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Polskie Archiwum Hydrobiologii existing as such since 1953, is a continuation of *Archiwum Hydrobiologii i Rybactwa* founded in 1926 under the editorship of A. Lityński; during the period 1926 to 1939 and in 1947, thirteen volumes of *Archiwum Hydrobiologii i Rybactwa* have appeared, volume XII, 3, 4, published in September 1939, being almost entirely destroyed due to war action.

The journal publishes original works reporting experimental results, descriptive works and theoretical investigations in every sphere of hydrobiology. The article must contain original research not already published and which is not being considered for publication elsewhere. Papers are published in the official Congress languages of Societas Internationalis Limnologiae (at present: English, French, Italian and German).

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INTRODUCTION

The present issue presents the papers delivered on the IBP Wetland Symposium, performed on 11--18 June, 1972, at Mokołajki (Poland). In the meeting 40 participants from 9 countries took part. 38 reports and short communications were delivered, and some organizational solutions connected with both elaboration and edition of Wetland-Biome issue were established.

Great biological and economical importance of a frontier area of water and land as well as of marshes, provoked a necessity to include this ecosystem into the International Biological Programme. An initiation of cooperation was "Project Phragmites" prepared by dr. J. Květ in 1968. The following meetings have been performed: on 1–10 September, 1970, in Danube Delta — Meeting on Macrophytes, organized by IBP-PF and UNESCO/IHD, on 3–6 June, 1971, in Budapest — Meeting of the SCIBP Conveners and Coordinators. In Wetland Symposium at Mikołajki it was proved how much it is still to make. It was decided that group will continue its internationally coordinated activities, in some form, after the termination of the IBP, in view of the importance of wetlands as components of the biosphere. The next meeting of the Wetland Working Group will probably take place in 1974.

Polish Academy of Sciences and IBP Central Office have aided considerably their assistance in organization of the Wetland Symposium, by covering the costs of participance of several scientists.

Many thanks are due to our colleagues of the Organizing Committee for their contribution to arrange the meeting, to the managers of Institute of Ecology of Polish Academy of Sciences and the heads of Hydrobiological Station at Mikołajki for their help and assistance in the organization, and to the colleagues of Department of Applied Limnology, who deserve the credit for the enjoyable climate of the meeting.

Doc. dr. Andrzej Szczepański

POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	1—7	1973

M. PLANTER

PHYSICAL AND CHEMICAL CONDITIONS IN THE HELOPHYTES ZONE OF THE LAKE LITTORAL

Department of Applied Limnology, Institute of Ecology, Polish Academy of Sciences, Świerczewskiego 14, 11-730 Mikołajki near Mrągowo, Poland

ABSTRACT

Some physical and chemical conditions in the helophytes zone of the lake littoral were analysed. Chemical compositions of littoral sediments, littoral water, and interstitial water filling the space among the solid particles of littoral sediments were determined. Investigations were carried out at 108 sites in 12 lakes with various trophy in the Mazurian Lakeland.

The littoral occupies a large area in the majority of Polish lakes — sometimes up to 1/3 of the total area, forming a convenient environment for various plants. The area overgrown with helophytes, found mainly on shallows, constitutes 9.3 to 12.3% of the total lake surface area (Bernatowicz, Radziej 1964).

Because of its area and specific chemical and physical conditions, the littoral zone favours many chemical and biological processes and is certainly of great importance for all the processes taking place in a water body.

In view of the increased interest in helophyte production and in their economical exploitation as well as ecological significance, this paper deals with the estimation of certain physical and chemical conditions, mainly in that zone of lake littoral which is occupied by helophytes. The littoral without plants is not very large in the investigated lakes.

The present paper is a part of the research programme of the Department of Applied Limnology on production, morphometry, life condition and biology of common reed.

The physical and chemical conditions in the littoral have been estimated on the basis of analyses of water, sediments and interstitial water filling the space among the solid particles of sediments. The samples were collected from the middle of August to the beginning of October of 1969. The seasonal changes of the chemical composition of interstitial water were examined from May to November 1970. The investigations were carried out at 108 sampling sites in 12 lakes with various trophy in the Mazurian Lakeland (Table I).

Table I. The characteristics of the investigated lakes

Lake	Area (ha)	Maximum depth (m)	Area covered by helophytes		Trophic type	Number of stations
			ha	%		
Bełdany	941	46			eutrophic, holomictic	9
Flosek	4	6			dystrophic	2
Jagodne	943	37	92	9.8	eutrophic, holomictic	14
Kotek	42	2.5			eutrophic, polimictic	6
Lisunie	14	8.5			eutrophic → dystrophic	5
Mikołajskie	460	28	39	8.5	eutrophic, holomictic	15
Skonał	9	5.5	1.5	16.7	eutrophic, holomitic	5
Smolaczek	2	5.5			dystrophic	2
Szymon	154	3	34	22.1	eutrophic, polimictic	6
Śniardwy	10,970	23	754	6.9	eutrophic, polimictic	12
Tałtowisko	327	39.5	43	13.1	β-mesotrophic, holomictic	12
Tałty+Ryńskie	1831	51	122	6.7	eutrophic, holomictic	20

Lakes Kotek, Skonał and Szymon are small, shallow and eutrophic. The dystrophic type is represented by mid-forest lakes Flosek and Smolaczek. The small and shallow Lake Lisunie is described by some authors as eutrophic with a tendency to dystrophy. The remaining large lakes are eutrophic or of a moderate trophy, e.g. the β-mesotrophic Lake Tałtowisko.

The following relations have been found in the materials analysed.

Littoral sediments are mainly composed of organic material, calcium carbonate and silicate. The same elements also dominate in the bottom sediments of lakes in the Suwałki district (Stangenberg 1938). Taking into consideration the above components, the investigated littoral sediments can be divided into four types (Fig. 1): I — "siliceous with a dominance of silicates and small amounts of other elements"; II — "siliceous with a higher amont of calcium carbonate" — silicates are the main component, and $CaCO_3$ constitutes from 20 to 40% of the sediment;

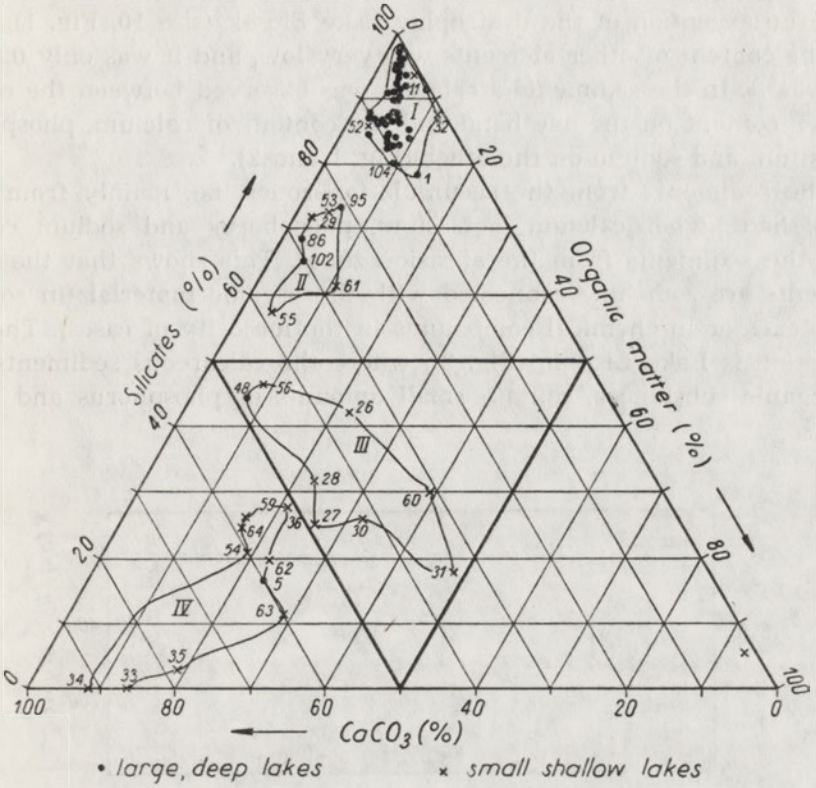

Fig. 1. Types of littoral sediments: I — siliceous, II — siliceous with a higher amount of $CaCO_3$, III — mixed, IV — calcareous

III — "mixed" — each element constitutes less than 50%; IV — "calcareous" — with a higher amount of calcium carbonate than is that of the organic matter and silicates.

The "siliceous sediments (I type — Fig. 1) show the predominance of abrasion processes. The silicates are a product of mechanical, physical and chemical destruction of lake shores. This type of sediments is found in large lakes with a narrow littoral platform.

The "siliceous with a higher amount of calcium carbonate" sediments (II type — Fig. 1) show that the accumulation of allochtonous or autochtonous material starts to predominate in the littoral. This type of sediments is found on some sites in small lakes, and in larger lakes ones, in bays sheltered from the wave action.

The "mixed" and "calcareous" sediments (III and IV type — Fig. 1) show a decisive predominance of the accumulation processes over abrasion. These two types of sediments are usually found in small and quiet lakes.

The "organic" type of sediments, distinguished for bottom sediments by Stangenberg (1938), has not been found in the examined lakes with the exception of the dystrophic Lake Flosek (site 10, Fig. 1).

The content of other elements was very low, and it was only 0.1, 0.01 or 0.001%. In the sediments a relation was observed between the organic matter content on the one hand and the content of calcium, phosphorus, potassium and sodium on the other (Fig. 1 and 2).

The sediments from the accumulation zones, i.e. mainly from small lakes, had higher calcium, potassium, phosphorus and sodium content than the sediments from the abrasion zones. This shows that the above elements are somehow connected with the organic material (in sorption complexes or in chemical compounds in the majority of cases). The only exception is Lake Lisunie (Fig. 2), where the calcareous sediments, rich in organic substances, contain small amounts of phosphorus and potassium.

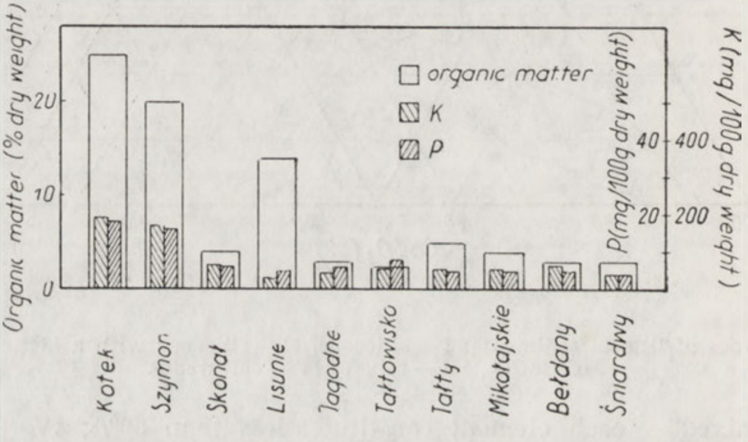

Fig. 2. Organic matter, P and K content in littoral sediments

In some of the investigated lakes, the types of littoral sediments were greatly differentiated. For example, in Lake Skonał all four types of sediments were found (sites 52—56, Fig. 1).

The chemical composition of littoral water was similar to that of the majority of surface waters of freshwater reservoirs (with the exception of waters of dystrophic lakes). In any one lake, the chemical composition of water in various places of its littoral was not much differentiated. Only the isolated and more shallow parts of the littoral show differences in the composition of their waters. Pieczyńska (1971) found much higher concentrations of various substances there than (compared with) in the littoral water.

A lack of differentiation in the content of the principal ions in littoral water of the investigated sites resulted from the constant exchange of littoral and pelagial waters. The chemical composition of the littoral water depended on the trophic type and character of each lake, but it did not on the composition of littoral sediments.

The chemical composition of interstitial waters of near-shore zones of lakes is not well known. In Polish literature, this problem has not yet been discussed. The only exceptions are the investigations in the emergent psammolittoral by Wiszniewski (1934) and Stangenberg (1934).

In the present paper, certain physical and chemical properties of interstitial water from lake littoral have been examined. The knowledge of the chemical composition of littoral sediments and of the water contained in them is important from the point of view of nutrient content and exchange processes between the sediments and lake waters.

The interstitial water of littoral sediments is in the zone of plant root system and is a source of nutrients for aquatic macrophytes.

The chemical and physical properties of interstitial water are different from the properties of littoral water.

The interstitial water was slightly acid or neutral, its pH was 6 to 7, while the littoral water was neutral or slightly alkaline.

The conductance of interstitial water, which is proportional to the total amount of ions in the water, was much higher than that of the littoral water (Fig. 3). The conductance varied from 400 to more than 1000 μS, while in littoral water it was 250 to 350 μS. The interstitial water also had a higher concentration of ions of calcium, magnesium,

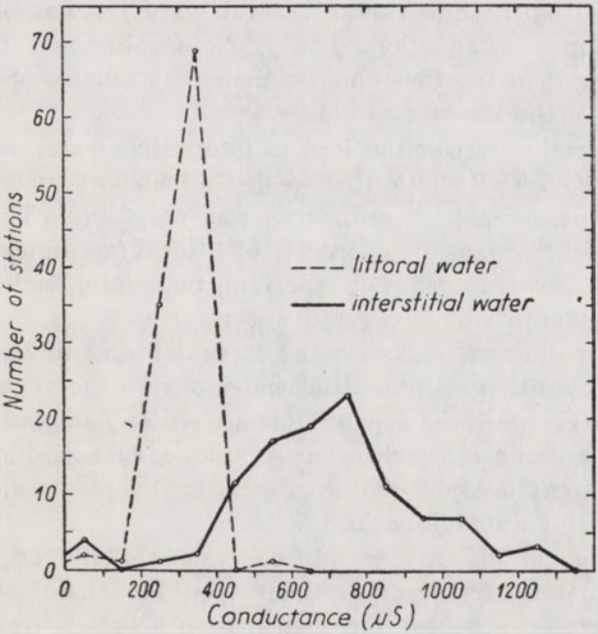

Fig. 3. Frequency of occurrence of specific conductance

amonium-nitrogen and a higher alkalinity (Fig. 4). The littoral water had lower values of these elements.

The main elements of interstitial water, influencing its conductance were calcium, magnesium and hydrocarbonate ions.

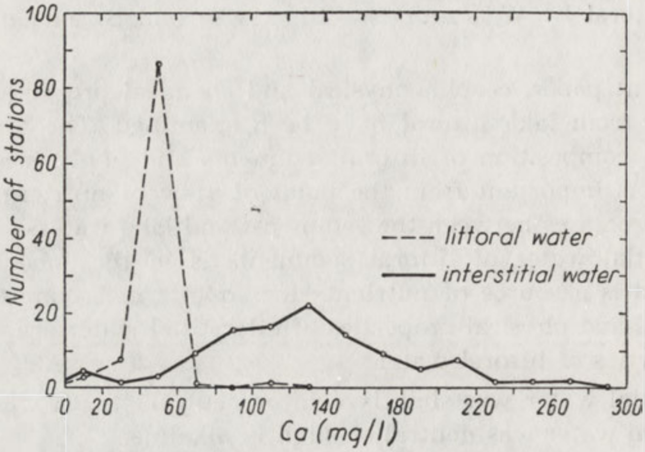

Fig. 4. Frequency of occurrence of calcium concentration

The interstitial water contained more iron and phosphates than the littoral water, as it was found on the basis of the investigations of seasonal changes of its chemical properties.

The concentration of phosphates in the interstitial water was 30 to more than 1500 µg/l, while in the littoral water it was below 10 µg/l during the summer stagnation. The iron concentration in interstitial water was more than 100 times higher than that usually observed in the surface waters of the investigated lakes.

The concentration of calcium ions in interstitial water was correlated with its alkalinity. The relation between the calcium concentration and quantities of this element in sediments was not found. There was also no direct relation between the character of littoral (accumulative or abrasive) and the concentrations of magnesium, potassium, sodium, chlorine, amonium and alkalinity of interstitial water.

The above statement, and also the irregular and unrelated changes of chemical composition of interstitial water during the vegetation season show that this composition depends on an entire complex of co-acting factors. These are the mineralization processes, carbon dioxide content, redox potential, exploitation of the substratum by plants and the inflow of waters from the drainage basin.

The influence of an intense mineralization of the organic detritus accumulated on the surface of sediments, on the chemical composition of interstitial water was best demonstrated in a broad "isolated" littoral of Lake Śniardwy (Fig. 5).

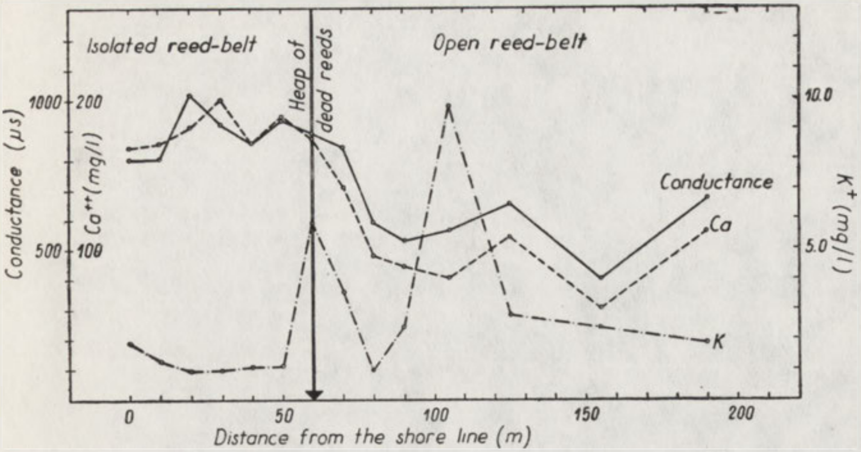

Fig. 5. Changes of composition of interstitial water in the reed-belt in Lake Śniardwy (4.VII.1968)

The conductance of this water and calcium concentration was much higher in the "isolated" part of this littoral than in the "open" part with strong wave action.

Analysis of physical and chemical conditions on the investigated littoral sites show a significant differentiation of habitats for helophytes. A comparison of the nutrients content in littoral and interstitial water suggests that the latter is a source of many plant nutrients. Therefore it can be assumed that helophyte stands take part in the exchange of nutrients between the littoral sediments containing water and the littoral water, by taking up nutrients from the substratum and returning them to lake water in the mineralization process.

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R. G. WETZEL and R. A. HOUGH

PRODUCTIVITY AND ROLE OF AQUATIC MACROPHYTES IN LAKES. AN ASSESSMENT

W. K. Kellogg Biological Station, Michigan State University,
Hickory Corners, Michigan 49060, U.S.A.

ABSTRACT

The present understanding of wetland primary productivity is discussed in terms of methodology and existing generalities. Emphasis is given to voids in our knowledge of macrophyte physiology, particularly in control mechanisms of photosynthesis and respiration, with discussions of some recent data and suggestions for avenues of future research. Interrelationships of the shifting contributions of emergent and submersed macrophytes, of attached and eulittoral algae, and of phytoplankton to the total primary productivity of lakes are indicated in relation to increasing fertility. Macrophyte-microflora interactions, mediated in part by secreted organic matter, are treated in an evolutionary context, and the continued inappreciation of the importance of the littoral flora to the entire metabolism of most lakes is reemphasized.

1. INTRODUCTION

Much of the emphasis of the International Biological Programme on wet land ecology has centered on an evaluation of the productivity of marsh and aquatic flora. Data are sought on production rates among varying climates, floral composition and community structure, and a host of community parameters. Major environmental parameters, e.g. nutrient concentrations of the sediments and water, and biotic interactions regulating growth have been investigated with varying degrees of success.

The enormous complexity of the littoral flora and attendant community, as well as physiological heterogeneity, has forced most investigators to employ generalized techniques of assaying production. The most common approach is to estimate a composite type of community net production employing organic biomass techniques. Full cognizance is given to the importance of corrections for grazing losses, disease, fragmentation, carry-over of annual production among perennial aquatic angiosperms and macroalgae, and many other serious confounding factors (cf. Westlake 1963, 1965).

The littoral region consists of a massive complex of many microhabitats. Variance in distribution of plants of the littoral community is extremely high. This heterogeneous distribution is a minor difficulty in comparison to the high variability in organic composition (even within a given monospecific stand), annual increments of root or rhizome biomass, and grazing losses. A most important difficulty is estimation of turnover rates among populations of perennial species. Moreover, we have a nearly total ignorance of the physiological and biochemical variations among aquatic and emergent angiosperms, a group that has secondarily developed an array of morphological and physiological adaptations enabling invasion of the relatively stable aquatic habitat.

No simple method exists for estimating rates of growth among such heterogeneous communities. Measurements of net production likely are made most effectively by very detailed analyses of changes in organic biomass. One can ask if the variance encountered in these analyses of production is too high to permit detailed resolution of causal mechanisms regulating growth. Even under ideal conditions of essentially monospecific, uniform macrophytic stands coupled with extensive sampling replication, variance is exceedingly high (e.g. Rich et al. 1971). As is apparent to most workers, validation depends upon the resolution demands of the hypothesis in question. Also apparent to serious workers in wetland ecology, the degree of resolution possible at the present time is not very great, particularly in regard to the most commonly employed correlation analyses. The use of semi-natural or manipulative experimental approaches employing controlled growth conditions (e.g. Westlake 1966, 1968, Wetzel 1969, Dykyjová 1971) is a highly essential direction of investigation.

Alternatively, very few assays of in situ metabolism of littoral macrophytes have been made. In view of the large gaps in our knowledge of the physiology of these plants, this situation is fortunate. Many of the results of in situ studies, especially employing oxygen change techniques, are likely of questionable value or totally erroneous (Wetzel 1965, Hartman, Brown 1967). Results from the radiocarbon uptake methods are confounded by variable rates of refixation of respired carbon (cf. discussion below).

2. WETLAND AND AQUATIC PRIMARY PRODUCTIVITY

Comparisons of plant productivity among wetland communities have been given greater resolution by the intensive and improved investigations under the auspices of IBP. Results have clarified productivity of these communities in comparison to terrestrial and marine environments. Moreover, much of the detailed analyses of integrated community investigations is providing badly needed insight into some of the major interactions (e.g. faunal grazing, community structure) affecting production and productivity.

The generalities, set forth in the excellent reviews of Westlake (1963, 1965), that the zones of highest productivities of wetland and aquatic communities exist in the emergent (reedswamp) region of the littoral-wetland complex, and the lowest in the submersed zone, have been confirmed for fertile sites. Coordinated studies are providing further insight on growth factors and interactions regulating growth, e.g. light, shading effects, etc. These generalities essentially stand for fertile sites, and they will be improved only slightly in resolution of fine details of variations in community growth. These generalities are not necessarily applicable, however, to less fertile sites (see discussion below).

