far narrower than that of the generative offspring.

The total number of seeds produced by an individual is more or less the same in every depth interval of the reproduction zone (Table 1). According to its condition, *L. dortmanna* produces few fruits, each with many small seeds, or a larger number of fruits, each with fewer seeds which are then bigger. Slightly more seeds are produced only by individuals growing under the least favourable habitat and topographic conditions, i.e., close to the upper (near shore) and the lower (deepest-lying) limits of the reproduction zone.

Analysed against the growing-depth gradient, *L. dortmanna* shows a directional type of plastic reactions. In both of the populations studied (Figs. 9, 10) it is positively correlated with the growing content of organic matter in the sediment (Fig. 2), that is, with its increasing fertility and biological and chemical activity.

6. POLISH SUMMARY

Praca jest trzecią, a zarazem ostatnią częścią studiów poświęconych ekologii *Lobelia dortmanna*. Obiektem badań były morfologicznie dojrzałe osobniki, które rosły w coraz głębiej położonych fragmentach fitolitoralu dwóch jezior (rys. 1), na piaszczystym podłożu fitocenoz dwóch zbiorowisk roślinnych.

W gradiencie wzrastającej głębokości modyfikowana jest wielkość, pokrój i płodność *L. dortmanna* (rys. 3 – 5, 7, 8). Bardzo czułym wskaźnikiem zmieniających się warunków biotopowych jest powierzchnia asymilacyjna, która u osobników rosnących na głębokości 1.41 – 1.70 m, w porównaniu z osobnikami zebranymi tuż przy brzegu, jest niemal sześciokrotnie większa, liście są trzykrotnie dłuższe, a ich liczba wzrasta dwukrotnie (rys. 3). Bardzo plastyczna jest również łodyga kwiatostanowa (rys. 4). Jej wysokość waha się od kilkunastu centymentów (na brzegu) do niemal półtora metra na głębokości 1.40 m. Przyrost ciężaru osobnika odbywa się pomimo zmieniającego się rozkładu zagęszczenia populacji *L. dortmanna* i *Littorella uniflora* (rys. 5). Najbardziej stabilny jest ciężar kłącza, którego masa zależy przede wszystkim od wieku rośliny.

U coraz bardziej zanurzonych osobników generatywnych systematycznie wzrasta długość i szerokość owoców (rys. 3), a także ich liczba w kwiatostanie, zmniejsza się natomiast produkcja nasion w owocu (rys. 7). Płodność jest wprost proporcjonalna do stanu dorodności rośliny (rys. 8) i zależy m. in. od ilości dostępnego pokarmu. Modyfikowane są obydwa sposoby rozmnażania, lecz liczba i dorodność potomstwa wegetatywnego zmienia się w dużo mniejszym zakresie niż potomstwa generatywnego.

Suma nasion wytwarzanych przez osobnika jest w każdym przedziale głębokości strefy rozrodczej mniej więcej stała (tab. 1). Stosownie do swojej kondycji, *L. dortmanna* tworzy dużo drobnych nasion w niewielu owocach lub zwiększa liczbę owoców, zmniejszając w nich zawartość nasion, które są wówczas dorodniejsze. Nieco więcej nasion mają tylko okazy rosnące w najmniej korzystnych warunkach siedliskowo-topograficznych, tj. blisko górnej (przybrzeżnej) i dolnej (najgłębiej położonej) granicy strefy rozrodczej.

W gradiencie wzrastającej głębokości *L. dortmanna* wykazuje ukierunkowany typ reakcji plastycznych. W obu badanych populacjach (rys. 9, 10), jest on dodatnio skorelowany z coraz większą ilością materii organicznej w osadzie (rys. 2), tj. ze wzrastającym stopniem jego żyzności, a także biologicznej i chemicznej aktywności.

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