Very little is known of photosynthetic efficiencies, physiology of in situ photosynthesis, respiration, photorespiration, and dynamic environmental parameters affecting this metabolism. Furthermore, evolutionary interrelationships and physiological adaptations of the wetland angiosperms to aquatic environments are almost completely lacking in detailed analysis. Efforts must be made in these directions simultaneously with those on details of community structure, net production, and species interactions if we wish to gain insight into the complexities of heterogeneous and dynamic metabolism of aquatic macrophytes, associated microflora, and their true functions in the aquatic ecosystem. Generalities will surely emerge as the components differing in fine detail are coupled.

3. RESPIRATION

Photosynthetic carbon fixation of aquatic macrophytes is balanced by losses of respiratory CO_2 and secretion of soluble organic compounds, and photosynthetic efficiency is influenced directly by the rates of these processes. In calculations of primary productivity, the respiration rate is usually assumed to be the same in light as in the dark, for lack of evidence to the contrary. Physiological evidence increasingly suggests that such an assumption is erroneous in many cases. The normal process of mitochondrial or dark respiration may be inhibited in the light in some plants, perhaps by suppression of glycolysis (Jackson, Volk 1970). Furthermore, efficient refixation of respired CO_2 in the light is probably a universally common event in submersed aquatic plants. These processes would restrict loss of respiratory CO_2.

Alternately, the phenomenon of photorespiration, well known in terrestrial plants (Tolbert 1963, Zelitch 1964, Gibbs 1970, Goldsworthy 1970, Jackson, Volk 1970, Hatch et al. 1971), enhances loss of CO_2 and may be a significant factor in reduction of photosynthetic efficiency of aquatic macrophytes. In this process CO_2 is generated in the light as a result of oxidation of glycolic acid, a direct product of C_3 Calvin cycle photosynthesis. The rate of this reaction is highly influenced by, and is proportional to, oxygen concentration, light intensity, and temperature. Glycolate metabolism is also enhanced when low CO_2 limits photosynthesis. The rate at which photorespired CO_2 is actually lost from the plant depends on the efficiency of CO_2 refixation.

Terrestrial plants in which all cells photosynthesize by the C_3 Calvin cycle can lose up to 50% of fixed carbon immediately in photorespiration depending on environmental conditions. Those plants in which photosynthesis proceeds through the C_4 β-carboxylation pathway in mesophyll cells efficiently refix CO_2 both from dark respiration and from photorespiration in the C_3 bundle sheath cells, and little or no CO_2 is lost from these plants in the light.

C_3 and C_4 plants can be distinguished by the following combination of characteristics, any one of which is reasonable evidence for the distinction (adapted from Black 1971, and from review articles noted above): C_4 plants have highly developed bundle sheath cells in leaf cross-sections, with unusually high concentrations of organelles and starch accumulation (elucidated by use of iodine-potassium iodide stain); C_3 leaves lack this differentiation. Photosynthesis is difficult to light-saturate in C_4 plants, while in C_3 plants saturation illuminance is in the range of 10,000 to 45,000 lux. Photosynthetic temperature optima are 30-40°C in C_4 plants, 10-25°C in C_3 plants. Photosynthetic CO_2 compensation points are low for C_4 plants (0-10 ppm CO_2), and high for C_3 plants (30-70 ppm CO_2). Response of apparent photosynthesis to O_2 concentration is not detectable in C_4 plants, and shows increasing inhibition above 1% O_2 in C_3 plants. Response of photorespiration (CO_2 release in light) to O_2 concentration is not detectable in C_4 plants, but shows increasing enhancement with increasing O_2 in C_3 plants. Glycolate synthesis and glycolate oxidase activity are low in C_4 plants relative to C_3 plants. An extensive and growing list of C_3 and C_4 species exists (Hatch et al. 1971), with obvious implications as to presence or absence of photorespiration, but the list consists entirely of terrestrial plants; little is known of the role of photorespiration in aquatic plants.

Emergent hydrophytes are exposed partially to environmental conditions similar to those of terrestrial plants and photorespiration undoubtedly can be extensive. The C_4 photosynthetic system thus is likely of adaptive value in many emergent hydrophytes, particularly in regions of high temperature and high light intensity, and also in situations where salt content of the environment adversely affects internal CO_2 and water balance (Bjorkman 1971, Slatyer 1971). In the latter context, Spartina, the dominant plant of the salt marshes of the East Coast of the United States, appears to be a C_4 plant (Black 1971). There is some evidence that *Typha latifolia* is a C_3 plant with relatively low rates of photorespiration (McNaughton 1966, 1969, McNaughton; Fullem 1969); limiting mechanisms are not known in this case.

Submersed hydrophytes are exposed to lower maximum O_2, light, and temperature relative to air, and photorespiration correspondingly may be of lesser magnitude than in terrestrial plants. Also, the greater resistance of water to diffusion of CO_2 relative to air (Raven 1970) and presence of massive internal gas lacunae likely retard loss of CO_2 from submersed hydrophytes and facilitate refixation of CO_2 regardless of presence or absence of the C_4 photosynthetic system. The C_4 system may not be of adaptive value in submersed hydrophytes generally, but this has yet to be determined. There is no question that the evolution of an extensive internal lacunal system in submersed angiosperms constitutes an array of interrelated morphological and physiological adaptations related to efficiency of gas utilization, buoyancy — light availability interactions, plasticity to water movements, etc.

Using a ^{14}C-assay developed to evaluate photorespiration in submersed hydrophytes, Hough, Wetzel (1972) found that *Najas flexilis* (Willd.) Rostk. and Schmidt refixes respired CO_2 efficiently in the light, similar to the activity of C_4 terrestrial plants. However, photorespiration was inducible inasmuch as release of CO_2 was enhanced by high O_2 concentrations in the light but was unaffected by O_2 in the dark (Fig. 1).

This response normally is found only in C_3 plants; recent analyses of the first (<15 seconds) fixation products, as well as leaf cross-section anatomy and starch distribution, also indicate that *Najas flexilis* is a C_3 plant (Hough unpublished). Thus, although apparent or net photorespiration in this plant does not result in great losses of CO_2 to the extent that a C_4 metabolic system would be of great adaptive value, the observed influence of O_2 on release of CO_2 in the light nevertheless affects photosynthetic efficiency significantly. Midday depression of ^{14}C fixation in natural macrophyte communities (Wetzel 1965) could be explained by onset of photorespiration with rising O_2 concentrations, light, and temperature. Data of Carr (1969) on light and dark respiration in *Ceratophyllum demersum*, also measured as $^{14}CO_2$ evolution from prelabeled plants, suggest refixation of respiratory CO_2 in the light similar to that found in *Najas flexilis*. These results cast some doubt on the assumption (Wetzel 1964) that, in short-term ^{14}C fixation productivity measurements for macrophytes, incorporated ^{14}C would not be respired and recycled appreciably. Although this likelihood was indicated previously without supporting evidence (Wetzel 1965), it is now clear that most certainly the ^{14}C assay for productivity measurements underestimates net photosynthetic rates.

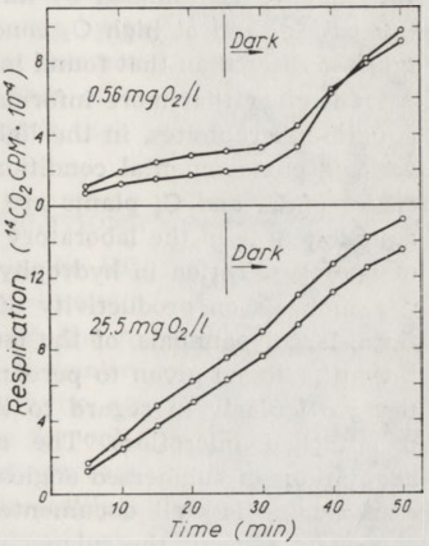

Fig. 1. Effect of dissolved oxygen concentration on respiration of *Najas flexilis* in the light and dark. Cumulative $^{14}CO_2$ cpm evolved into growth medium flowing past pre-labelled plants in tubular chambers. 2150 lux at all chambers for 25 min, then dark; 22°C, pH 8.1, flow rate 20 ml/min. Two lines in each graph represent duplicates (from Hough, Wetzel 1972)

A few other studies relating to photorespiration have been made in aquatic macrophytes, including effects of O_2 on photosynthesis in *Elodea canadensis* (Kutiurin et al. 1964) and Sagittaria (Bjorkman 1966), CO_2 compensation point in some marine macroalgae (Brown, Tregunna 1967), and compensation point and photosynthetic temperature optimum in *Myriophyllum spicatum* (Stanley 1972). These studies all generally suggested presence of C_3 metabolism and varying magnitude of net photorespiratory response, again likely because of varying CO_2 refixation efficiencies.

While dark respiration rates of *Najas flexilis* did not change with variations in O_2 concentrations (Hough, Wetzel 1972), dark respiration is enhanced by high O_2 in many other submersed hydrophytes (Pannier 1957, 1958, Gessner, Pannier 1958, Owens, Maris 1964, McIntire 1966, Westlake 1967, McDonnell 1971, McDonnell, Weeter 1971). During daytime in the latter species, the effect of O_2 on photorespiration and dark respiration would be additive (although this may be confounded by inhibition of dark respiration at high light intensities), and at high O_2 concentrations total release of CO_2 could be much greater than that found in *N. flexilis*.

It is clear that more information is needed on rates of respiration in aquatic macrophytes, in the light as well as in the dark, in response to varying environmental conditions. Until these and the other characteristics of C_3 and C_4 plants are more fully investigated in a variety of aquatic plants in the laboratory and in situ, a full assessment of the role of photorespiration in hydrophyte productivity cannot be made.

Emphasis on productivity of hydrophytes has centered on emergent flora, largely annuals, of the temperate region. Relatively little consideration has been given to perennial populations of submersed macrophytes, particularly in regard to the metabolism of associated populations of attached microflora. The morphological and certain physiological adaptations of submersed angiosperms to the aquatic milieu from terrestrial origins is well documented (Arber 1920, Sculthorpe 1967). In certain aspects, the submersed habitat is less severe than the terrestrial, e.g. thermal stability, nutrient availability from sediments, water, etc. These ameliorated parameters permit growth, reduced to be sure in temperate regions, to continue all year (cf. for example Borutskij 1950, Rich et al. 1971). This pattern of growth is likely much more common than generally believed. It is apparent, however, that many aquatic parameters (e.g. retarded gas exchange, reduced light, etc.) counterbalance advantages. Nonetheless, there are indications, alluded to above, that an array of morphological and physiological compensations exists indicating a high degree of plasticity to changes in the littoral environment on diurnal, seasonal, and geological bases. Investigations of these facets are only beginning and are needed for a proper assessment of parameters regulating primary productivity.

4. SECRETED DISSOLVED ORGANIC MATTER

The loss of major fractions of recently synthesized organic carbon as secreted dissolved organic compounds has been demonstrated for a few submersed and floating angiosperms (Wetzel 1969, Khajlov 1970, 1971, Wetzel, Manny 1972, Hough, Wetzel 1972). Well known among planktonic algae, this loss of organic carbon during active metabolism of submersed macrophytes represents a significant reduction in net photosynthetic efficiency. The secretion may well represent an incomplete adaptation to the totally aqueous medium. Functionally, however, the secretion of labile organic compounds by submersed hydrophytes enhances the development of a highly productive epiphytic community of microflora (Allen 1971, Wetzel, Allen 1971). Nutrient interactions, both organic and inorganic, exist between the submersed macrophyte and epiphytic algal and bacterial populations that are lacking in the greatly diluted planktonic regime. Indeed, the relationship of this apparent decrease in photosynthetic efficiency by loss of dissolved organic carbon could be viewed as a symbiotic interaction between community components and, moreover, an evolution of an ecosystem community adaptation to environmental conditions that impose physiological stress upon the macrophytes.

5. PRODUCTIVITY INTERRELATIONSHIPS

In spite of the significant inroads that the IBP has made into the question of the magnitude of wetland productivity, there continues to be an overwhelming inappreciation of both the magnitude and of the functional impact of the littoral flora to the entire metabolism of lake ecosystems. Freshwater benthic and epiphytic algae have been cited (Westlake 1963) as usually accounting for only a small part of the production of communities where they are present. Nearly all of these estimates are based on biomass analyses in fertile sites without any real determination of turnover rates of the populations. In extremely hypereutrophic waters where light is severely attenuated by biogenic turbidity, such may be the case (Fig. 2). In less fertile sites, however, the algae attached to the substrata (Wetzel 1964, Hargrave 1969, Kalff, Wetzel 1972) or to macrophytes (Allen 1971, Hickman 1971, Pieczyńska 1971, Rich et al. 1971, Wetzel et al. 1972), constitute a dominant, if not the major, site of autochthonous primary productivity. Regeneration rates of these algae on natural substrata are generally much greater than commonly estimated by growth on artificial substrata (cf. Wetzel et al. 1972) and exhibit a steady continuous growth with a population stability not common among phytoplankton populations (Allen 1971). Their contribution to detrital carbon metabolism constitutes a major impact on the system metabolism (Wetzel et al. 1972), both in the form of particulate detrital carbon in benthic carbon metabolism, and as dissolved detrital organic carbon which contributes to regulation of pelagic photosynthetic and heterotrophic metabolism in an array of simultaneously interacting direct and indirect pathways (Wetzel 1968, 1971).

Submersed macrophytes commonly constitute increasingly greater importance to the total primary productivity of lakes until fertility of the system reaches the point of severe light attenuation (Fig. 2). This light limitation is usually associated with intense phytoplankton productivity. At a given latitude, maximum growth of phytoplankton is rapidly reached where population densities are self-limiting by self-shading effects beyond which growth can be increased only by greater turbulence and light availability than occurs under natural conditions (Wetzel 1966).

As the emergent vegetation assumes greater dominance in a lake ecosystem and eventually encompasses a majority of the lake basin, an exceedingly productive combination of littoral macrophytes and attendant microflora develops (Fig. 2). Attached, largely epiphytic, algae and especially eulittoral algae (=pseudoperiphyton; pseudoplankton; tychoplankton) develop strongly in association with the emergent flora.

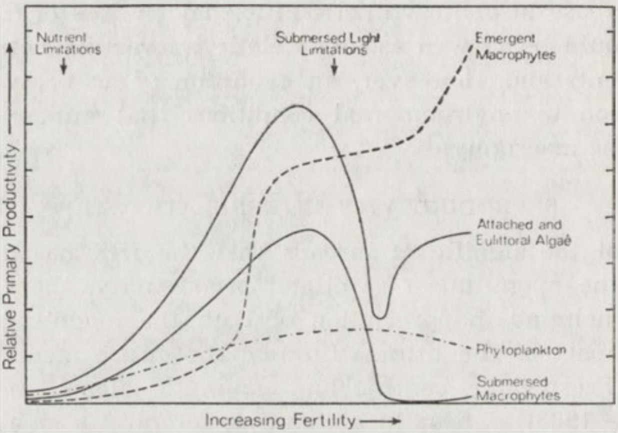

Fig. 2. Generalized relationship of primary productivity of emergent and submersed macrophytic flora, attached and eulittoral (tychophytoplankton) algae, and phytoplankton in lake ecosystems of increasing fertility

A large majority of the lakes of the world are small and have a morphometry such that the ratio of colonizable littoral zone to pelagic zone of production is large. In these cases there is little question that macrophytic vegetation and, most importantly its attendant microflora community, constitute a major impact on the lake ecosystem. The distinction of what constitutes allochthonous production (e.g. eulittoral, terrestrial, etc.) and what is part of true autochthonous lake production is a highly artificial distinction and has, indeed, led to an artificial anthropocentric treatment of natural mechanisms of ecosystem metabolism. It has long been recognized that all components of the watershed are influential in regulation of lake metabolism. Integrated data on the functional impact of these components on the entire system are essentially non-existent (cf. Wetzel et al. 1972). The concept of a lake as a microcosm must finally be laid to rest. Foremost in functional impact on the system as a whole and regulation of rates of eutrophication in most lakes is the littoral complex of macrophytes and associated microflora.

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B. GOPAL

A SURVEY OF THE INDIAN STUDIES ON ECOLOGY AND PRODUCTION OF WETLAND AND SHALLOW WATER COMMUNITES

Department of Botany, University of Rajasthan, Jaipur-4, India

ABSTRACT

The paper gives a brief account of the Indian researches on aquatic vegetation (especially of the wetlands) and puts on record the hitherto published (and some unpublished) data on the production of macrophytes. Salient features of autecology of several investigated species have been pointed out and attention is drawn to the urgent need of intensive autecological studies.

1. INTRODUCTION

Wetlands, sometimes referred to as marshlands, have been recognized as separate ecosystems transitional between purely terrestrial and aquatic ones and form the subject of a separate theme under the PT section of the IBP. It is difficult if not impossible, to demarcate well defined boundaries of the wetlands, and therefore, it is more appropriate to include shallow waters in the wetland habitats[1]. This provides for a close liasion between PT and PF sections. The Indian programme of IBP did not originally include any PT project which could be grouped under wetland theme (*IBP News* 13) and the projects under PF section (*IBP News* 17) also did not give a balanced consideration to macrophytes. Thus, there has only little effort been devoted to the study of the wetland habitats in India and that too not under the banner of IBP. I will, however, attempt to present a brief survey of the literature to assess our present state of knowledge which may be made use of in the synthesis of wetland data being attempted here.

2. THE VEGETATION

In India, there are numerous large and small, temporary or permanent shallow freshwater bodies harbouring a variety of marshland vegetation. During the monsoon, especially in the northern parts of the country, the shallow depressions (up to 2 m deep) get filled with water. Soon from the underground perennating parts, rapid growth occurs of several

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[1] The workshop has since provided a definition of the wetlands to include the various situations in different climatic regions.

marshland species and the submerged and free floating species follow closely. At the retreat of the monsoon, there flourishes a luxuriant marshland vegetation throughout the winter and later as the summer approaches, the vegetation turns again into a meadowland in which the underground parts perennate. Thus, these habitats display the process of succession (termed as seasonal succession by Dudgeon 1921) in which every year the hydrosere alternates with a xerosere (Misra 1944, 1946).

The most important species in Indian wetlands include: *Typha angustata, Cyperus exaltatus, C. rotundus*, several other species of Cyperus and Scirpus, *Eleocharis plantaginea, Hygrophila auriculata* (*Asteracantha longifolia*), *Oryza sativa*, Marsilea species, *Monochoria vaginalis, Phragmites sp.* (in Kashmir), *Ipomoea aquatica, Paspalum scorbiculatum, Eichhornia crassipes, Spirodela polyrhiza* and other lemnids, and *Azolla pinnata*. These species can be seen even forming large single species stands. Several other hydrophytes of usually deeper waters are also commonly met with in shallow waters.

The vegetation of the shallow waters and marshlands had been first studied by Mukerji (1921, 1926), Agharkar (1923), and Biswas (1927). Later these studies were undertaken as part of investigations on breeding and control of mosquitoes, and Biswas, Calder (1936) published the first extensive list of aquatic and marshland vegetation of India and Burma. More comprehensive ecological studies including an analysis of the habitat factors and the vegetation dynamics were later made by Misra (1944, 1946). Since then, there have been several publications dealing with the vegetation of such habitats all over the country but unfortunately most of them deal mainly with floristics and the zonation along water depth gradients. These workers (Sen 1959, Mirashi 1954, 1958, Vyas 1965, Jha 1965, Kaul, Zutshi 1967, and several others) have classified the aquatic vegetation into traditional free-floating, submerged, submerged-floating leaved, rooted submerged, emergent and marshy types. Hogeweg, Brenkert (1969) for the first time employed a different system of classification based largely on the growth-form classification of Hartog, Segal (1964) in which the various phenophases in the life cycle of a plant were taken into consideration along with the ecophases. I suggest that before attempting at any classification of the aquatic and marshland vegetation under Indian situations, enough autecological information has to be gathered about the various taxa since they exhibit immense phenotypic plasticity and adaptability to the ever-changing situations of the unstable habitat. The phenophases are greatly modified under diverse ecophases in which the species thrive well.

3. THE ABIOTIC ENVIRONMENT

Several investigations have been made on the limnology of deep waters and larger fish ponds in India (studies of Ganapati, Sreenivasan, Suxena, Zafar and the Hyderabad School, and various Fishery Research Institute Centers and University Departments). However, comparatively few and incomplete studies on wetland habitats are available. The data on hand from various sources (Misra 1944, 1946, Gopal 1968, Gupta 1968a, Jha 1968, Sahai, Sinha 1969, Srivastava 1950, Mitra 1955, 1964, 1969) show that the pH of both the soil and water remain on the alkaline side being mostly between 7.5 and 11.0. The total alkalinity reaches upto 50 ppm with as much as 250 ppm calcium. The calcium usually gets precipitated and is found as encrustations over submerged macrophytes as Hydrilla and charophytes, and is also shown by the abundance of molluscs. The dissolved organic matter content reaches upto 25 ppm in comparatively clear waters and even more in highly polluted waters. The dissolved oxygen content varies appreciably during different seasons and also diurnally between values as low as 1 ppm as high as 40 ppm. Nitrates and phosphates range between 0.1 and 1.5 ppm. The bottom waters always have high concentration of nitrates, phosphates, calcium, carbonates and bicarbonates, and lower concentrations of free CO_2 and dissolved oxygen.

4. COMMUNITY PRODUCTION

To my knowledge, there have been only two major studies on the community production. In one of them at Varanasi, Jha (1968) studied a 0.4 ha semi-permanent shallow fish pond in the Banaras Hindu University Campus. A maximum biomass of 554.7 g/m^2 was recorded and the annual net primary production was 353.5 g/m^2. The same pond showed 51.6 g/m^2 annual production of fish (fresh weight basis). Of the total production, about two-thirds are contributed by the emergent and marshland species alone, i.e. *Eleocharis plantaginea* and *Cyperus exaltatus.* In terms of energy values, macrophytes produce about 1200 kcal per year, the phytoplankton contribute 215 kcal per year and the fish about 52 kcal per year. Highest daily rates of production for macrophytes were 4.5 g/m^2/day during the monsoon while the lowest rate was 0.14 g/m^2/day during spring. A turnover value of 64% and maximum photosynthetic efficiency of 0.58 has been reported. In another study of the same pond, conducted for only a short period, a much higher standing crop biomass (only aboveground) has been reported by Ambasht (1971). He recorded 2.21 kg/m^2 biomass of the emergent species alone. Sinha (1970) in a similar study of a shallow lake (Ramgarh Lake) at Gorakhpur reported a net annual production of 7.38 kg/m^2 for macrophytes of which the attached emergent and other marshland plants alone contributed about 5.0 kg/m^2. A comparison of these values with those listed for fresh water marshes of other parts of the world by Westlake (1965) shows that the tropical and subtropical wetlands are as much or even more productive as those in temperate regions. While the values given by Jha (1968) seem to be an underestimate of the situation, the results of Ambasht (1971) and Sinha (1970) indicate that the emergent vegetation of the Indian wetlands (lying under subtropical climatic region) is highly productive and could produce more where the substratum remains under water all the year round.

5. PRODUCTIVITY OF IMPORTANT MOCROPHYTES

Some data has been gathered on the productivity and maximum biomass of few common macrophytes of wetland habitats. These values have been obtained by harvest method and utilizing the values of minimum and maximum biomass over the growth period for the computation of daily production rates. The data are presented in Table I. It is seen that a very high rate of dry matter production is obtained in many of these species. The highest reported value is for a wild variety of *Oryza sativa* (33.3 g/m^2/day) followed closely by that of *Phragmites communis* (28 g/m^2/day) and by quite high values for Cyperus species, *Monochoria vaginalis, Typha angustata, Salvinia auriculata, Eichhornia crassipes* and *Eleocharis plantaginea*.

However, a comparison of the data presented here with that compiled by Westlake (1965) from various sources shows that the Indian wetland species do not produce much more than those of temperate regions. Freshwater swamp species have been reported to produce as much as 75 t/ha dry matter under warm temperate and tropical conditions (Perude 1958, for *Arundo donax). Scirpus lacustris* (cf. Westlake 1965) and *Cyperus papyrus* (Pearsall 1959) are among other highly productive species with annual dry matter production of 46 and 70 t/ha respectively. The high values of net annual production for Phragmites and Typha in Kashmir (Kaul 1970) are under comparable temperate conditions and may even be overestimates. A study of Typha under subtropical conditions is being made and may reveal the difference. *Oryza sativa* (wild) produces 31 t/ha — the highest among species investigated so far and this is very close to the 40 t/ha annual production of the cultivated variety of the same species in New South Wales (Westlake 1965). However, it is noteworthy that the daily productivity of the wild variety is about 50% more than that of the cultivated one. The rate of production is also governed by the density of the species as is true for free-floating

Table I. Data on productivity of certain macrophytes of Indian wetland and shallow water habitats

Species	Annual net production (t/ha)	Maximum rate of productivity (g/m^2/day)	Author
Phragmites communis (aboveground only)	44.00	ca. 28.0 *	Kaul (1970)
Typha angustata	32.00	15.5 *	Kaul, Vaas (1970)
Oryza sativa	31.00	33.3	Sinha (1970)
Eleocharis plantaginea	...	ca. 7.0 *	Pandey (1969)
Cyperus rotundus	5.9	3.7 *	Pandey (1969)
Cyperus spp.	1.07	14.7	Sinha (1970)
Eichhornia crassipes	6.15	3.8	Sinha (1970)
	...	3.5—9.5 **	Das (1968)
Spirodela polyrhiza	8.02	3.5—4.7 ***	Sinha (1970)
	...	1.0—2.4 **	Das (1968)
Azolla pinnata	2.80	1.8—4.7 **	Gopal (1967)
Hydrilla verticillata	3.64	2.6	Sinha (1970)
Najas graminea	5.23	3.5	Sinha (1970)
Potamogeton pectinatus	3.79	1.5	Sinha (1970)
Monochoria vaginalis	10.35	13.3	Sinha (1970)
	1.44	...	Gupta (1968)
Sagittaria sagitifolia	9.0	4.5	Sinha (1970)
Polygonum glabrum	4.5	6.7	Sinha (1970)
Rumex dentatus	1.8	8.0	Sinha (1970)
Spirodela and other duck-weeds	3.5	1.8 *	Kaul (1970)
Salvinia natans	...	10.5 *	Kaul (1970)
Salvinia auriculata	...	12.8	Gopal (unpubl.)

* Values have been calculated from biomass and growth data of the author investigating the species.

** Values are for different conditions during the growth period.

*** The lower value is for "summer form" and the higher value for "winter form" of the species.

species like *Eichhornia crassipes*. It produces 3.5 to 9.5 g/m^2/day under different conditions and densities. The maximum productivity of hyacinth in India is still near the lower values reported in United States 7.4 to 22 g/m^2/day (data of Westlake 1965, based on Penfound, Earle 1948, and Dymond 1949).

It is thus observed that while the Indian marshland and shallow water species have daily productivities greater than those of other climatic regions in many cases, the net annual production is much lower. This can be accounted for the marked seasonal variations in temperature and precipitation. The high temperature and extremely dry conditions of the summer months are prohibitive to growth and indeed, most of the marshlands turn into dry beds with little or no vegetation aboveground. The most favourable growth period for majority of the species is between the retreat of the monsoon and mid--winter (late August to December).

6. AUTECOLOGY OF WETLAND SPECIES

A few species of wetlands (including shallow waters) have been investigated autecologically by various workers. The following account gives certain common observations of interest. In all the aquatic and marshland plants, the vegetative reproduction is more prominent than the sexual reproduction and in many cases it completely eliminates the latter, e.g. in Marsilea species, *Eichhornia crassipes,* etc. This is accomplished by underground rhizomes and other perennating tubers, turions, etc. *(Eleocharis sp., Marsilea sp., Cyperus spp., Hygrophila auriculata,* duckweeds). These propagules in general have a long viability and also tolerance to desiccation in soil (Gopal 1966, Das 1968, Tripathi 1968, Pandey 1969). However, in several species *Marsilea spp., Eichhornia,* duckweeds) the viability is found to be lost or considerably decreased on air-drying (Gopal 1966, Das 1968). Apical dominance has been noted in most of the tubers (Gopal 1966, Anonymous 1969). Seed germination in several species as *Hygrophila auriculata* (Gupta 1968), *Pistia stratiotes* (Datta, Biswas 1969), *Hydrilla verticillata* (Mitra 1955, 1964), *Ipomoea aquatica* and *Alternanthera sessilis* (Datta, Biswas 1968, 1969) has been studied and found to be influenced by the light intensity and quality. In general, the light is an essential requirement. Most of the species of marshlands have been found to show best growth under experimental conditions when they are grown in soils at field capacity. Water-logging is detrimental to growth in many species. The growth is also much influenced by the pH, dissolved oxygen content and temperature conditions. The plants appear to be quite sensitive to temperature fluctuations (especially the free-floating ones) as they enter or come out of the dormant phase swiftly. In duckweeds (Spirodela) several forms as summer and winter or spring forms, have been recognized on this basis (Das, Gopal 1969). The light relations of some species have been studied but there seems to be great adaptability to varying light conditions among all these plants.

Another feature of great interest is the large phenotypic variability among both marshland and shallow water plants. This has invariably been correlated with the water level and soil moisture regimes (Gopal 1968, Das 1968). The adaptability among these plants to the dynamic habitat is so great that any attempt at their control measures remains futile. The estimates of their productivity vary over a wide range and are not easily comparable unless the habitat conditions are specified.

It has also been concluded in most of the investigations on rooted submerged or emergent or marshy species that the edaphic factors (pH redox potential, nutrient availability) are as important for their growth as for any terrestrial species (cf. Misra 1938, Gopal 1971).

Lastly, it is noted that very little work has been done on the hydrological role of these plants. A preliminary study on the evapo-transpiration rates from a cover of hyacinth, Salvinia and duckweeds has yielded information which should caution us in making use of our productivity data. Several times (5 to 10) more amount of water is lost through the cover of these plants than that from the free water surface. It has been suggested in literature that the high rates of production (for example, of Eichhornia, cf. Westlake 1965) coupled with the great nutritive value of these plants (Boyd 1968) may be economically exploited and these plants may rather be cultivated instead of trying their eradication. If the water economy of these plants is taken into consideration, all the human efforts at water conservation would be wasted for the production of little protein! We need urgent investigations into the water relations of the wetland and shallow water plants before their high production values may deceive us.

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D. F. WESTLAKE

AQUATIC MACROPHYTES IN RIVERS. A REVIEW

River Laboratory, Freshwater Biological Association, Wareham, Dorset, England

ABSTRACT

The typical communities and growth forms of aquatic macrophytes in rivers are briefly described. The problems of identifying the causal relations between species distribution, productivity and environmental factors are discussed with particular reference to the many correlated and interacting factors in the river environment. The effects of various important factors are then reviewed. On a world-wide scale temperature is probably the most important factor. Within a region the general chemistry of the water favours certain species and their detailed distribution and productivity are determined by local variations in irradiance, flow, nutrients, management and dynamic interactions between the plants and flow.

1. INTRODUCTION

Shallow, clear-water rivers that are not overshadowed and are not excessively rapid, oligotrophic or polluted are dominated by submerged aquatic macrophytes, which are more important in such water bodies than in most other types. The margins are lined with emergent plants, which extend to cover vast deltaic areas where rivers enter lakes, seas or regions without slope. The faster flowing, more specialized habitats have characteristic communities and species but as the flow decreases the plant populations come closer to those of lakes, ponds, swamps and marshes.

There are few experimental studies of the effects of environmental factors on these communities and this review can do little more than point to some obvious relations between some environmental factors and the composition of the communities and the growth of the plants.

Many statements will be made without the support of adequate detailed evidence but are included to contribute towards the "challenging hypotheses" that are required to help with the task of synthesis of results of the International Biological Programme.

2. GROWTH FORMS

It is convenient to describe the floras in terms of the growth forms that predominate (Hartog, Segal 1964). The characteristic submerged communities of temperate flowing waters contain batrachiids (e.g. *Ranunculus peltatus, Callitriche platycarpa*), myriophyllids (e.g. *Myriophyllum spicatum, Ranunculus fluitans)* and some elodeids (e.g.

Potamogeton pectinatus, Zannichellia palustris). In warmer waters vallisneriids are often present (e.g. *Vallisneria spiralis, Sagittaria lorata*) and in some very large and long rivers even pleustohelophytes such as *Eichhornia crassipes* may develop large populations. In the most rapid waters only haptophytes (e.g. *Fontinalis antipyretica, Podostemon olivaceum)* can survive.

The marginal vegetation is normally composed of helophytes, generally similar to lakeside communities in specific composition (e.g. *Phragmites communis, Alisma plantago-aquatica, Rorippa spp.)* but with a restricted range of species. The reasons for the infrequence of many lakeside species are not clear, but problems of dispersal and establishment are probably important. Some of the species favoured by the frequent deposition of silt and by relatively well-aerated soils (e.g. *Glyceria maxima)* are particularly common. Characteristic communities of weak-stemmed adventitiously-rooting dicotyledonous plants (e.g. *Rorippa nasturtium-aquaticum, Veronica beccabunga, Apium nodiflorum)* often extend from the margins, or from shallow areas, if flows are low during the summer.

3. ENVIRONMENTAL FACTORS

Much has been written about factors controlling the distribution of aquatic plants but the complexity of the field situation is often not recognized and oversimplified explanations are common. The neat, tidy and simple situation found in good physiological experiments, with only one variable factor, rarely occurs. If a factor is defined as limiting when an increase in its intensity produces an increase in the plants response, then normally there are many partially limiting factors, any of which can be changed to give rise to a change in growth rate. It should be remembered that some factors may be negatively limiting, i.e. in increase in such a factor produces a decrease in growth. To simplify the problems it may often be possible to recognize a hierarchy of limiting factors, ranging from those which are more or less constant for long periods (e.g. many aspects of water chemistry) or over wide regions (e.g. annual solar irradiance), to those which change markedly over short distances (e.g. water velocity), or rapidly with time (e.g. instantaneous solar irradiance).

The nature of the problem to be investigated thus defines a few of the factors involved as the most important, and a change in the terms of reference can completely alter the situation. The most rewarding investigations are those which enable particular factors to be successfully isolated.

Many factors are interrelated and the most easily measured value may be only remotely or non-linearly related to the real causes of a particular effect. Such problems are particularly difficult to unravel in the field and the possible factors may not be separable experimentally. For example velocity and silting are broadly correlated, but a mid-stream measurement of velocity may have little connection with the actual velocities affecting the deposition of silt around a stand of plants, and the degree of silting will be dependent on the degree of turbulence and the supply of silt. The actual mechanisms by which a typical species of high velocity sites is replaced by a typical species of slow velocity sites may involve the sensitivity of the plants to shading, to nutrient supply from the flowing water, to nutrient supply from silt, to attack by silt-inhabiting invertebrates, and to physical damage; as well as the obvious rooting abilities of the plants and the effects of all these factors on the relative ability of the plants to compete. It as extremely difficult to set up experiments which keep all factors constant except one; a change in velocity normally produces changes in silting and invertebrate populations.

Such situations can easily give rise to loose and misleading statements. Consider a plant growing in slow moving water containing a high concentration of a nutrient. Under these conditions the nutrient close to the plant may be severely depleted because mass transfer is not occurring in the neighbourhood of the plant and diffusion cannot transfer the nutrient sufficiently rapidly. It is not useful to say that the concentration of the nutrient is limiting, although it is true that a large increase in the concentration in the main body of water would increase the growth rate. It is better, but still not very useful, to say that the concentration of the nutrient near the plant is limiting. It would be correct to say that the nutrient supply to the plant is limiting, but a really quantitative model can only be constructed by considering the interactions of the concentration gradient, water velocity, turbulence, the shape of the plant, the concentration in the plant as affected by the rate of utilization (which is in turn affected by the supply of other nutrients) and the effects of temperature on supply and utilization; which all affect the rate of transfer of the nutrient from source to sink.

LIGHT AND TURBIDITY

These are treated together, since the main effect of turbidity is to reduce irradiance with depth. However turbidity may also have a direct effect by abrading plants when water velocities are high (Haslam unpubl.), and an indirect effect on the rate and nature of silting.

As a consequence of bank shading, surface reflection and attenuation by the water, dissolved and suspended materials, the light available to a submerged plant is considerably less than that reaching a terrestrial plant. A plant growing under 1 m of clear river water receives about 50% of the incident visible irradiance (vertical attenuation coefficient, log base 10, about 0.3; Westlake 1966 b), which is comparable with many lakes. However many rivers have coloured or turbid water derived from leaching and erosion in the drainage basin or from pollution, so that attenuation is much greater, and much more variable than in lakes. Large rivers may also have dense potamoplankton populations attenuating the irradiance. Conditions where only 1% of surface irradiance reaches 1 m are common and in many large rivers the irradiance at 1 m is negligible (Westlake 1966 b).

This means that plants are restricted to parts of the river bed shallow enough to receive sufficient irradiation. A cross-section of the River Thames at Reading (Berrie 1972) gives a good example of the influence of irradiance, as affected by shading and depth, on plant distribution. Where Salix trees hang over the water, plants are absent. Elsewhere *Acorus calamus* occurs along the margins and *Nuphar lutea* extends down the sides to about 2 m, where the irradiance is 2–3% of the surface. The river bottom, at 4 m, is devoid of plants.

Some plants are particularly sensitive to shading. In chalk streams *Ranunculus penicillatus var. calcareus* (subsequently called *R. calcareus*) soon disappears from shaded waters and is replaced by *Callitriche spp.* or, in more extreme conditions, by bryophytes. *R. calcareus* is unable to colonize the bottom deeper than 1.5 m and such areas are often occupied by *Potamogeton perfoliatus* or mosses (Dawson unpubl.). Floating plants, or floating-leaved plants once they have reached the surface, are little affected by turbidity. Some correlations of particular species with degree of turbidity can be found (Haslam 1971) but most of these are probably the result of responses to other factors correlated with turbidity.

There will also be more specialized responses to the level, duration and spectral composition of the irradiance, but very little is known about these in aquatic plants. After long, warm days some heterophyllous batrachian species of Ranunculus produce laminate leaves (Cook 1966). Flowering may also be a response to day-length (e.g. *Rorippa nasturtium-aquaticum*, Bleasdale 1964). Seeds of some lake species of Potamogeton are known to require red light for germination (Spence et al. 1971). The general level of irradiance produces light and shade responses in the morphology and physiology of plants.

WATER VELOCITY

This is likely to be the most important factor affecting the specific composition of river plant communities and is a factor peculiar to rivers, though wave action in lakes may have some similar effects. However it is not often clear whether the effects are direct, through physical control of establishment, physical damage or physical effects on metabolic rates, or indirect through the effects of water movement on the substrate or the fauna.

In his analysis of river communities in Britain Butcher (1933) subdivided the communities of each major water type into communities characteristic of different degrees of water velocity, correlated with different bottom deposits (very fast, rocks; fast, stones; moderate, gravel; slow, sand; very slow, silt; negligible, mud). In the very fast reaches the plants are mainly mosses (e.g. *Fontinalis antipyretica* or *F. squamosa*). *Ranunculus spp.* and *Myriophyllum spp.* are typical of the stony and gravelly stretches. *Potamogeton spp.* become more abundant in slower waters. *Elodea canadensis* is typical of the slowest flows and littoral helophytes become important, especially *Sparganium erectum.* Haslam (1971) has demonstrated some of these correlations with flow and type of bottom.

Floating plants are obviously the most affected by problems of establishment, but, if the river is long and slow enough to allow time for significant reproduction while they drift downstream, populations may develop. Many other plants, which could grow if anchored, are restricted in distribution by failure to establish in fast flowing water. Thus *Rorippa nasturtium-aquaticum* can only develop near the banks or where dense beds of other plants reduce the flow enough for seedlings or drifting pieces to take root. Establishment also depends on successful dispersal of seeds, spores and fragments in the first place. This is facilitated within river basins by flow, but is extremely difficult between different basins. *R. calcareus* is absent from many limestone streams in Northern England although it is widespread in Southern England and grows well in the limestone streams if introduced.

Physical damage may take the form of breaking shoots or leaves, pulling plants from the bottom or eroding the bottom. Haslam (unpubl.) finds considerable differences between species in experimental conditions. For example *Sparganium emersum* (found in slow flow) is easily broken by pulling and turbulence, while *Ranunculus spp.* (found in higher flows) are less easily damaged. Plants not easily uprooted have low resistance to water flow and well developed rooting systems. Plants of gravel reaches (e.g. *Ranunculus* spp.) have relatively short roots but they are produced readily at every node from a flexible stem lying close to the gravel, and are tough and contorted around the stones. Plants of silt and mud (e.g. *Elodea canadensis*) may also have numerous nidal roots but the stems are more erect and when damaged the distal portions are easily lost since they are not rooted. However their roots are long and a high proportion of each root remains buried even when much of the superficial deposits are eroded. The natural growth pattern may also be important since plants perennating by underground rhizomes will be better able to survive winter spates than species with turions or overwintering green shoots. The differences between rivers with winter and spring floods (temperate rainfall) and summer floods (snow-melt) may be important in relation to growth cycles of different species. Frequent loss of plant material reduces the relative growth rate.

Metabolic effects of flow influence the exchange of materials between the plant and the water, especially the uptake of carbon dioxide and mineral nutrients. The photosynthesis of submerged plants is affected by the rate of water movement (James 1928, Westlake 1966 a), presumably because carbon dioxide sources cannot diffuse across the boundary layer around the leaves fast enough, and because the thickness of this layer depends on velocity. Natural growth will often be partially limited by flow acting through the control of the rate of supply of a nutrient, but which nutrient is most important will depend on a complex balance of requirements, sources, uptake routes, concentrations and velocity (see also under chemical factors). It is possible that *Ranunculus calcareus* requires fast, hard waters because it has a high growth rate which can only be sustained by a clear water with a high concentration of available carbon (bicarbonate), which is maintained close to the leaves by the high velocity.

WATER CHEMISTRY

The general chemical nature of the water, calcareous or non-calcareous, eutrophic, oligotrophic or dystrophic, is correlated with particular floras. Each type has species which are only found in that type, species which are most successful, and species which are never found. However the number of species that are absolutely restricted to particular waters is small and most species are capable of some growth in unfavourable waters, especially if free from competition or grazing.

Butcher's (1933) first division of river communities was into four groups of increasing calcium content (about 10, 50, 100 and over 200 mg/l calcium carbonate respectively). Some examples of species that are limited in distribution are *Potamogeton polygonifolius* and *Ranunculus flamula*, in less than 120 mg/l $CaCO_3$, and *Ranunculus calcareus* and *Hippuris vulgaris*, more than 100 mg/l $CaCO_3$. (These values are mainly from personal experience and may not hold for all waters). *Potamogeton lucens* and related hybrids, *P. pectinatus* and *Myriophyllum spicatum* are other species characteristic of calcareous waters, while *P. gramineus* and *M. alterniflorum* are found in more calcium-poor waters. It is not known if the causal factor is really the calcium or commonly correlated factors such as pH, conductivity or nutrient level.

Limiting nutrients in most rivers are likely to be carbon, nitrogen, phosphorus or potassium. Iron deficiencies are not apparent but little is known about iron concentrations and supply in rivers. Much more carbon is needed (roughly 250 C to 20 N to 15 K to 1 P) but the total available carbon is often in much greater concentration, except in enriched low calcium waters or in waters of high pH where plants requiring free carbon dioxide are growing. Carbon dioxide may be obtained from sediments, either by diffusion through air spaces inside the plant from the roots or by creation of locally raised concentrations within weed beds. Other nutrients may also be obtained from the sediments as well as directly from the water. The relative importance of nutrients will depend on their concentrations in water and sediments, their mass transfer by flow, their diffusion coefficients, the permeability of leaves and roots and the plant's demand (internal concentration). The equilibrium constants of various forms of the solutes, especially carbon dioxide, may also be involved.

In many of the chalk-streams of Southern England the total annual throughput of dissolved inorganic carbon, nitrogen, phosphorus and potassium is over 40 times the amount in the total biomass of plants in the river (Westlake 1968, Ladle, Casey 1971). If any of these nutrients are to affect the rate of growth either the rate of transfer from water to plant or the throughput during the season of maximum growth must be involved. In the larger streams the supply of carbon is probably partially limiting but in some small, densely weeded streams potassium and phosphorus concentrations fall during the spring as it is taken up (Casey, Newton in press.). Normann (1967) and Stake (1967) have found similar decreases in nitrogen and phosphorus in small polluted streams with dense vegetation, during the growing season.

In short experiments the uptake of nitrogen and phosphorus only becomes saturated at concentrations far higher than in most natural waters (NH_4^+ — 5 mg N/l, Schwoerbel, Tillmanns 1964 a, b; PO_4^{---} $>$ 2–5 mg P/l, Schwoerbel, Tillmanns 1964 c, Normann 1967). However it is probable that such experiments give a short period of uptake from concentrated media which is higher than can be sustained over long growing periods (cf. Mulligan, Baranowski 1969, growth not limited above 0.2 mg N/l, 0.07 mg PO_4^{---}/l).

Aquatic plants seem relatively insensitive to chemical pollution and are more affected by associated factors such as turbidity and accumulation of organic deposits. *Potamogeton pectinatus* seems to be particularly resistant to pollution and favoured by eutrophication.

BOTTOM DEPOSITS

Although the distribution of plants is often related to the nature of the bottom it seems likely that this is only the result of correlations with flow, which is the real causal factor. In nutrient-poor waters organic deposits or fresh inorganic deposits may however be an important source of nutrients. Haslam (1971) shows correlation diagrams relating the distribution of some species to flow and to substrate, which have similar shapes in both cases.

TEMPERATURE

The geographical distribution of species is influenced by the general level of temperature in the climate and particularly by the occurrence of frosts.

In general temperature has no special effects in rivers. However spring-fed streams have a relatively high temperature in winter and a lower temperature in summer. *R. calcareus* in such streams flowers earlier than downstream though the biological mechanisms and significance of this response are far from simple (Dawson unpubl.). *Vallisneria spp.* have become established in cool temperate waters where heated effluents maintain warmth during the winter.

4. BIOTIC FACTORS

The vegetation of particular sites is often highly dependent on man's activities; either directly through water management or indirectly through grazing by domestic animals. The dominance of *R. calcareus* in chalk streams is almost certainly due to the regular cutting that has been practized for hundreds of years. The very patchy and illogical distribution of vegetation on many river banks is probably related to the growth of mutually exclusive clones from fragments dispersed by dredging.

5. VEGETATION DYNAMICS

Short-term instability is a characteristic of river vegetation. Records of the occupation of particular sites often show frequent changes in species and biomass (Butcher 1933, Hoogers, Weij 1971, Ladle, Casey 1971) which arise from constant interactions between seasons, flow, sediments and plant species.

The example discussed by Ladle, Casey (1971) is particularly useful. At the end of winter a typical shallow chalk stream has much exposed gravel with scattered clumps of *Ranunculus calcareus*. These thicken and spread and by May many have reached the surface and are beginning to accumulate sediments. Seedlings and drifting pieces of *Rorippa nasturtium-aquaticum* establish in these regions of reduced velocity, along the edges and in midstream, as the flow of the river decreases. The Ranunculus becomes weakened by the reduced velocities and the shading of the emergent Rorippa and starts to die except at the edges of the weed beds, where the flow is concentrated in narrow channels of fast water with gravel bottoms. After the Ranunculus dies the Rorippa is only held by small roots in soft sediments and, weakened by autumn frosts, autumn floods can easily dislodge the buoyant plants. Finally the bare gravel is exposed, generally where Ranunculus was growing the year before, and the new patches of Ranunculus are distributed along the edges of the summer channels.

The success of such communities is dependent on adaptations of the species to exploit instability. If Rorippa had a more efficient rooting system the sediment deposits would become stabilized and colonized by species starting growth earlier in the year than Rorippa, and they would then eliminate the Rorippa from the community.

6. SUMMARY

Communities of plants in flowing waters contain a range of characteristic growth forms which are closely correlated with water velocity. Their specific composition and productivity is governed by a complex of inter-related factors but particular factors can be recognized as more important at different levels of the study of their distribution in time and space.

On the widest regional basis the distribution of species is primarily governed by temperature and dispersal problems. Even on a much smaller scale dispersal problems can limit the occurrence of species to a restricted number of the possible habitats.

Within a region the general chemical nature of the waters selects ranges of species which may flourish, and within a water type further restrictions on the distribution of species are imposed by spates and water velocity, irradiance (shading, turbidity and depth), management, pollution and sediments. The detailed distribution is often an unstable mosaic but a regular pattern in time often develops from the interactions of the plants and flow.

These factors also affect the productivity of sites. Irradiance and temperature are nearly always partially limiting. Carbon supply may be important in slow, well-lit waters, rich in mineral nutrients, but these nutrients may be more important in poor waters. Physical damage reduces the relative growth rate.

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	41—50	1973

W. SZCZEPAŃSKA and A. SZCZEPAŃSKI

EMERGENT MACROPHYTES AND THEIR ROLE IN WETLAND ECOSYSTEMS

Department of Applied Limnology, Institute of Ecology, Polish Academy of Sciences,
Świerczewskiego 14, 11-730 Mikołajki near Mrągowo, Poland

ABSTRACT

The role of various external factors in controlling the helophyte production was discussed as well as both intra- and interspecific interactions. It has been found that reed is susceptible to influence of other helophytes, the response being the production decrease or even retreat from other species. Preliminary results of investigations on allelopathy were presented. Both pathways and mechanisms of return of allelopathic substances, nutrients and metabolites to environment were discussed.

Plants inhabiting any biotope are in very close contact with the surrounding environment. This contact is directed both from the environment to the plants, as plants get from the environment all materials necessary for their life, and from the plants to the environment, as plants give to the environment many products of their life processes. Generally speaking, plants modify the landscape to a large extent. This modification and influence on the environment has a dual character. The exchange and transformation of energy is of the order of tonnes per ha per year. The transpiration of a reed stand is for an example 3—10 thousands of tonnes per ha per year, $1.6 \cdot 10^{12}$—$5.5 \cdot 10^{12}$ cal/ha/year. The photosynthesis is of the order of $1.6 \cdot 10^{10}$ cal/ha/year, i.e. about 45 t/ha/year. The decomposition is of the same order as the production and thus disperses this energy.

The second part of this dependence with the environment is the exchange and transformation of "information". Organic substances stimulate processes at the cellular level as particular molecules, and on the level of plants in picomicrograms. Their main task is the steering and informing, and they are not important in the balance of masses. These substances are the hormones acting within plants, and pheromones and allomones acting between plants (Whittaker, Feeny 1971). Studies on these substances were possible only after the development of such analytical methods as gas chromatography or mass spectrography.

There is no boundary between these types of contact of plants with environment. There is a continuum of transpiration water, CO_2, assimilation water and so on at one end of the range, and a small substances and phytoncydes at the other one.

All these factors influence plant life and production. Therefore, for the estimation of their influence, it is necessary to study production without the added complication of variable external biotic factors. The influence of internal and allelopathic biotic factors can be noticed only in such situation.

There is not much data on the dependence of production on the environmental conditions. The data on the production in natural environments are dependent on the whole complex of factors, thus they are of limited significance for this particular problem. More evidence comes from culture experiments, but there are only a few of those.

The culture experiments from our laboratory, are the basis for this discussion of biotic dependences. Most observations were made on common reed (*Phragmites communis* Trin.), so the conclusions are valid only for this species, and cannot be applied to other plants without further investigations.

Common reed is an eurytopic plant with very few specific habitat requirements, and it is very tolerant of unfavourable conditions. Its development and production is most probably summarized as production dependent on the environmental capacity. The development is proportional to the fertility of environment, and in the experimental conditions with limited fertility the reed has a low potential maximum level (Fig. 1). Reed plants grown from seed reach 130 cm on eutrophic mud,

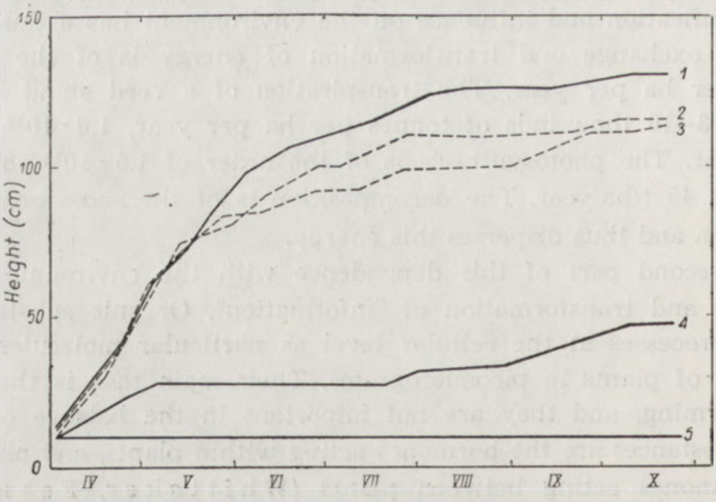

Fig. 1. Growth rate of *Phragmites communis* on different soils. 1 — lake mud, 2 — mud+bog peat, 3 — mud+sand, 4 — sand, 5 — bog peat

several milimeters on a peat soil, about 40 cm on a washed sand from lake littoral, and about 110 cm on a mixture of mud, sand and peat. Growth of reed seedlings cultivated on a poor substratum can be inhibited. Translocation of such seedlings to better conditions or enriching their substratum permite further growth.

Szczepańska (1973) obtained similar patterns of reed production (Fig. 2) when investigating mutual influences of aquatic plants.

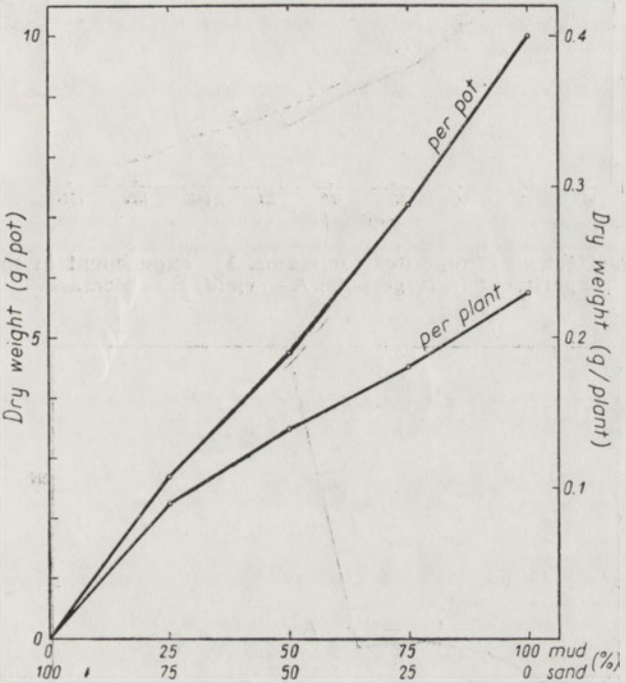

Fig. 2. Growth of *Phragmites communis* on mixed soils (mud+sand)

Here, there is an obvious dependence of production on the environment fertility. It was also found that production is not limited by the total level of fertility, but by the quantity of nutrients available for each individual. Using various densities of sowing in pots, plant size was inversely proportional to the sowing density, but total biomass per unit of soil volume was nearly the same and not dependent on the pot volume (Fig. 3). This was also found for *Typha latifolia*, although some tests were anomalous (Fig. 4).

It can be thus stated with considerable probability that there is intraspecific competition among macrophytes for nutrients in short supply, and that autoinhibition occurs rather seldom (McNaughton 1968).

It was not possible to determine the minimum density for intraspecific competition, as competition affected production even with only

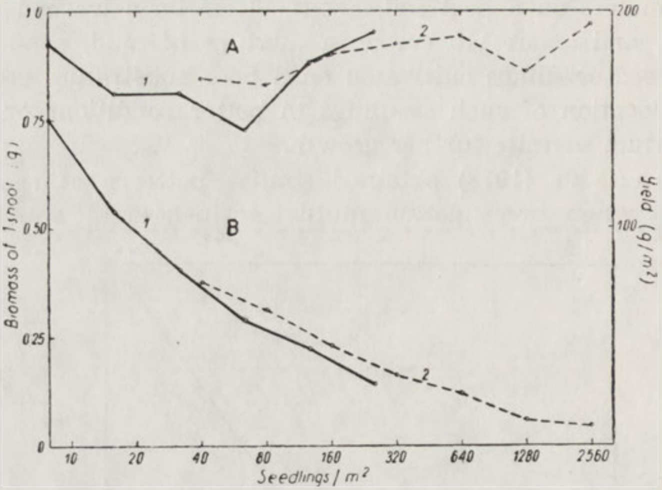

Fig. 3. Crowding effect on *Phragmites communis*. 1 — experiment in small pots, 2 — experiment in large pots. A — yield, B — biomass

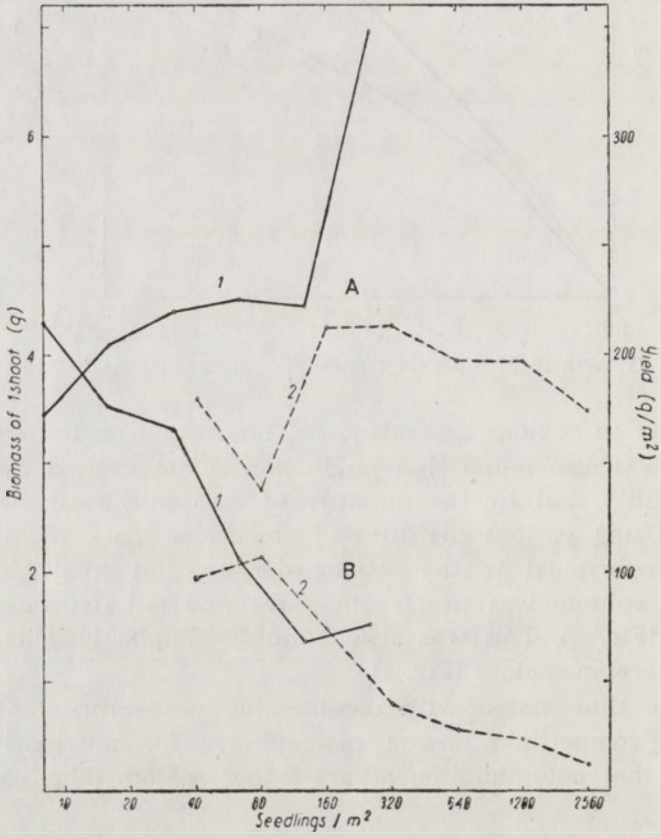

Fig. 4. Crowding effect on *Typha latifolia*. 1 — experiment in small pots, 2 — experiment in large pots. A — yield, B — biomass

8 plants per m², which is much less than that occurring in the field (50 plants per m²).

The problems of the theory of plant competition were analysed by de Witt (1960) in his very interesting monograph. This author is mainly interested in field crops and production dependences among various species. However, he assumed a limitation for this theory for perenials with vegetative reproduction, stating that the growth of individuals do not influence neighbouring plants, and is not dependent on them. Such simplification, suitable for analysis of grain crops, excludes the interspecific competition which is a subject of our investigations.

The following possibilities can be expected when analysing the influence of plants on each other: mutual stimulation, mutual inhibition, inhibition and stimulation in the same time. In the last of these, the production of a mixed stand will increase or decrease as a result of the opposite processes, depending on the predomination of first or second possibility.

The pairs of species investigated by Szczepańska (1973) showed neither mutual stimulation nor inhibition. In all cases mutual growth one of the species increased relative to the other, but joint production was in 7 cases lower than that calculated theoretically from monospecific

Table I. Changes in production of plants competing with *Typha latifolia* as per cent of monospecific culture (=100%)

Species	*T. latifolia*	Competing species	Total production (%)
Acorus calamus	180	70	125
Glyceria aquatica	159	83	143
Phragmites communis	140	39	90
Equisetum limosum	139	68	103
Typha angustifolia	114	36	74
Carex sp.	112	84	98
Heleocharis palustris	54	123	89

Table II. Changes in production of plants competing with *Phragmites communis* as per cent of monospecific culture (=100%)

Species	*P. communis*	Competing species	Total production (%)
Carex Hudsoni	152	67	110
Glyceria aquatica	114	99	107
Carex acutiformis	105	84	94
Acorus calamus	100	124	112
Equisetum limosum	88	120	104
Heleocharis palustris	81	111	96
Schoenoplectus lacustris	63	149	106
Typha latifolia	39	140	90

cultures. In eight cases it was higher than the theoretical one (Table I and II).

Table I shows that *Typha latifolia* is a species relatively increasing in mixed stands. Only *Heleocharis palustris* can decrease its development. *Phragmites communis* usually develops worse than the other species with which it was grown. This possibly explains the frequent occurrence of common reed in monospecific stands. As reed has very small demands on the environment, it can grow in monospecific stands in our climatic-edaphic conditions unless the environment is greatly altered. When the habitat conditions allow other species to invade a reed stand, the rapid development of the other species eventually stops the growth of reed.

T. latifolia in such situation will tend to prevent the immigration of other species. This species tends to migrate into stands of other species.

This discussion should be treated as a hypothesis which needs further investigation, and not as a proved statement.

The mechanisms of the mutual influence of plants is still not known. The literature is very scarse, and it is almost lacking for aquatic macrophytes.

It is known that exudates of certain plants inhibit other plant species (Bleasdale 1956, Ralski, Makowiecki 1962, Muller 1966, Muller, Moral 1966, Tukey 1969 a, b, Plhák 1971 and others). The character and chemical composition of exudates are little known (Lerner, Evenari 1961, Chang, Bandurski 1964, Itai, Vaadia 1965, Richter et al. 1968). All these papers deal with terrestrial plants. There is a complete lack of data for wetland vegetation. The observations of allelopathy, i.e. of this kind of interspecific contacts, are in papers of McNaughton (1968), Szczepańska (1971), Szczepański (1971). We have started in our laboratory the research on isolation and identification of allelopathic substances. The work is still in progress and the obtained results are so far scarse.

The influence of extracts of various macrophytes on germination of *Lepidium sativum* was investigated. The germination of seeds of aquatic plants could not be used for a bioassay because of the difficulty of obtaining seeds of high viability, and of breaking dormancy in the case of reed.

Not all investigated macrophytes inhibit the germination of cress seeds. Species whose extracts show inhibition include Glyceria, Scirpus and Equisetum (Fig. 5). However, results showing no influence of particular species on cress germination are not valid for other plant species. Each species should be investigated separately. *Glyceria aquatica* has the strongest inhibiting effect on the germination of Lepidium. The other reason for choosing this species is that its hay is toxic for cattle

(Włodarczyk 1955). Haslam (1971) noted that Glyceria is one of the species with the strongest suppresive effect on Phragmites.

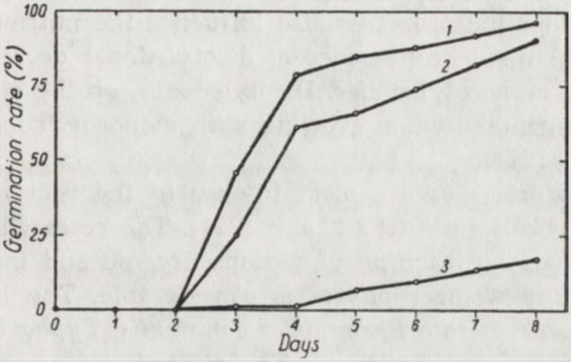

Fig. 5. Germination rate on *Lepidium sativum* on extracts of different plants: 1 — Equisetum, 2 — Scirpus, 3 — Glyceria

The isolation of the active substances is still incomplete. Now we can give only some introductory information. 1. Drying of plant material do not stop activity of the active substance (SA). 2. Heating up to 100°C do not stop activity of SA. 3. SA can solve in polar solvents (water, acetone, methanol, ethanol). 4. SA do not solve in nonpolar solvents (petrol ether, benzin, chlorophorm, methylen chloride, hexane). 5. The smell of almonds accompanies the SA in fractions from chromatography column with silica gel. It is known that Glyceria contains cyanide glycosides. We do not know whether these compounds are the SA whether they are accompanying inactive substances. 6. The chromatographic separation on paper or sephadex shows that apart from the main SA there are at least two other compounds with inhibiting properties, although they are in much smaller quantities. 7. SA occurs in water from mud collected at the Glyceria stands. However, its quantity is low in comparison that found in plants.

The allelopathic substances can occur outside the plant, by being actively excreted or by passively dissolving in water, or by being the products of plant decomposition (Goatley, Lewis 1966, Muller 1966, Tukey 1969 a, Clarke, Humphreys 1970, Grodziński 1970).

Apart from the volatile substances of the terpene type (Muller, Moral 1966), various organic and inorganic substances are leached from plants by atmospheric falls and fog (Tukey, Tukey 1962, Tukey 1970). In this way plants can manage the cations and remove some metabolites accumulated on the leaf surfaces (Mecklenburg et al. 1966). The quantities of substances leached in this way are strikingly high. Bhan et al. (1959) found that 24 hr of rain leaches 8% of K and 15% of Mg content from banana leaves. The problem of nutrient circulation in plants was shown a long time ago (Buchenau 1883), but because of inadequate methods, results were dubious. Recently the introduction of isotopic techniques permitted the detailed study of this problem. The allelopathic processes also influence the nutrient management of competing plants. The presence of dicotyledones decreases the potassium intake by monocotyledones. Dicotyledones, on the other hand, have a lower calcium intake when growing with monocotyledones (Daftardar, Savant 1971).

Allelopathic processes are most intense in the root system and the active part of rhizosphere (Haslam 1971). The research in our laboratory showed that the leaching of various organic and inorganic compounds from emergent macrophytes is considerable. The leaching of nutrients was observed from *Phragmites communis, Typha latifolia, Glyceria aquatica, Alnus sp., Salix sp.* The subject of leaching are PO_4^{---}, $N\text{-}NH_4^-$, $N\text{-}NO_3^-$, N org., Ca^{++}, K^+, Na^+ and the organic compounds.

Similarly, about 6.0 mg of K is leached from 1 m² of a reed stand. This process is within certain limits, proportional to the period of leaching. Long lasting rains cause greater leaching than short-term storms, although the rate of precipitation is larger in the latter. The length of time between storms influences the quantities which can be leached on any one occasion. A one day break between rains is enough to allow measurable leaching during the next rain. Substances are more easily leached from Glyceria than from reed, and its leaves are more easily moistened. Not all substances are leached at the same rate. Potassium and phosphates are leached the quickest — during several minutes.

Aphids influence the character and quantity of leached substances. Reed leaves infected with aphids released more salts than non-infected ones: 2—3.5 times more potassium, above 3 times more ammonium nitrogen, about 50 times more phosphates and 2—4 times more organic compounds. If honeydew, faecals and exuvia of aphids are added to the above figures, then the total losses are clearly significant in the plant nutrient budget.

There is one more way of releasing nutrients from plants — through the transpiration stream. Nemeriuk (1970) found, when analysing this phenomenon, that 1 l of transpired water contained 6—19 mg of ions ($Ca > Na > Mg > K > HCO_3 > SO_4 > Cl$). The figures were derived from investigations on several species of terrestrial plants. If the same order of magnitude is applied to aquatic macrophytes, then a square meter of a reed stand releases 3 g of ions during the vegetative season.

The terrestrial plants lose nutrients through leaching which are thus returned to the earth, where they collect. Emergent macrophytes release the nutrients to water, enriching it in this way. Littoral plankton and periphyton grow in these nutrients. It should be also remembered that emergents get nutrients from the soil and interstitial water, but leaching and decomposition move the nutrients to the water.

The antagonism among the emergents and the algae have an allelopathic character. Among the submerged macrophytes and algae there is a possible allelopathic influence, and a very severe competition for nutrients (Fitzgerald 1969).

Taking into the consideration all possible ways of leaching of various substances from living plants we see that plants have ways of allelopathic influence at their disposal. Also the significance of macrophytes in the formation of biological relationships and in the circulation of nutrients is more important that generally accepted.

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W. SZCZEPAŃSKA

PRODUCTION OF HELOPHYTES IN DIFFERENT TYPES OF LAKES

Department of Applied Limnology, Institute of Ecology, Polish Academy of Sciences, Świerczewskiego 14, 11-730 Mikołajki near Mrągowo, Poland

ABSTRACT

Species composition of rushes in Suwalki Lakeland is more diversified than that in Mazurian Lakeland. The less diversified rushes in both lakelands are those in eutrophic lakes. In Mazurian Lakeland, biomass of rushes plants increases from mesotrophic to pond-like lakes and in the latter it is twice as high as in the former. In Suwalki Lakeland, it is lesser in pond-like lakes than in mesotrophic ones. The lowest biomass was found in eutrophic lakes. Biomasses were more differentiated within the limits of the same lake type than between various lake types. *Schoenoplectus lacustris* in mixed communities was of somewhat higher individual weight than that in pure belts. Individual weight of *Typha angustifolia* was higher in pure than in mixed belts.

1. INTRODUCTION

The role of vascular plants in a lake is of different significance. In some lakes, all the processes occurring in a water body are depending on vascular plants, in other ones their role is minimal. It depends on different factors among which the most important are morphometry of a water body and fecundity of both water and soil.

According to Bernatowicz (1971), 9–12% of lakes area in Poland are overgrown with emergent plants, and 18–28% — with submersed ones. About 1/3 of all the lakes area is overgrown with plants. Bernatowicz et al. (1968) indicated that productivity of macrophytes cannot be ignored when an energetic balance of a lake is estimated. Rich et al. (1971) calculated 48.3% of primary production in Lake Lawrence being produced by macrophytes.

Both species compositions in lakes and species biomasses are very differentiated. In littoral of some lakes, there is only one plant species, mostly reed; other lakes are characterized by diversified species composition. It is interesting whether such a situation is connected with a type of a lake or not.

The aim of the present paper was to estimate macrophyte biomasses in different types of lakes in Suwalki Lakeland and Mazurian Lakeland.

The paper is a part of the complex researches on macrophyte production in the mentioned lakelands. It concerns the production of reed-belts containing more than 10% of biomass of plants associating with reed as well as the production of the other rushes plants vegetating purely and/or in communities. Data on production of pure reed-belts will be presented in Szajnowski (1973).

2. MATERIAL AND METHODS

In the selected sampling places, at depth of 0.5 m, there were 0.25 m² areas separated with the respective frame, of which all the plants were cut at the same bottom. A sample was plant material taken from 3 frames of Suwalki Lakeland and of 5 frames of Mazurian Lakeland. In the field laboratory, samples were classified among species groups, dried for 48 hr at 84°C (Project Phragmites 1969) and weighed.

Typological data on the lakes were taken from Stangenberg (1936, 1937), Olszewski, Paschalski (1959) and completed with data of investigations made in Department of Applied Limnology (unpublished).

30 lakes were investigated; 14 sampling places were in mesotrophic lakes, 34 in eutrophic and 14 in pond-like lakes. In Suwalki Lakeland, the material was sampled from 26 sampling places in July 1967, and in Mazurian Lakeland — from 36 sampling places in August–October 1969.

3. RESULTS

33 species characteristic for mid-European lowland rushes were found in the investigated lakelands (Table I). None of these species vegetates at the border of its occurrence range. In Suwalki Lakeland 29 species were

Table I. Species found in rushes of Suwalki and Mazurian Lakelands

Species	Lakeland					
	Suwalki			Mazurian		
	Meso-trophic	Eutro-phic	Pond-like	Meso-trophic	Eutro-phic	Pond-like
Acorus calamus L.	+	+	+			
Batrachium circinatum (Sibth) Hbr			+			
Carex rostrata L.	+	+	+			
Carex sp.			+		+	
Ceratophyllum demersum L.	+					
Chara sp.	+		+		+	
Cladium mariscus (L.) Pohl.		+				
Elodea canadensis Rich.	+		+			
Equisetum limosum L.	+	+	+		+	+
Fontinalis sp.	+	+	+		+	
Glyceria aquatica (L.) Wahlb.					+	
Heleocharis palustris (L.) R. Sch.	+				+	
Hydrocharis morsus-ranae L.		+	+	+		+
Juncus sp.					+	
Lemna trisulca L.	+		+		+	
Myriophyllum spicatum L.	+		+			
Myriophyllum verticillatum L.		+	+			
Nymphea alba L.		+	+			
Nuphar luteum (L.) Sm.	+		+	+	+	+
Phalaris arundinacea L.				+		
Phragmites communis Trin.	+	+	+	+	+	+
Potamogeton natans L.	+	+		+	+	
Potamogeton lucens L.	+					
Potamogeton perfoliatus L.		+			+	
Potamogeton sp.			+		+	
Ranunculus linqua L.	+		+			
Sagittaria sagittifolia L.			+			
Schoenoplectus lacustris (L.) Palla	+	+	+	+	+	+
Sparganium ramosum Huds.	+		+		+	+
Stratiotes aloides L.	+					
Typha angustifolia L.	+		+	+	+	+
Typha latifolia L.					+	
Utricularis vulgaris L.	+	+	+			

found, and in Mazurian — 19 species. 15 species were common for both lakelands. The environments of Suwalki Lakeland are more differentiated — there occurred more species, and more species in one sample were found: up to 10 (up to 6 in those of Mazurian Lakeland). Frequency of samples with different numbers of species from both lakelands is compared in Fig. 1. In Mazurian Lakeland, as far as 45% of samples came from monospecies rushes, 28% — from bi-species rushes, and only 27% of samples contained three or more species, while in Suwalki Lakeland all the samples contained at least 3 species. The greater floristic diversity of rushes in Suwalki Lakeland shows its connection with a lake type. On the average, in rushes of mesotrophic lakes in Suwalki Lakeland 5.3 species were found, of eutrophic lakes — 3.4 species, and of pond-like lakes — 6.8 species. The respective figures for Mazurian Lakeland are 2.3, 2.0 and 2.0 species. In Suwalki Lakeland, only in eutrophic lakes were small numbers of species, while in Mazurian Lakeland all the types of lakes were such in this respect.

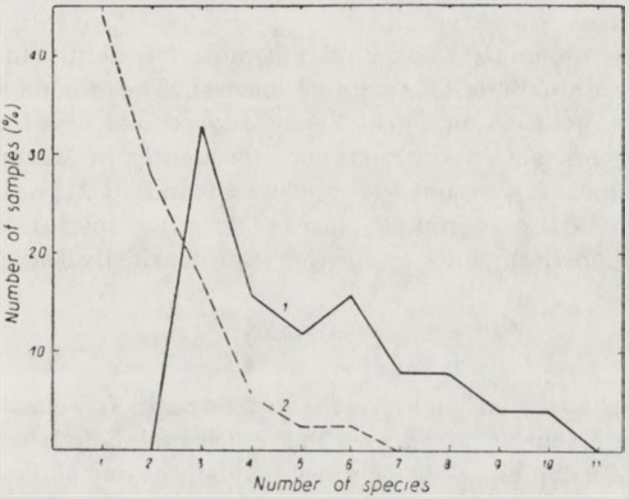

Fig. 1. Frequency distribution of samples with different number of species. 1 — Suwalki Lakeland, 2 — Mazurian Lakeland

The greatest biomass of rushes in Suwalki Lakeland was found in mesotrophic Lake Wigry (984 g/m²), while in Mazurian Lakeland — in pond-like Lake Szymon (1620 g/m²). Comparison of mean biomasses of various lake types (Table II) indicates that in Mazurian Lakeland they are more differentiated than those in Suwalki. The respective coefficients of variability are 30.8 and 16.1%. The biomass of rushes of mesotrophic lakes is the lowest in Mazurian Lakeland, and the highest in Suwalki Lakeland; and that of the latter is the lowest in eutrophic lakes (Table II).

The coefficients of variability of biomass within the limits of the same lake type are rather high: 42–57.6%. Thus they are significantly higher than those of various lake types, above discussed, what clearly pointed out the material being markedly differentiated. Height of the coefficient is not clearly influenced by the number of samples since even in the most numerous group — Mazurian eutrophic lakes — it is 52%.

Table II. The biomasses of rushes in various lake types

Lake type	Biomass (g/m²)	
	Suwalki	Mazurian
Mesotrophic	600	453
Eutrophic	437	590
Pond-like	565	834
Coefficient of variability (%)	16.1	30.8

Phragmites communis was found the most frequently in all the investigated lakes (in 60% of sampling places). The second place takes *Schoenoplectus lacustris* (in 40%). *Typha angustifolia* was found in 30% of sampling places, but it occurred more frequently in Mazurian than in Suwalki Lakeland. *Equisetum limosum* was found in 21%, and *Phalaris arundinacea* in 12% of sampling places. The other species, which vegetate mostly in small amounts in rushes, were markedly less frequent.

Phragmites communis Trin.

It is more shapely in Mazurian than in Suwalki Lakeland. Maximum weight of one Mazurian stalk was 38.1 g (Skonał Lake), while that of Suwalki — 21.4 g (Iłgiel Lake). The mean weight of one stalk of Mazurian eutrophic lakes was 16.6 g, and that of Suwalki – 10.5 g. Szajnowski (1973) found also great differences in reed biomasses when investigating the material coming from pure reed-belts: in Mazurian Lakeland, in 1969 biomass was 165% (1502 g air dried weight/m²) of that in Suwalki Lakeland (910 g/m²); in 1970 it was even 180% comparing with that in Suwalki.

Schoenoplectus lacustris (L). Palla

In pure belt, biomass of *S. lacustris* was 225–453 g/m², on the average 339 g/m². Mean dry weight of one shoot was 1.93 g, and mean height was 164 cm. In mixed communities, mean dry weight of one shoot was 2.34 g, and mean height — 171 cm. A dependence between biomass and substratum type was observed: *S. lacustris* grew best on soft substratum with great amount of organic debris. In such soil conditions dry weight of shoot was up to 4.58 g, and height — 212 cm.

Typha angustifolia L.

In pure belt, biomass of *T. angustifolia* was 480—1620 g/m², on the average 1026 g/m². Mean weight of one shoot was 21.1 g and maximum weight — 27.5 g. Maximum biomass of one shoot in mixed communities was up to 31 g; it was not stated, however, that *T. angustifolia* in mixed communities had usually greater biomasses. It should be emphasized that both maximum and minimum biomasses of *T. angustifolia* in pure belts were found in plaures of a pond-like lake.

Equisetum limosum L.

Dry weight of one shoot was found to be 0.98–3.27 g. *E. limosum* occurred in all the types of lakes, somewhat more frequently in Suwalki Lakeland. Clear dependence on substratum was not observed; it grew both on mud and on dense, sandy soil, more frequently on the latter.

4. DISCUSSION

There is a rich literature on productivity of rushes in particular lakes, but no physiographical elaborations nor papers on limnological types of lakes. Most of phytosociological descriptions do not comprise data on macrophyte production.

High variability of the presented material makes interpretation difficult. Probably this variability reflects the situation in nature, since increase of the number of samples does not decrease the coefficient of variability. (It was 46% at 4 replications, 42% at 10, and 52% at 27). Apart of these restrictions, the material is sufficient to conclude about production of rushes in the investigated lake types.

Occurrence frequencies of rushes species recorded in the present paper is similar to those observed by Bernatowicz, Radziej (1964) in Mamry Lake complex, where predominating species were *Phragmites communis, Schoenoplectus lacustris,* and *Typha angustifolia.* Dąmbska (1961) found somewhat different arrangement when investigating phytosociology of lake communities in Pomerania: *Schoenoplectus lacustris, Phragmites communis, Glyceria aquatica* and *Typha angustifolia* were predominating species, and *Sparganium ramosum* was very frequent. Kępczyński (1960) found even more differentiated arrangement in rushes communities in Skępskie Lakes: *Phragmites communis* and *Scho-*

enoplectus lacustris were also predominating, but *Typha angustifolia*, the fourth species in Dąmbska (1961) and the third one in the present paper was only the thirteenth. *Equisetum limosum* was the third species there. Certainly, direct comparisons of occurrence frequencies of plants, found in the three regions, are not possible to be done due to very differentiated areas investigated. However, it is permissible to compare the sequences of species as to their frequency. Thus in rushes from various lakelands, *Phragmites communis* and *Schoenoplectus lacustris* were the most typical species, and the other were *Glyceria aquatica, Typha angustifolia, Sparganium ramosum* in Pomerania (Dąmbska 1961), and *Equisetum limosum, Phalaris arundinacea* in Skępskie Lakes (Kępczyński 1960).

Small amounts of species forming rushes communities in eutrophic lakes, observed in the present paper, were stated in the other papers, too. Dąmbska (1961) stated the poor or extremely poor species compositions in rushes of eutrophic lakes (mean deep lakes in her definition) comparing with pond-like lakes (shallow, muddy lakes — as above) and mesotrophic lakes. It would be interesting to find the reasons of the observed species monotony.

In the Mazurian Lakeland, there were great differences in production between particular lake types: in pond-like lakes it is twice as high as in mesotrophic lakes. In Suwalki Lakeland, such differences are low, and a differentiating factor is number of species in a community.

Statistical analyses showed that the presented material was not sufficient to explain the relationships between the production and the number of species in a community. But non-existence of such a relationship cannot be excluded.

Szczepańska (1971) found experimentally that the biomass of *Typha latifolia* cultivated together with *Phragmites communis* was higher than in the monoculture. In field investigations, it was found that individual biomasses of *Typha angustifolia* were higher in mixed than in pure belts. However, both an arithmetic mean and a median calculated for individual weights of *Typha angustifolia* vegetating in a pure belt ($\bar{X}=21.1$ g, $\bar{M}=20.6$ g) were higher than those in a mixed belt ($\bar{X}=17.6$ g, $\bar{M}=15.6$ g). The differences are 20% for the arithmetic mean and 32% for the median, the latter being the more representative value. It should be indicated that *Typha latifolia,* the species investigated in experimental cultures (Szczepańska 1971), was found only sporadically in the presented material, in amounts insufficient to be interpreted.

Schoenoplectus lacustris was another species, dependence of which on associating species has been found. Mean weights of one shoot is higher by about 17% when it vegetates in a mixed community. In other species such dependences were not found.

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K. FIALA

GROWTH AND PRODUCTION OF UNDERGROUND ORGANS OF *TYPHA ANGUSTIFOLIA* L., *TYPHA LATIFOLIA* L. AND *PHRAGMITES COMMUNIS* TRIN.

Department of Botany, Czechoslovak Academy of Sciences, Stará 18, Brno, Czechoslovakia

ABSTRACT

The seasonal changes in the rate of dry weight increase in underground organs of both *Typha angustifolia* and *Typha latifolia* are characterized by two maxima: one occurs in July to early August, the other takes place in late September and October. In Phragmites, the habitat influences apparently the rate of both total underground and rhizome dry matter production as well as the distribution of the biomass into different kinds of organs. A close relationship was found between the number of rhizome sections observed in a soil profile wall (at −30 to −70 cm) and the rhizome biomass of Phragmites.

1. MATERIAL AND METHODS

During 1969 and 1970, small polycormones (see Pénzes 1960) of *Typha angustifolia, T. latifolia* and *Phragmites communis* were cultivated in small shallow fishponds near Hlohovec and Lednice in southern Moravia (48°50′N, 16°48′E, altitude 175 m). Before planting the seedlings from which the small polycormones were started, 1 mm mesh diameter silon nets (supported by polythene sheets), 1 to 9 m^2 in area, had been buried in the mud 10 to 20 cm below the bottom level. The silon net facilitated the extraction of rhizomes and roots from the mud during the harvest. Each of five consecutive destructive harvests during the first growing season comprised 4 to 5 *Typha angustifolia,* 3 *T. latifolia* and 3 *Phragmites communis* polycormones. During the second cultivation period only three harvests were performed, consisting of 3 to 4 *Typha angustifolia* and 2 to 3 *T. latifolia* polycormones, each polycormone being treated as a separate replicate (see Fiala 1970 b, 1971 b).

Eight stands of *Phragmites communis* were investigated at seven sites which were situated in the littoral zones of managed fishponds, in marshes, on flooded arable land and in swampy backwaters in three regions of Czechoslovakia (southern Bohemia, southern Moravia and southern Slovakia). Methods of assessing the biomass, rhizome density and characteristics of habitats are described by Fiala 1970 a, and in print).

The changes in the reserve content in rhizomes of Phragmites of various age were studied in a polycormone at the northern shore of the Nesyt fishpond at the end of the 1971 growing season. The upper part (about to 50 cm under the bottom level) of 4 to 5 rhizomes of the same age, carrying terminal aerial shoots, was analysed. For the determination of total carbohydrate content, fresh rhizomes were extracted for 3 hr with 2% HCl and the photometric method of Nelson (1944) was used. The volume of rhizomes was estimated in a gauged glass cylinder (see Jeník 1954).

2. RESULTS AND DISCUSSION

The seasonal growth of underground organs in both *Typha angustifolia* and *T. latifolia* is characterized by two periods with high rate of dry weight increase: one is high summer from July to early August (in Central Europe), when the leaf area reaches the largest values (see Květ et al. 1969, Květ 1971 and Van der Valk, Bliss 1971), and the other is autumn from late September to October. The former period is marked by great increments in rhizome biomass, while the latter period is characterized by the accumulation of reserves in underground organs. The relative growth rate (RGR) of underground shoot bases, rhizomes and roots shows just one summer maximum, while the autumn maximum occurs only in the roots (for more details see Fiala 1971 a, b).

For the growth of both underground and aerial organs of the species under study, not only the biomass increments of new rhizomes but also the shift of reserves to older parts of the rhizome system are significant. They are also typical for other perennial plants (see Iwaki, Midorikawa 1968, Iwaki et al. 1969, Mutoh et al. 1968). The seasonal changes of bulk density (dry weight/fresh volume) in both new and old (living) rhizomes of *T. latifolia, T. angustifolia* and *P. communis* are shown in Fig. 1 and 2. The species of the genus Typha are characterized by an approximately two-year growing cycle. In the course of the second growing season, most of the shoots are fertile and the rhizomes of the same age connecting these shoots are dead at the end of their second growing season (see also Westlake 1968, Dykyjová 1971 c). Only a part of both the rhizomes and shoots which grew at the end of the

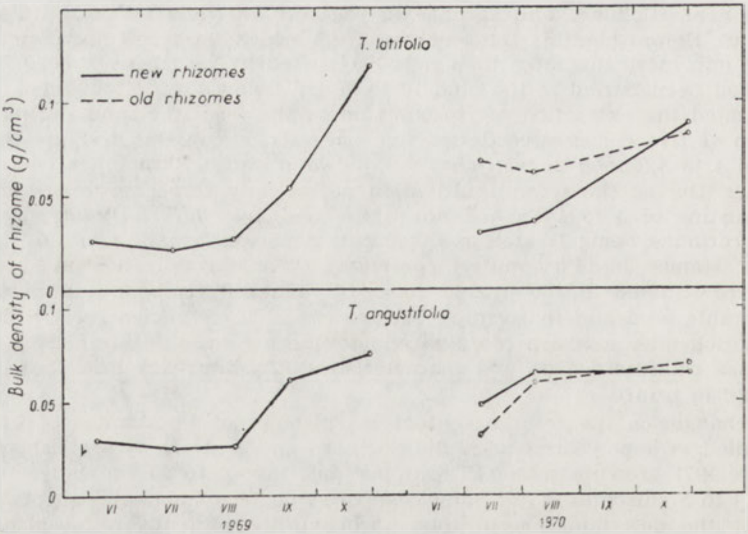

Fig. 1. Changes of bulk density (dry weight/fresh volume) in new and old living rhizomes of *Typha latifolia* and *Typha angustifolia* during the first (1969) and second (1970) seasons of cultivation

preceding growing season and are still sterile, survive the second growing season.

In most cases, the rhizomes of Phragmites live for more than three years (see Hürlimann 1951, Westlake 1965, 1968, Haslam 1970, Fiala in print). The changes in the carbohydrate content and bulk density in the rhizomes of different age are shown in Fig. 3. The critical period for the growth of the underground organs, especially for the formation of new rhizomes and lateral shoots, is the fourth growing season of the main rhizome carrying terminal aerial shoots (in the case of the Phragmites stand at the Nesyt fishpond).

A considerable decrease in the values of bulk density and carbohydrate content in the rhizomes of terminal shoots of Phragmites at the end

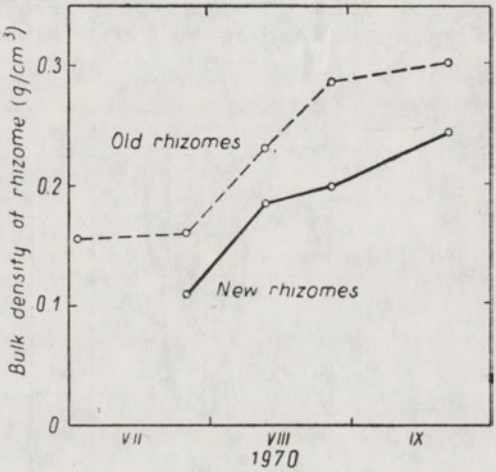

Fig. 2. Changes of bulk density (dry weight/fresh volume) in new and old living rhizomes of *Phragmites communis* during one season of cultivation (1970)

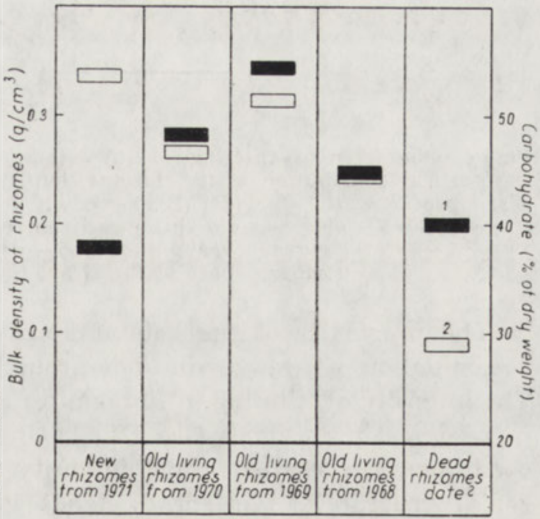

Fig. 3. Changes of bulk density (1) and total carbohydrate content (2) in rhizomes of various age of *Phragmites communis*. Recorded at the northern shore of the Nesyt fishpond in October 1971

of the fourth growing season is a sign of great mobilization of reserves from old rhizomes in spring of that growing season; on the other hand, it indicates a comparatively small storage in autumn. At the end of the third growing season, a great number of hibernating buds (lateral shoots for the next year, see Fig. 4 A) grow from the terminal and old lateral shoots. The lateral shoots of the fourth, and even the fifth, growing season are much thinner and shorter than the terminal and lateral shoots of the preceding years (see Kaikko 1934, Krasovsky 1962, Orekhovsky 1969, Haslam 1969). The irradiation conditions are worse, the shoots often die off; and the density of reed stands usually decreases in the second half of the growing season (see Květ et al. 1969, Květ 1971). At the end of the fourth growing season, the lateral buds for the fifth growing season grow only sporadically, and the rhizomes of the Phragmites stand at the Nesyt fishpond perhaps die off during the fifth growing season.

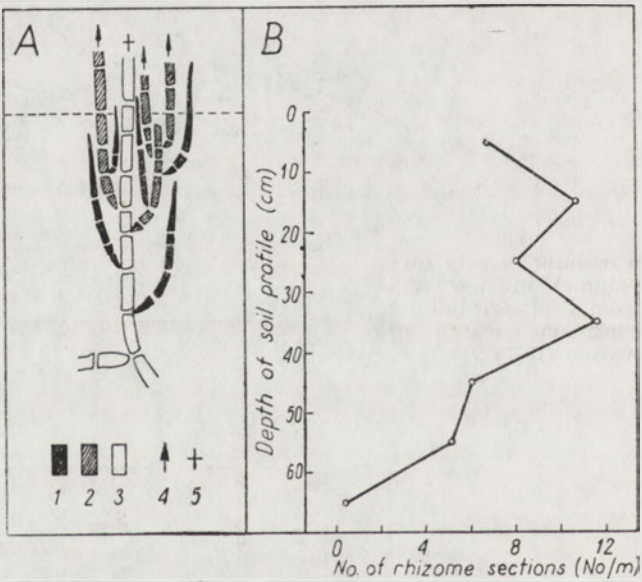

Fig. 4. Character of tillering in the stand of *Phragmites communis* (A) and the vertical distribution of its rhizome density (i.e. number of rhizome sections in a soil profile wall 1 m wide) (B). 1 — newly formed rhizomes and hibernating buds (from 1971), 2 — one-year old rhizomes (from 1970), 3 — two-year old rhizomes (from 1969), 4 — lateral current year's shoots, 5 — dead terminal shoots. Recorded at the northern shore of the Nesyt fishpond in October 1971

The properties of the habitat apparently influence the intensity of accumulation of reserves in underground organs (see Davidson 1969). The intensity of tillering in Phragmites is probably related to the amount of reserves in rhizomes (see Fiala in print). Under the given habitat conditions, the character and intensity of tillering determine the horizontal structure of Phragmites stands which is related to the amount of biomass both in the aerial and in the underground parts (see Ondok 1970, 1971, Fiala 1970 a). Phragmites stands with an extensive rhizome system, with a low rate of tillering, and with stems forming rather inconspicuous primary clusters (about 10 to 20 cm in diameter) on the one hand, and large clusters (about 3 m in diameter) on the other hand, produce a relatively smaller amount of rhizome biomass than stands which are characterized by highly conspicuous small clusters of stems (smaller than 160 cm in diameter). This results in a close relationship between the number of Phragmites rhizomes in the soil profile wall (in −30 to −70 cm layer, see Fig. 4B) and their biomass (see Fig. 5).

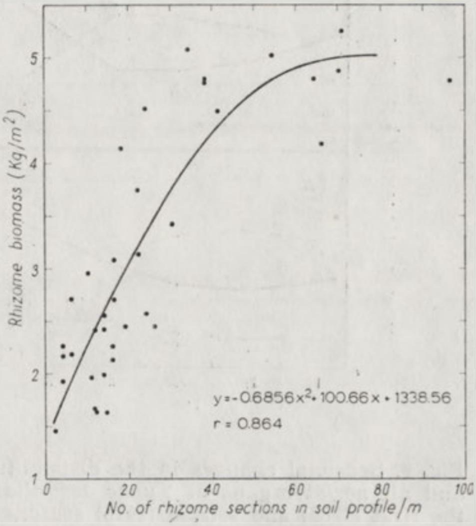

Fig. 5. The relationship between the number of rhizome sections encountered in a soil profile wall 1 m wide (at −30 to −70 cm) and the rhizome biomass of *Phragmites communis*. Recorded in 3 regions of Czechoslovakia (southern Bohemia, southern Moravia and southern Slovakia)

The biomass of the underground organs of Phragmites (produced in the course of several years) reflects differences between habitat properties much better than the shoot dry weight (Isambaev 1964, Krasovsky 1962, Rudescu et al. 1965, Fiala et al. 1968, Dykyjová, Květ 1970, Fiala 1970 a, Fiala, Květ 1971, Dykyjová 1971 a, b, Husák 1971, Schierup unpubl.). Great differences exist in dry matter distribution to various organs. The values of the rhizome dry weight/shoot dry weight ratio varied (in the Phragmites stands under study) in a relatively wide amplitude — approximately from 1.5 to 5.5. In eutrophic habitats, which in late summer passed to limosal to terrestrial ecophase, this ratio was lowest; in ecotopes with relatively balanced hydrological relations (the littoral ecophase only) it surpassed 3.0. The values of the root dry weight (in our case only from the 0 to −20 cm layer, representing about 70 to 80% of total root biomass) to shoot dry weight ratio varied from very low values (about 0.1) to about 4.5. The rate of dead root decomposition is probably one of the factors which cause great differences in root dry weight of various Phragmites stands.

As shown by the great differences in the dry weight of underground organs/shoot dry weight ratio in Phragmites, it is not possible to estimate underground biomass from aerial parts mechanically by using a value of this ratio.

Seasonal changes in dry weight distribution in individual underground organs and in all aerial parts of *Typha angustifolia* and *T. latifolia* polycormones during two cultivation seasons are summarized in Fig. 6.

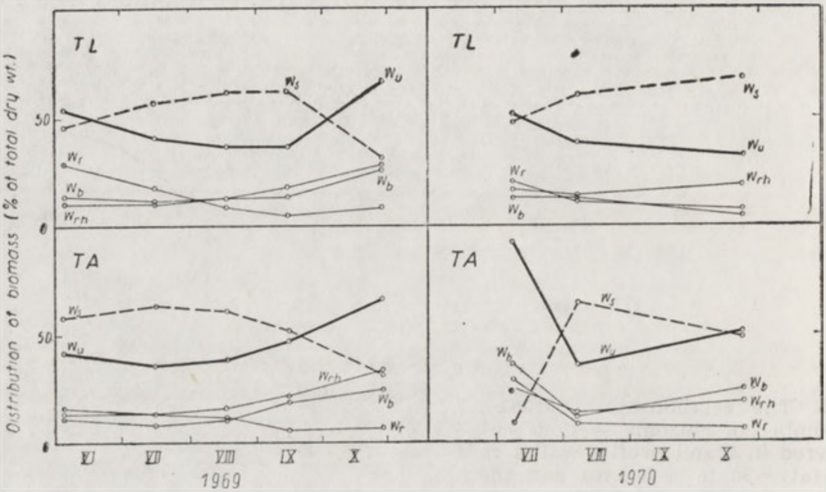

Fig. 6. Seasonal changes in the distribution of biomass into individual underground and all aerial organs of *Typha latifolia* (TL) and *Typha angustifolia* (TA) during the first (1969) and second (1970) seasons of cultivation. W_r — roots, W_{rh} — rhizomes, W_b — underground shoot bases, W_u — total underground, W_s — all aerial organs

In the first half of August (the first cultivation season), the total dry weight increment of underground organs reached about 60% of the production of aerial parts recorded in the same period. At the end of the first growing season, the annual net production was approximately twice as high as that of the aerial parts. The annual increment of underground organs amounted to about 90 and 30%, respectively, of the aerial shoot production in *Typha angustifolia* and *T. latifolia* at the end of the second cultivation season (for calculation see Iwaki et al. 1969). The results of the second year of cultivation are much closer to the relations in mature stands of Typha, for fertile shoots which were absent in the first year, make themselves felt in the dry weight of aerial parts.

The values of annual increments of Phragmites underground organ biomass will probably differ in different habitats. The estimation of the annual net production of rhizomes (obtained by dividing the living rhizome dry weight by their age), assessed in two different habitats, was approximately 60% in one stand (Nesyt fishpond) and only 30% in another (Šakvický fishpond), of the maximum biomass of aerial parts. The data obtained are only approximate; they reveal the complexity of the annual increment assessment of total underground organ biomass in *Phragmites communis* stands.

It may be expected, however, that in some stands the annual underground production of Typha and Phragmites stands reach higher values (see also Hejný 1960, Dykyjová et al. 1971, Westlake 1968, Szczepański 1969, Burian 1971, Van der Valk, Bliss 1971, Schierup unpubl., Fiala in print) than estimated for some terrestrial plant communities (see Iwaki, Midorikawa 1968).

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	67—71	1973

A. SZCZEPAŃSKI

CHLOROPHYLL IN THE ASSIMILATION PARTS OF HELOPHYTES

Department of Applied Limnology, Institute of Ecology, Polish Academy
of Sciences, Świerczewskiego 14, 11-730 Mikołajki near Mrągowo, Poland

ABSTRACT

Three types of arrangement of chlorophyll in assimilating parts of helophytes were distinguished: 1. The highest chlorophyll concentration near the leaf tip and even decrease downwards (Typha, Glyceria, Equisetum), 2. The highest concentration at 1/3 of the plant height and decrease both downwards and upwards (Acorus, Scirpus), 3. Almost even distribution in the whole leaf and little decrease only at the topical and basal parts (Phragmites). An importance of such a chlorophyll distribution for interpretation of biological productivity of helophytes was discussed.

The vertical stratification of the light climates in the natural productive system are similar, and independent on the kind of system.

The light conditions in waters of Wigry Lake (Stenz 1937), in crop fields (Ničiporović 1970) and in a layer of lungworts (Kershaw, Harris 1971) are of the same type apart from basic differences among the environments and the primary producers species forming the producers associations (Fig. 1—3).

Data on the light climate in a reed stand were given by Dyky-

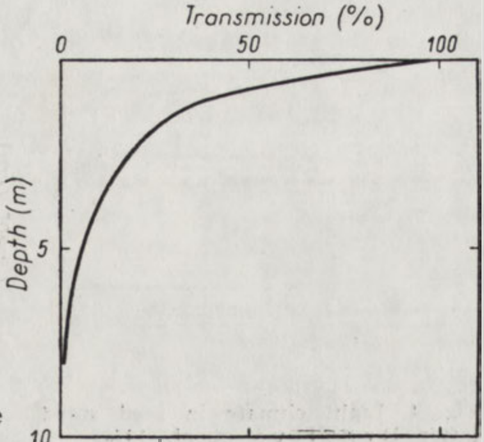

Fig. 1. Light transmission in Wigry Lake (after Stenz 1937)

jová et al. (1970). In their community the light climate is also the same (Fig. 4). It is obvious that a light climate patterned in this way leads to differentiation of other microclimatic factors. The significant life pro-

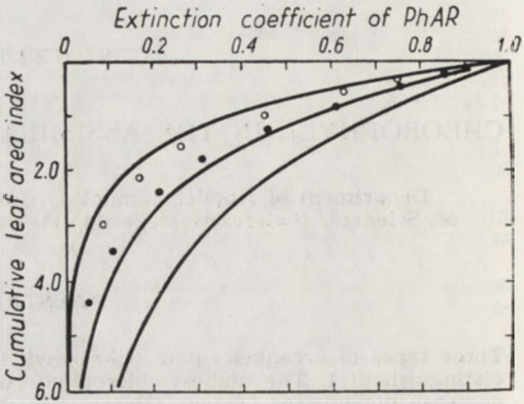

Fig. 2. Light climate in crop field (after **Ničiporović** 1970)

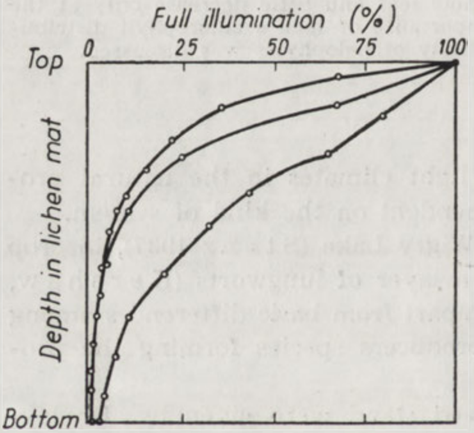

Fig. 3. Light climate in lichen mat (after **Kershaw, Harris** 1971 modified)

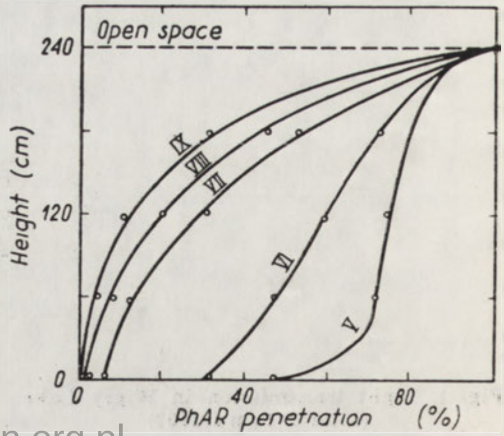

Fig. 4. Light climate in reed stand (after **Dykyjová** et al. 1970)

cesses of plants can also be supposed to be stratified in a similar way. This problem has not been much investigated previously and there are only a few papers dealing with it (Rychnovská 1967).

The activity and quantity of chlorophyll in different layers of a plant stand is one of the factors determining the primary production. Analysing this problem, we measured the quantity of chlorophyll in various parts of leaves or assimilating parts of several species of macrophytes dominant near Mikołajki. The chlorophyll content was determined spectrophotometrically from the acetone extracts of homogenized tissues and calculated per unit of fresh weight.

At least three types of arrangement of chlorophyll concentrations are found.

I. The highest concentration of chlorophyll is found near the leaf tip (apex). The chlorophyll quantity decreases evenly downwards, with a possible rapid decrease near the change to the leaf sheath. Typha, Glyceria and Equisetum among the plants investigated have this type of differentiation (Fig. 5).

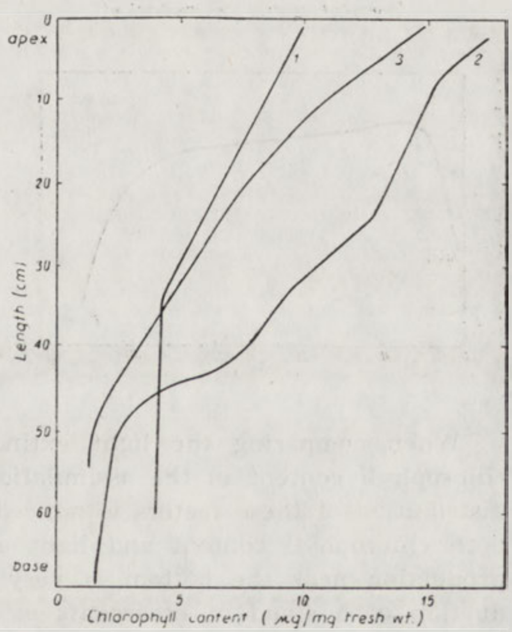

Fig. 5. Chlorophyll content in various helophytes. 1 — *Equisetum palustre*, 2 — *Glyceria aquatica*, 3 — *Typha angustifolia*

II. The highest concentrations are found at about 1/3 of the plant height. The chlorophyll quantity per unit fresh weight of leaf shoot decreases both downwards and upwards. This type was found for Acorus and Scirpus (Fig. 6).

III. The chlorophyll content is spread almost evenly, only the topical and basal parts having lower concentrations. Such a distribution was found in *Phragmites communis* (Fig. 7), which has a different spatial orientation of the leaves to the species mentioned above. Most reed leaves are more or less horizontal.

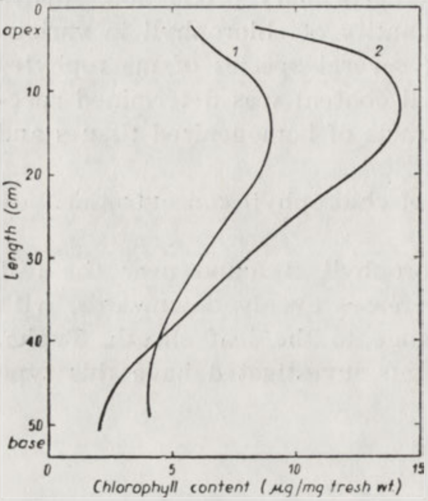

Fig. 6. Chlorophyll content in various helophytes. 1 — *Scirpus lacustris*, 2 — *Acorus calamus*

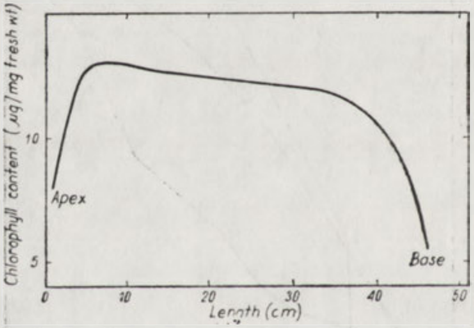

Fig. 7. Chlorophyll content in *Phragmites communis*

When comparing the light extinction in a reed stand with the chlorophyll content in the assimilation parts, a stricking similarity of distribution of these factors is noticed. In the lower part of the stand, both chlorophyll content and light are low. Thus the photosynthetic production near the bottom is very limited. Nearly the whole production of a stand of emergents is achieved in its upper part. This is also probably a reason why the lower leaves of common reed are lost in the middle of summer (Willer, Wodden 1943). These leaves are, by then, in low light and their production is less than their respiration. However, this problem should be carefully studied from the point of view of ecophysiology. It is worth stressing that reed leaves have nearly twice the chlorophyll concentration than the other plant species investigated.

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	73—75	1973

J. KRÓLIKOWSKA

TRANSPIRATION OF CERTAIN MACROPHYTES IN VARIOUS CONDITIONS[1]

Department of Applied Limnology, Institute of Ecology, Polish Academy of Sciences,
Świerczewskiego 14, 11-730 Mikołajki near Mrągowo, Poland

ABSTRACT

The studies concentrated at the estimation of transpiration of *Phragmites communis* Trin. in natural conditions and of *Typha latifolia* L. with the influence of herbicides 2,4-D-Na and MCPA. It was found that transpiration intensity of reed increases with the increase of air temperature and insolation and decreases with the increase of the relative air humidity, during a day. During the vegetation season, the maximum value of the transpiration was recorded at the end of July and the beginning of August. Transpiration of reed growing on land was lower than that growing in water. Leaves of reed without panicles transpired more than those with panicles. In the investigations with herbicides it was found that 2,4-D-Na and MCPA in high concentrations inhibited transpiration and growth of cattail, and decreased the chlorophyll and water contents in its leaves.

The studies of transpiration of *Phragmites communis* Trin. and *Typha latifolia* L. were carried out, as there is an increased interest in production and utilization of helophytes, and because the water budget of plants is strongly connected with their production. Both these species can be cultured in green houses, and therefore are convenient for the experiments.

The studies concentrated at the estimation of transpiration of Phragmites in natural conditions and transpiration of Typha in experimental conditions, i.e. with the influence of herbicides. These chemicals reach the waters with atmospheric falls and as a result of wind action.

The transpiration intensity of Phragmites was investigated on two sites: one in the littoral (in water) and the other one on the shore of Mikołajskie Lake, during the vegetation season of 1969. With help of a method of quick weighing the changes of transpiration during the

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[1] A summary. The full papers: Transpiration of reed (*Phragmites communis* Trin.). *Pol. Arch. Hydrobiol.*, 1971, 18, 347–358. Physiological effects of sodium salts of 2,4-D and MCPA on *Typha latifolia* L. *Pol. Arch. Hydrobiol.*, 1972, 19, 333–342.

season and during the day, the influence of panicles on leaf transpiration, and dependence of leaf transpiration on their age were determined.

It was found that the transpiration intensity of reed increases with the increase of the fresh weight of plant during the vegetation season. Transpiration increased till the middle of summer and later on decreased. The maximum value was recorded at the end of July and the beginning of August. Transpiration of reed growing on land was about 40% of the value obtained for reed growing in water, also the height of former was about 30% lower than the latter.

The transpiration of land reed during the day time was lower than of reed growing in the littoral (in water). Maximal transpiration was observed on both sites from 11 a. m. to 1 p. m. The transpiration intensity increased with the rise of temperature and insolation, and decreased with the increase of the relative air humidity. Night measurements did not show transpiration.

The parallel measurements of transpiration on plants with and without panicles were made and it was found that leaves of reed without panicles, the assimilation area of which was about 40% smaller, and fresh weight about 60% lower of plant with panicles, transpired 50% more than the flowering plants. It was also found that younger leaves in the upper part of plant have stronger transpiration than the older leaves in the lower part.

The investigated reed bed was infected with *Ustilago grandis* Fr. and the influence of this parasite fungus on transpiration was estimated. It was found that this fungus decreases the leaves transpiration about 50%.

It was calculated that a reed bed with a density of 54 plants per 1 m^2 (Szczepański unpubl.) can transpire during a day 2.23 kg of water per 1 m^2 of reed bed.

The investigations of *Typha latifolia* transpiration in the experimental conditions under the influence of commercially available popular herbicides "Pielik" and "Chwastox" were carried out in 1971. The active substances in these preparations are sodium salts of 2,4-D and MCPA. The changes of plant transpiration, chlorophyll and water content, and of plant growth caused by these chemicals were estimated. The chemicals were poured to the mud surface in plant pots. The investigated plants were sown on mud from eutrophic lake and cultured on it with constant water supply. Such application of herbicides is similar to the natural way of reaching the helophytes by herbicides.

It was found that 2,4-D stimulates the Typha transpiration in 24 hour from its application only during the period of intense growth of this plant at the beginning of the vegetation season. In other time the solutions of 2,4-D in concentrations 50, 500, and 5000 mg/l inhibited the transpiration 2, 14 and 28% respectively, as compared with control plants. The longer was the time of the influence of herbicides on plants, and the stronger was their solutions, the more inhibited was the transpiration intensity. The strongest concentrations of 2,4-D and MCPA decreased the transpiration in 61—72% as compared with the control after 192 hr of action. The cattail influenced by these herbicides changed its colour to yellow-grey already after 48 hr, began to loose turgor, and epignastic changes on its leaves. Plants withered after several days of treatment with the strongest concentrations of herbicides. The chlorophyll and water content in cattail leaves also decreased in the leaves in experimental conditions. The growth of cattail decreased about 70% as compared with control plants (after 8 days of treating with the solutions of 2,4-D and MCPA of 5 g/l concentration).

POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	77—78	1973

E. PIECZYŃSKA

THE FATE OF MACROPHYTE PRODUCTION IN LAKES [1]

Department of Hydrobiology, University of Warsaw, Nowy Świat 67, Warszawa, Poland

The literature on the fate of macrophyte production in lakes is very poor. The most frequent subject of investigations is the loss of macrophyte biomass before the period of maximal biomass, and these data are necessary for estimating the annual production on the basis of biomass during the period of maximal growth. The majority of these papers provide us with and estimate of general biomass loss without mentioning whether they are due to grazing, the death of plants or to wave action. There are only a few quantitative results on the effect of particular factors on the loss of macrophyte production in lakes.

Higher aquatic plants undergo various decomposition processes, the intensity of which depends on the properties of particular species and also on the complex of biotic and abiotic environmental factors. Also certain parts of plants, particularly those above and below the ground are subject to various changes. The following possible fate of macrophytes in lakes has been discussed:

1. The macrophytes can be consumed by phytophagous animals and thus be included into the circulation of matter and energy flow through the grazing food chain. Literature provides data on grazing of macrophytes by mostly of littoral invertebrates, many fish species, birds, mammals and terrestrial insects.

2. The macrophytes die and the dead material is used up in processes of microbiological decomposition and by detritus-feeding animals. In this case they join the circulation of matter and energy flow through the detritus food chain. During these decomposition processes the dissolved organic matter is being secreted by the dead cells.

3. The macrophytes are mechanically damaged due to different factors but most frequently due to wave action, activities of fauna

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[1] A summary of the report presented.

(destruction of macrophytes during feeding, building cases, mining etc.) and due to the activities of man. The partly damaged plants, which are detached from the substrate, die (are decomposed in the detritus food chain) or live for some time (are utilized in the grazing food chain and secret dissolved organic compounds into water).

4. The excretion of dissolved organic compounds by live plants is the next fate of macrophyte production in lakes.

5. The macrophytes can be exported beyond a given ecosystem and thus they are primarily being exploited by man (either for industry or weed control). The terrestrial animals (birds, mammals, insects, reptiles), which feed on macrophytes, also have some share in the export. They use for food either live plants or the detritus coming from decomposing plant material.

The subsequent fate of partly decomposed macrophyte material is greatly differentiated and takes place in various parts of the water body (not only in the littoral but also in the pelagial and profundal in which, as a result of water motion, the macrophyte remains are found in various stages of decomposition).

The final fates of organic matter produced by macrophytes in a given lake ecosystem are: a) mineralization, b) export beyond an ecosystem and/or c) accumulation in bottom sediments.

The results of studies on the fate of macrophytes in several Mazurian lakes conducted by the Department of Hydrobiology, Zoological Institute, University of Warsaw have been presented in the report.

POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	79—100	1973

S. M. HASLAM

SOME ASPECTS OF THE LIFE HISTORY AND AUTECOLOGY OF *PHRAGMITES COMMUNIS* TRIN. A REVIEW

Botany School, University of Cambridge, Cambridge, England

ABSTRACT

Phragmites Adans. is widely distributed and variable. Variation in e.g. size and longevity of aerial stem and leaf is both environmental and genetic, though there is a genetic correlation between growth cycle and climate. Phragmites tolerates a wide range of water and soil regimes, but being sensitive to competition it tends to be limited by this in the drier and more eutrophic parts of its range. The optimum habitat conditions for germination and early establishment are more stringent than for the adult, and differ to the typical environment of the adult. Variation within and between populations is discussed in relation to population type, biotype and short-term and small scale differences in habitat.

1. INTRODUCTION

Phragmites Adans. is widely distributed, and is currently divided into three species (Clayton 1967). *P. mauritianus* Kunth. is confined to central Africa, *P. karka* (Retz.) Trin. ex Steud. occurs in Polynesia, N. Australia, tropical Asia and N.C. and W. Africa, while *P. communis* Trin. sensu stricto, the commonest, occurs from the tropics (e.g. Africa, America) to over 70°N, and is most abundant in temperate regions of the northern hemisphere (Clayton 1967; C. E. Hubbard, personal communication; Haslam 1972).

The altitude range depends on climate (i.e. partly on latitude). Phragmites is typically a sea level and lowland plant, and is confined to these places in Shetland (ca. 60°N). In Central Scotland it reaches ca. 330 m (Spence 1964), further north and east in Sweden, ca. 670 m (Samuelson 1934). Southwards, it reaches ca. 1910 m in the Alps (ca. 47°N) (Bittmann 1953), and ca. 3000 m in Tibet (ca. 30°N) (Ridley 1930).

The relevant literature indicates Phragmites is more widespread and abundant in Europe, perhaps because suitable habitats are more frequent there.

Phragmites is very important in mesotrophic, oligotrophic and some eutrophic reedswamps, and is an initiator of, and a stage in, hydroseres. In areas of intermittent shallow flooding, it commonly dominates with human interference. It is a frequent subordinate in damp habitats of magnocaricetum, parvocaricetum, grassy and heathland communities, scrub and woodland. At the landward side of saltmarshes, Phragmites commonly marks the transition to freshwater swamp (Chapman 1960).

Phragmites can grow in most wet places, except those with extreme nutrient deficiency or high salinity. Thus it can occur with any species growing in damp, shallowly-flooded or reedswamp habitats.

2. VARIATION

Phragmites varies genotypically and environmentally, and as both physiological and morphological characters are concerned, this is of ecological as well as taxonomic interest. Variables include characters related to climate, such as length of growing season and response to frost, and documentation is missing from most parts of the world. Hence this account, based on only a few countries (mainly Britain and Malta), may be inapplicable elsewhere.

The three present Phragmites species (Clayton 1967) differ in:

Texture of lower surface of leaf blade,
Shape of leaf tip,
Length of rhachilla hairs,
Number of branches on lowest node of panicle,
Length of branch of panicle below the spikelets,
Shape or size of glumes and lower lemma.

All these, however, vary within each species, and the variations overlap between the species, so that species determination is on the balance of these characters, not on a clear-cut distinction between them.

The forms earlier considered subspecific and varietal (e.g. Hegi 1906), have — such as have been tested — proved environmenal in origin (Rudescu et al. 1965). The characters concerned include:

Height[1],
Diameter,
Leaf size,
Legehalme production,
Panicle size,
Floret number,
(Perhaps chromosome size, Tischler 1918).

Additional variables shown to be environmental by transplant tests in Britain and Malta include:

Date of emergence etc.,
Branching of undamaged shoots,
Stem longevity,
Branching of the stem in the second year,
Colouration (purple) of exposed internodes,
Rhizome diameter,
Leaf texture,
Leaf rigidity,
Leaf colour,
Fruit viability,
Size of germinated seedlings.

Further variables presumed from field evidence to be environmental include:

Straightness of stem,
Hardness of the mature stem,
Length of stem with sheaths, shorter than internodes, and the relative lengths of these exposed parts of internodes,
Internode length,
Susceptibility to reedbug (see later),
Longevity of sheaths on the dead stem,
Leaf shape.

There are also differences which prove constant under long-term transplants, or which recur in plants grown from seed. These are presumed genetic in origin, and include:

Height,
Diameter,
Date of emergence, flowering etc.,
Stem longevity,
* Branching of the stem in the second year,
Hardness of the mature stem,
Colouration of young shoots,
Hairiness of young shoots,
* Inflorescence colour,
Fruit viability,
* Length of dormancy,
* Frost sensitivity.

Further variables, shown by different clones in the same, uniform marsh and thus presumed genotypic, include:

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[1] All characters are of aerial shoots unless otherwise stated.

* Between British and Maltese material only.

Straightness of stem,
Length of stem with sheaths shorter than internodes, and the relatives lengths of these exposed parts of internodes,
Colouration (purple) of adult shoots, particularly of exposed internodes,
Hairiness on longer internodes,
Susceptibility to rust (Puccinia),
Susceptibility to reedbug (see later),
Colour of young shoots,
Ability of young shoots to withstand drying,
Legehalme production,
Longevity of sheaths on the dead stem,
Leaf shape and size,
Leaf rigidity,
Leaf colour.

Also see Dykyjová (1970).

These lists indicate that, within one region, the common differences between Phragmites stands may be of either genetic or environmental origin. (See also Toorn 1972).

The Phragmites biotype is determined by these characters. The population type (see below) depends only on habitat, although characters such as height pertain to both sources of variation. To interpret performance, characters of biotype and population type must be recognized and separated. There is also short-term or small-scale variation with minor changes in habitat.

Height (and rarely diameter as distinct from height) may be important in competition, but otherwise the physiological differences are ecologically important, and the morphological ones are not.

The genetic variation in growth cycle with country of origin ensures Phragmites is in equilibrium with climate.

Interpretation of biotype differences can be difficult. Many habitat factors are concerned, and as there is usually only one biotype per stand, only long-term transplants can show whether the biotypes of neighbouring marshes are genetically similar.

3. GERMINATION AND ESTABLISHMENT

Potential germination varies between panicles, habitats, seasons and biotypes. A further complication is that in some biotypes apparently full potential germination occurs in ordinary laboratory conditions (e.g. Szczepański, personal communication), while in others stringent conditions of e.g. temperature are required.

Germination is often negligible, and most seedlings, including those in reedswamps, die before maturity. Old reedbeds, however, may be ca. 1000 years old (e.g. Rudescu et al. 1965), and vegetative spread is considerable, so a few surviving seedlings would maintain the populations.

The proportion of fruits that are not set varies from ca. 2 to ca. 100% (e.g. Curran 1969, Gustafson, Simak 1963). The failure described in Curran (1969) was due to a meiotic abnormality, and was greater in $2n=48$ than in $2n=96$ material. Potential germination of mature fruits is often ca. 70—90% (e.g. Szczepański, personal communication).

Within one panicle, percentage germination appears constant, but between panicles from one small plot it may vary from 2 to 96%. Biotypes differ, varying e.g. from 2 to 25% between clones grown together at the laboratory, and such transplanted clones often have increased germination, e.g. 1% from field material, in the same year as 70% from previously transplanted material. Annual variations at the same place vary between at least 0.5 and 50%, presumably because of weather differences during flowering or seed setting.

Claviceps spp. infection may be absent (as in Malta), or reach over 90%, and infected fruits are non-viable.

The duration of viability is variable. Germination in Switzerland decreased after two years, but still occurred after 5 years (Hürlimann 1951). British and Maltese seed appears to retain viability better when stored in Britain than in the more humid climate of Malta. First-year fruits stored for six weeks in a desiccator, in 50% and in 100% humidity showed little difference in germination.

Phragmites germinates on damp soil or filter paper, on wet soil or filter paper, and under 1 cm of water. It does not germinate under 5 or 15 cm of water (Spence 1964), and so cannot germinate on the soil in reedswamps. (Young seedlings are drought-sensitive, and those on the upper side of fallen panicles normally die).

Up to 3% sodium chloride does not apparently decrease germination.

A few fruits germinate in the dark, more in low light, but higher light (indoor daylight) is needed for maximum germination. In one test results were 2, 4 and 7%, but proportionate differences may vary with biotype. Germination is therefore, likely to be low under a litter mat.

Constant temperature (at least at 18°C and 30°C) is unsatisfactory, germination of British and Maltese fruits seldom reaching 0.5%. Low temperatures, e.g. 5—10°C, are equally unsatisfactory. Maximum (i.e. the full potential) germination may occur in glasshouses, especially in warm Malta, but the (few) British biotypes tested show about double the glasshouse germination when fruits are placed above a waterbath alternating between 30°C and at least 10°C below this. A high and fluctuating temperature is apparently preferred and this can occur in the top soil in spring. Day and night differences of over 20°C are common in Cambridge, England, maximum temperatures frequently reaching 28°C. (Also see Bittmann 1953). Vernalization of British and Maltese fruits has no apparent effect.

Thus germination varies, but is often low, due to either faulty fruits or unsuitable habitats. Habitats optimal for germination differ from those in which the adult plant is most common.

When the first leaf is full-grown, seedling size varies. Small seedlings, with low viability, may occur sparsely among normal ones; or may compose, in any one year, the entire crop from a biotype. Extra-large seedlings occur in some biotypes, but, in the clone tested, the character disappeared when the parent material was transplanted.

Plants with ca. 10 shoots can be deemed established. Usually, each shoot is taller and from a longer rhizome than the one before. A 10-shoot plant is usually over ca. 30 cm high, so can survive ca. 20 cm flooding; it has roots over 20 cm down, and rhizome to survive some drought; it has horizontal rhizomes to tolerate frost; and food stores to tolerate some shading, grazing, burning etc. It is thus viable in normal hazards, though still too short to grow in reedswamp habitats.

Seedlings take from 3 months to over 3 years to reach this 10-shoot stage. Before this, mortality is high, so the chances of survival decrease when seedlings develop slowly. Hence habitat affects mortality through growth rate as well as through lethal hazards.

Growth is slow in drought, though the harm done depends on other conditions also. Water 5 cm below ground is usually unsatisfactory, but with high light and temperature, water 10 cm down is tolerated well; it is also slow with shade; with low temperatures (25°C night and 35°C day temperature are the most favourable of those tested); with salt (many young seedlings and some older ones die in 1% sodium chloride); and with mineral deficiency. On unflooded and unsilted peat (at least in fens), seedlings are stunted by phosphate deficiency. If the water rises to ground level, growth is normal, but young seedlings are likely to drown in over ca. 2–3 cm of water. Hence establishment on peat is very difficult.

Hazards during establishment vary with the region. Drought is the main hazard in the open dry summer habitat in Malta. In the dense summer vegetation in Britain, shading, drowning, frosting (in spring or autumn) are potential hazards and the low temperatures prolong the vulnerable stage (Haslam 1971 a).

Recently, establishment has been recorded in semi-flooded gravel pits, with an open habitat, mineral soil, and wide range of water levels. Even so, it occurred in only ca. 3 of the 6 years studied. It has also occurred at the back of a saltmarsh (Ranwell, personal communication) and on silted peat cleared by severe frosts, with establishment speeded by a warm spring (E. A. Ellis, personal communication).

Most small clones seen, however, are very old (e.g. Spence 1964).

4. VEGETATIVE PROPAGATION

Rhizomes and legehalme spread the plant within an area. Rhizome fragments can propagate downstream or, with animal transport, upstream and between catchments. For establishment, fragments need to lodge in negligible current etc., with part in or on the soil, most wet, and part in air or dry soil.

Fragments commonly arise from human interference (ditch cleaning, ploughing etc.), but also from rodents (water rats, coypu etc.) and perhaps other animals (also see Fiala, Květ 1971).

5. THE DEVELOPMENT OF THE MATURE POPULATION

Mature, flowering stands develop from seed or rhizome fragments in 2—3 years at best (Dykyjová et al. 1971), but take very much longer in poor conditions. Once maturity is reached, Phragmites behaviour is the same, irrespective of actual age. A mature young plant (e.g. 4 m diameter) can spread by ca. 1 m/year in each direction in habitats where the shoots remain sparse, ca. 1—2 m/year in dense stands, and more if the clone can potentially form, and the habitat actually induce, legehalme. Each year, there is ca. 1 (—2) m of new horizontal rhizome proximally per plant, and perhaps 0—10 m distally, the length depending on habitat. Vertical and (in good conditions) oblique rhizomes grow in addition. Phragmites, given sufficient time, will occur throughout that part of the habitat which is suitable for it, and will be dense or sparse depending on conditions.

6. DEGENERATION

Senescence has not been recorded in Phragmites populations. Individual rhizomes live 3—6 or more years. Bad treatment damages, and, if severe, kills populations — but this not death from old age. Degenerating stands occur where blanket bog has overgrown a mesotrophic valley bog and Phragmites, now in oligotrophic peat and being grazed, is depauperate (see below). Degeneration also occurs in a dry fen where the water level is lowered and the suppressive power of competitors increased. Here, shoots from 3-year rhizomes are small, and 4-year rhizomes are mainly dead. Height, density and population type are lowered (in one fen this was recorded for 14 years e.g. Haslam 1970 a). The floating plaur mats described by Pallis (1916) were without, and unable to grow, horizontal rhizomes, and so were non-viable (Haslam 1969 a) but Rudescu et al. (1965) found horizontal rhizomes in plaur from the same region.

7. THE ADULT PLANT

PERFORMANCE IN RELATION TO THE INORGANIC ENVIRONMENT

The variation in Phragmites behaviour in different latitudes, longitudes and altitudes is inadequately known. As Phragmites is sensitive to environment, and shows physiological variation, the results presented here may not be applicable to all countries.

Water regime

Phragmites grows well when permanently submerged up to ca. 1/2—3/4 of its modal height. In lakes this height is determined by nutrient status, temperature etc. and hence maximum water depth ranges from 4 m in eutrophic or warm lakes (P. Denny, Szczepański, personal communications) to 0.75 m in an oligotrophic Scottish loch. Lake stands tend to be sparser than swamp ones, perhaps because of worse aeration and better insulation (see below). (Also see Haslam 1972, Matiuk 1960).

Phragmites also grows well (over 2 m high) with the water level ca. 6 m below ground in the dry climate of Malta, and records consistent with this come from other countries. In wet fens etc. horizontal rhizomes are usually 0.5—1.8 m down, but in dry habitats they may be lower, e.g. dense only below 1 m with the water level ca. 1—1.5 m down.

Annual fluctuations range from ca. 5 cm to ca. 2 m, and tidal fluctuations of ca. 1.25 m occur (Haslam 1972).

Most Phragmites grows in still or stagnant waters, and it occurs in the most stagnant conditions recorded in Britain, though it decreases in the larger stagnant areas in the Netherlands (J. van der Toorn, personal communication). Flow brings aeration, and much flow brings scour, in which Phragmites is sparse or absent. Phragmites is less sensitive to scour than some *Glyceria maxima* (Buttery, Lambert 1965) but more so than e.g. *Sparganium erectum* and *Schoenoplectus lacustris*. In watercourses it is rare except in dykes etc. with negligible flow, and in lakes it usually avoides exposed shores. However, in deep waters in Uganda, where surface turbulence occurs together with a (presumably undisturbed) mud substrate, Phragmites colonises exposed shores (P. Denny, personal communication).

Aeration in lakes is through the standing shoots, whether living or dead. Hence if shoots cannot grow above water level, or if ice or waves remove dead reeds in autumn, Phragmites will be limited. Flooding the stubble decreases bud formation (Rudescu et al. 1965).

There are few effective competitors in habitats continuouly flooded or with intermittent deep floods; these few, however, may be very abundant locally, e.g. *Cladium jamaicense*, *Cyperus papyrus* (P. Denny, personal communication), *Typha angustifolia*. Effective competitors increase in drier habitats, and are numerous in never flooded marshes and usually remove Phragmites. In Malta effective competitors are absent, and Phragmites dominates in much drier habitats (see below).

In spite of the wide possible variation in water table, regularity is required for good Phragmites performance; that is, the water level should be similar each year at the same season. This is particularly so for variations from ca. +5 to ca. −10 cm from ground level, when the upper rhizomes have more temperature fluctuations if the water falls, and less if it rises. A dry spring in a normally flooded stand delays emergence, and hence flowering, by up to a month, and lowers modal height by e.g. 30 cm. A dry autumn in the same circumstances hastens shoot death. A wet autumn in a normally dry stand causes delayed (and so incomplete) maturation, and so low quality or unusable thatching reed. Unexpected deep floods in late spring may kill shoots, and lead to delayed or no emergence of replacements. A drop of 0.75 m in water level can make a stand depauperate. After ca. 4 years a stand adjusts to a new water regime but in the interim it is weakened and open to invasion (Haslam 1970 b).

Soil regime

Soil texture. Coarse substrates are usually nutrient deficient, and often exposed to scour, and are thereby unsuitable. Texture as such has little effect, except that buds narrow in ca. 10 cm of tarmac or ca. 50 cm of tough *Carex paniculata* tussock and so the shoots are usually small.

Major nutrients. A fine-particled mineral soil is satisfactory, a coarse one is less so (see above) and in nutrient-poor lakes Phragmites is often confined to areas of fine sediments (also see Hürlimann 1951). Nutrient-rich peat is also satisfactory. Performance is often lower on bog peat with light grazing; but as replacement shoots are decreased by low nutrients, the effect is largely due to grazing, except with extreme nutrient deficiency.

Fen peats with high calcium but low availability of other nutrients have restricted Phragmites populations with short internodes, some xeromorphy, leaves yellowing in July, and early shoot death. After adding phosphate, nitrate and potassium (phosphate is the most important), the shoots are normal, with increased height, density and flowering. Where the bedrock is hard and mainly acid (e.g. N. W. Scotland) Phragmites frequency and performance are high only on rock containing much calcium. Nitrogen is important in oligotrophic lakes (Spence 1964). Thus Phragmites can be limited by different nutrients, depending on the nutrient status of the area concerned. It can, however, grow in an exceptionally wide range of chemical status, e.g. pH 3.6 (Bittmann 1953) to 8.6 (Champan 1960). (Also see Bittmann 1953, Björk 1967, Hürlimann 1951).

Phragmites potentially grows well in eutrophic habitats. Effective competitors are usually few in nutrient-poor places, but more numerous and luxuriant in eutrophic ones. Consequently Phragmites is frequently limited by competition in the latter. Available nutrients in peat often increase on drier ground, so Phragmites in dry places is often denser in nutrient-medium than in nutrient-rich places, competitors growing better in the latter.

In dominant Phragmites small additions of nutrients have no effect, but eutrophic water in irrigation ditches increases the height of the nearby reed by up to ca. 50 cm. Intensive nutrient additions first mainly increase density, but later the biotype alters, reeds becoming larger and sparser (Björk 1967, personal communication). However, with exceptionally high nutrient status, performance appears to decrease (Szczepański, personal communication). The Giant reed may be attributed to high nutrient status (see Rudescu et al. 1965).

Nutrient uptake is mainly from the upper ca. 0.5 m of soil, by the branched horizontal roots of the upper rhizomes (Dykyjová, personal communication). Reeds develop basal roots in eutrophic water, and some uptake presumably occurs. Vertical roots from the lower horizontal rhizome reach over 2 m down in good conditions.

Rhizomes decay ca. 5—10 years after formation, leaves after ca. 1—3 years, and aerial stems after ca. 2—6 years (except where incorporated into peat). Thus a considerable quantity of nutrients are stored within the plant tissues.

Other chemicals. Various other chemicals locally affect performance, e.g. copper pollution causing harm and death (Chiaudani 1969), but only sodium chloride is of general importance. Phragmites is common in fresh and brackish water at the back of saltmarshes, and can advance over saltmarsh habitats (e.g. with *Spartina townsendii)* as these become further from the sea.

The lethal limit for a British biotype is 1.2% Cl in soil water 10 cm down (Ranwell et al. 1964), in Malta it is between 1.0 and 1.5% and as this is consistent with results from young plants of two British and one Maltese biotype, it may be generally applicable. A temporary increase to 2.5% Cl in a ditch normally containing below 1% led to all shoots becoming unhealthy or dying, and the next years density was low though the height was normal (i.e. bud formation was affected, bud size was not).

An inland reedbed flooded by salt water usually has a late-emerging (and so late-maturing), sparse, short crop. One flood was still affecting performance after 5 years. Recovery was even slower in another marsh, where more salt was left, though in another instance, with less salt, little harm resulted.

Sea spray can hinder the growth of immature internodes.

Reeds in permanently brackish water are often very hard (and thus good for thatching).

Salt encourages legehalme in biotypes potentially able to develop these.

Dry, salty and trampled habitats may bear the xeromorphic (with sharp leaf tips scratching skin) dwarf biotype, with shoots of ca. 5 cm modal height mainly in prostrate rosettes above the vertical rhizomes. Proximal shoots are the largest and the least affected morphologically. An equivalent mesomorphic biotype can develop in non-salty places, and of course all intermediates occur. Competition likewise affects distal shoots most.

Temperature

Temperature varies with the overall climate, the actual weather of any one season, and the special character of any one habitat (e.g. frost hollow, thick litter).

Average temperature of the growing season. Higher temperatures increase performance in dominant stands. Within Europe, performance increases southwards (e.g. Bittmann 1953), though there appears to be little further increase in Africa, perhaps because of biotype differences, or perhaps because temperature is already saturating. Many Swedish stands (Björk 1967) are taller than many British ones, in spite of occurring further north. This is probably due to biotype differences. (Also see length of growing season, below).

An exceptionally hot summer in Britain can increase height by ca. 0.5 m (Haslam 1972).

Average temperature of the non-growing season. Where winter temperatures are low, and frosts occur, Phragmites aerial shoots cannot grow, and the growing season is of course restricted to the other part of the year and, at least in Britain, it normally occupies most of this warm season.

The horizontal rhizomes are frost-tolerant (Haslam 1969 a) and grow in winter in Britain. Bud development is slowed in winter in Britain but not in Malta, suggesting low temperatures are responsible. A few buds emerge during dormancy. In Malta they mature. In Britain, they emerge in any warm spell and are quickly killed in the next cold spell. Thus dormancy is imposed.

Emergence in warm climates takes place when intrinsic dormancy ends, and in cold ones, when in addition, temperature rises. In Britain intrinsic dormancy ends around March, and emergence occurs between March and May (see Haslam 1969 c). In Malta dormancy is entirely intrinsic. In the colder winter of Poland, dormancy is mainly cold-controlled, winter emergence occurring in lakes, where the shoots grow up until they reach the overlying ice. About 50% of shoots emerge in winter, comprising most of those already formed (Szczepański, personal communication).

In Malta larger reeds live through the frost-free winter, and lateral shoots develop in their second (and perhaps third) year.

In autumn in Britain, shoots die roughly in parallel with the falling temperature. In a cold year, leaves and perhaps stems will be frost-killed early, while in a warm one, death will be at the same rate as in a (frost--free) glasshouse, except that lower parts of stems live longer in the latter.

Length and position of the growing season. The period of full growth is similar over a wide variety of countries, but the period between emergence and full growth varies, increasing in warmer climates. Shoot growth rate consequently decreases in warmer climates.

Between Britain and Malta there is a genetic difference in the duration of intrinsic dormancy. Polish material appears to differ genetically in the intensity of intrinsic dormancy, as intrinsic dormancy is slight. Emergence of Polish material occurs in April in Britain, indicating the late natural emergence is temperature-controlled. There are thus a range of biotypes with different, genetically controlled, growth cycles, adapted to the varying climates in which they grow (Table I).

Table I. Length and position of the growing season

Country	Month of main emergence	Last month of rapid growth	Duration of rapid growth (months)	Last month of full life	Duration of full growfh (months)	Authority
Canada	V	VI	2	VIII—IX	2—3	A. Hartgerink (personal communication)
Poland	V	VI	2	IX	3	A. Szczepański (personal communication)
Britain	IV	VII	4	IX	2	S.M. Haslam
Czechoslovakia	IV	VII	4	IX—X	2—3	J. Kvét (personal communication)
Roumania	II—IV	VI—VII	4—5	IX	2—3	Rudescu et al. (1965)
Malta	II	VII	6	X	3	S.M. Haslam

In North and Central Europe the growing season of Phragmites is similar to that of most of its associates, so competition is maximal. In Malta, most associates are winter-green, and competition is minimal.

Fluctuations between night and day temperature. In Britain the spring-formed buds (roughly half the total), are mostly developed under the influence of alternating temperatures, and some autumn-formed ones are temperature-dependent also. In non-flooded places, fluctuations increase in exposed places without litter, and also with burning, frosting and other fluctuating weather conditions. In Malta, in conditions otherwise comparable, night and day temperatures differ less. Emergence takes longer, and fewer buds develop in spring (Haslam 1969 c). Transplant tests show the difference is largely climatic.

Delayed emergence resulting from unexpected drying of soil in spring, may be due to the different temperature regime of the upper rhizomes, particularly as, if spring frosts occur also, the shoots are short and weak.

The insulating effect of litter is important in competition (see below).

Frosts stimulate bud development, but kill above-ground parts. Density is usually increased by low mortalities of young shoots, as frost-killed ones usually have 2—3 replacement buds.

Temperature regimes are more favourable when fluctuating, for both germination and bud initiation.

Light

Phragmites is more shade-tolerant than most species of open habitats, and it can be the main herb (though spare, short and flaccid) in damp woodland with a closed canopy. Treatment with low light can, however, kill shoots and prevent emergence the next year (Bernatowicz 1966). As only about half the rhizome reserves are utilized during emergence, the latter effect must be due to the disturbance (which is unfavourable, as with water and salt regimes, above).

In shade, inflorescences are fewer, and internodes and leaves both longer and more flaccid, though the latter effects are probably caused by high humidity as well.

Light is normally adequate for the good growth of the taller shoots, though a few small ones may be harmed by shading in dominant stands. Removing dead standing reeds does not increase growth; the resulting crop is often denser because of increased temperature fluctuations, but consequently also shorter. (See Haslam 1969 b, c, 1971 b). The distribution of light within reed stands is given by e.g. Hürlimann (1951), Willer (1949 a, b).

INTERNAL REGULATION

Production and performance vary from sparse to dominant stands, and also within dominant stands. Production differs between monodominant stands with variation in biotype and environment (e.g. Bernatowicz, Pieczyńska 1965, Björk 1967, Dykyjová 1970, 1971, Dykyjová, Květ 1970, Szczepański 1969).

If Phragmites can occupy space and refuse entry to other species then, ecologically, production is sufficient, and any increased production is superfluous. However, a stand able to resist invasion at one time may be suppressed by a new invader at a later period. Oligotrophic and deep water stands usually have few effective competitors, and eutrophic and dry ones, many (in North and Central Europe). Production increases from deep to shallow water, and with increasing nutrient status — and the likelihood of suppression increases also. Many causes of suppression are unrelated to production (see below), so, within dominant stands, high production does not necessarily increase resistance to invasion.

The advancing stand

These usually occur in changing habitats: those recently flooded, drained, dug or cleared, or like saltmarshes, newly formed.

An advancing margin may be kept sparse by e.g. competition or salt, or may be dominant. A sparse one resembles any other sparse stand except that the proximal rhizomes grow outwards from the margin.

A dense margin has three zones, that of the current years' advance, of the previous years' advance, and the uniform hinterland behind. Density is usually similar throughout (usually 100—200 per m^2, varying with biotype). Yet in the advancing margin these shoots come from first year rhizomes only, while at the back they arise from rhizomes of all ages. The normal density of a biotype may be achievable by intensive bud development from new rhizomes, or from variable development on rhizomes of varying age. A dense established stand has most of its shoots from rhizomes 2—4 (to 6) years old.

An advancing zone ca. 1—1.5 m wide comes from autumn-formed horizontal rhizomes. One ca. 1.5—2 m wide probably has a second band of proximal rhizomes, formed in spring or summer. This second proximal rhizome has no counterpart in established stands. When lateral buds develop soon after the terminal ones, they are nearly as wide as the terminals, and so the shoots are nearly as tall. If laterals develop later, their buds are narrower and the shoots much shorter than the terminals.

A few clones develop legehalme in the advancing zone (out of 25 clones examined, one had dense, and two sparse legehalme). Dense legehalme increase the advance by 3—5 m per year or even more, provided lateral shoots grow in summer, and horizontal rhizomes develop before the legehalme die.

The advancing margin may be as tall as the hinterland, which is common when the annual advance is of one proximal rhizome, or it may be shorter, as is common when a second proximal rhizome or legehalme develops. Provided a canopy forms, the height, in open habitats, is ecologically unimportant.

If an advancing margin meets unfavourable conditions, the density of horizontal rhizomes and terminal shoots is, for some years, unchanged, but few laterals develop and the stand becomes sparse. Both the physiological (advancing) state of the plant and the habitat must be suitable before buds develop freely (Haslam 1970 a).

The established stand

Environment, not biotype, determines population type. A restricted stand has no mode to the growth (height/number) curve, and is sparse, with shoots of all sizes equally distributed. Only a few laterals develop on older rhizomes, and their size decreases sharply with rhizome ageing. Populations are restricted by competition, nutrient deficiency, etc.

Most dominant and some co-dominant stands are optimal, with a negatively skew growth curve. Many of the abundant laterals, arising from wide buds, are nearly as tall as the terminals.

Sub-optimal populations, typical of sub-dominant stands, also have many laterals, but they are considerably shorter (i.e. from narrower buds) than the terminals, giving a central mode to the growth curve.

Depauperate stands have a positively skew growth curve, and often no really tall shoots. Laterals are frequent but are short, from narrow buds. These stands are common with some grazing, where the final replacement buds are small, and also occur in dry salty places, after severe drainage, and with summer cutting and competition.

All intermediates occur. Those between restricted and depauperate stands are usual in somewhat unfavourable habitats with slight grazing (Haslam 1970 a). Willer, Woddem (1943) describe similar variations in population height.

Within any population type, performance varies considerably with weather, nutrient status, litter etc. and with biotype (whether controlled by genotype or also by long-term habitat effects such as nutrient status or past management).

A monodominant stand in deeper water is protected by occupying the space, and by the water, which few competitors tolerate (Phragmites shades and suppresses submerged aquatic species). If density permits a closed canopy, this is a strong additional protection. The same applies in saltmarshes and some valley bogs where the initial protection comes from the sodium chloride or low nutrient status. Drier or nutrient-rich stands are protected by the closed canopy, occupancy of space, and the shallow water or litter or the absence of competitors in the neighbourhood, as appropriate. If none of the latter apply, Phragmites dominance is maintaned only by management.

Shoot density and height determine performance. The density of spring-formed buds, potentially great, depends on temperature fluctuations (see above). These fluctuations depend on climate, on the weather of the season in question, and water level, litter mat etc. Bud initiation is decreased by salinity, competition, lack of aeration, damage to upper rhizomes (recovery takes several years) and nutrient deficiency in (extreme instances or after summer cutting). The production of terminal buds from new horizontal rhizomes is affected only in extreme environments, while that of lateral shoots and rhizomes is very habitat-dependent. Thus adverse conditions easily make a stand sparse and restricted, but eradicate it only with difficulty.

Height is affected by bud width below ground, which determines potential height; and by the environment during growth, which determines actual height. Shoot height and diameter are correlated, but the regression varies with habitat and biotype.

Unusually narrow buds, within any biotype, occur with salinity, grazing (replacement buds), nutrient deficiency, competition, extra-high density, and sometimes in dry stands (flooded stands usually have wide buds, marsh ones my be wide or narrow).

Potential growth rate of shoots decreases in low temperatures, nutrient deficiency, salinity, competition, and unexpected drought or flood. Burning and high humidity can produce shoots unusually tall for their width.

Three processes thus control performance. Although the same factor may affect more than one of these, it does so in different ways. The relationship between height and density varies. A population of similar crop weight and habitat may consist of sparse large shoots or dense small ones, height and density being inversely related. A stand with a closed canopy is monodominant irrespective of shoot size. In more favourable conditions height or density may increase with little or no reference to each other. Where density increases without an improved habitat (as after burning), buds narrow and height decreases. Fourthly, height and density usually increase together when passing from an unfavourable to a favourable habitat of the same biotype (Haslam 1971 d).

Maximum density in favourable conditions with a closed canopy, is normally (from 30) 60—250/m^2 in Britain and Malta, varying with biotype. Increases up to ca. 600/m^2 have been induced in the field by burning etc., but even so these shoots do not fill the soil or the aerial space. Dykyjová et al. (1971) record an experimental plant with ca. 1500/m^2, so although bud density is normally regulated, the inhibition can be relaxed. Minimum density is of course less than 1/m^2.

Treatments applied to a plot affect only the shoots within that plot: stimulation of one vertical rhizome not being passed through the horizontal rhizome to other vertical ones.

The upper vertical rhizomes are sensitive to environment and control the performance of the aerial shoots. The horizontal rhizomes are less sensitive to environment and control the viability of the population.

Monodominant stands may be non-uniform. In a lake, ice, waves or animals may locally remove shoots in autumn, and lack of aeration makes next years' crop sparse in these places. In a marsh, thick litter patches may develop accidentally, and again patches of very sparse shoots result. As sparse shoots form little litter, density increases as the older litter decomposes. Similarly short-term patches of denser reed can result from thin litter. Where ditches supply eutrophic irrigation water, near-by reeds may be taller. Patchiness may also come from geese (Fiala, Květ 1971), coypu, cattle, burning, cutting, shading and disease. (See Haslam 1971 b).

THE EXTERNAL ORGANIC ENVIRONMENT

Management

Management aims at maintaining or obtaining Phragmites dominance and improving its production. The former is unnecessary in deep or salty water, as effective competitors are usually excluded. If flooding is intermittent and shallow or absent, woody plants and, especially in eutrophic places, many suppressive herbs can grow. Such reedbeds need intermittent clearing (of bushes), burning (selectively increasing Phragmites) or flooding. Commercial reedbeds are cleared and relatively dry in late winter, and so are not protected from invasion by litter mats, shading or deep water.

For high yields, burning is normally desirable and a regulated water regime and nutrient status are often so. (See Bittmann 1953, Haslam 1969 b, Rudescu et al. 1965).

Pests and diseases

These are frequent (Gaevskaya 1966, Haslam 1972) but only a few are of ecological or commercial importance, and these vary between different countries. In Malta, for instance, there is no appreciable damage.

Claviceps spp. can infect high proportions (e.g. over 90%) of fruits in many countries, and infected fruits are nonviable.

Various insects have larvae growing in stems ("reed bugs"). Infection is usually light, but a high infection (e.g. 80%) of *Arenostola spp.* can ruin patches in crops in Britain. Damage is avoided in flooded or cleared stands as the eggs overwinter on litter. Small shoots die if attacked, and though damage during emergence is replaced, a late replacement means late maturation, a low-quality crop, and increased competition because of the long period without tall shoots. If half-grown shoots are attacked, the mature base (ca. 30—60 cm) is left, the immature tip (ca. 10—30 cm) is lost, and narrow lateral shoots grow up from below. This is ecologically satisfactory as a closed canopy is formed, but the uneven reed is unsuitable commercially. Full-grown shoots are hardly affected by infection (basal infection is harmless, but the tip is lost if larvae move there). *Archanara dissoluta* causes a loss of up to ca. 50% in height, and ca. 40% in breaking strength of the fourth internode, in Poland (Durska 1970).

The gall-forming insects, particularly *Lipara lucens*, can locally cause considerable crop damage, but usually only a few shoots are infected.

Ustilago grandis infects buds or young shoots. Infected shoots later often thicken above, usually having many short internodes. In Poland the breaking strength of the fourth internode is halved, and flexibility decreases (Durska 1970).

Deightoniella arundinacea (*Napicladium arundinaceum*) causes short upper internodes and a lack of thickening in the stem, which remains flexible. In Poland the loss in breaking strength may be ca. 85% (Durska 1970).

Steneotarsonemus phragmitidis forms warts at the base and in the inflorescence, and causes curled leaves. In small patches the loss, in Poland can be ca. 35% in height and ca. 20% in breaking strength (Durska 1970). Also see Razumovskij (1968) and Roman, Roman (1964).

Macrofauna

Damage is of local importance only. Much of highland and heathland Britain has light but frequent grazing by sheep, cattle or horses. Phragmites is frequent on wet ground. It is tall in places too wet or soft for much access, and elsewhere populations range from sub-optimal to depauperate depending on the grazing intensity. Severe grazing, as in pastures, causes extreme depauperation or eradication.

In a vigorous Phragmites stand these animals eat growing reeds, trample and remove dead reeds and litter, and, if the soil is soft and the animals heavy, the upper rhizomes are damaged, thus lowering bud density for several years. All these open dominant Phragmites to invasion from other species. If invasion does not happen, and grazing does not recur, the population recovers in ca. 4 years. If a mixed Phragmites stand is damaged, the effect depends on the relative harm to each species. Phragmites is usually the most susceptible (see Fiala, Květ 1971).

Wild animals cause similar but normally less damage. Deer do little harm, but small clearances of litter could lead to the establishment of a competitor. Coypu, water rats etc. eat rhizomes and young shoots, and can clear and disturb soil in small patches (e.g. Fiala, Květ 1971). Geese can do similar damage (Fiala, Květ 1971).

Many animals live in reedbeds without doing harm, e.g. snakes, small birds.

Competition with other plants

Competition occurs when Phragmites and other species grow together in a mixed stand, when the proportions of each may alter; and also when an advancing margin of Phragmites meets other vegetation, or vice versa. Mixed stands are commonest at the wet, dry and eutrophic ends of the habitat range, and with human interference.

When two species grow together, their relations depend on the reactions of each to the habitat and their mutual interaction, so three processes are concerned. Monodominant stands are fairly stable, and a temporary weakening need have no long-term effect. Mixed ones are unstable, as a weakening of one species leads to an increase of another, and recovery from a temporary weakening may be impossible.

In mixed stands, Phragmites may be decreased (and hence competitors often increased) by unsuitable water or soil regimes or damage to shoots of rhizomes. When kept sparse or short in this way, Phragmites is not technically suffering from competition. Similarly, the other species in the stand may be limited by water or soil regimes, lack of aeration, pests or diseases. Most effective suppressors of Phragmites occur only in never-flooded or seldom-flooded places in mesotrophic or eutrophic habitats. A 10 cm change in water level, for instance, can alter the balance of dominance between Phragmites and *Calamagrostis canescens*.

Burning usually gives a selective advantage to Phragmites by increasing density and early emergence.

Phragmites harms other species mainly by shading. Shading depends on height and density, and so on both habitat and biotype. In drier places a litter mat hinders establishment from seed and the vegatative spread of short species.

Phragmites is easily suppressed by some species. Bushes succeed Phragmites mainly by shading, the Phragmites becoming sparse and subordinate. Herbs cannot ordinarily shade Phragmites. Species forming and unharmed by litter mats, e.g. *Agrostis stolonifera* and *Glyceria maxima* have an advantage, as Phragmites is weakened by litter (see above).

The below-ground control, possibly due to toxic root exudates is an important weapon against Phragmites. This decreases bud initiation and narrows buds and growing shoots, thus lowering both height and density. A community is often balanced between the ability of Phragmites to shade and so weaken the competitor, and that of the competitor to decrease Phragmites height and density and thus its shading power. Other ways of suppressing Phragmites, e.g. by lodging, are of lesser importance.

Combinations of factors may be important. A temporary fall in water level in an intermittently-flooded marsh, stopping flooding, weakens Phragmites as the water regime is disturbed. As litter remains dry throughout the winter, reedbug can increase and weaken Phragmites further. The presence of litter prevents much increase of bud density from frost. Because the ground is dry, species characteristic of dry marshes increase, and, by competition, weaken Phragmites yet more. In two years an abundant population can be reduced in this way to a few sparse shoots.

In a clone advancing from a dense hinterland there will be many terminal shoots from the horizontal rhizomes sent into the new area. In 2–3 years shoots will become dense enough to shade low-growing plants. So even if the below-ground control exerted by the other species prevents much lateral bud development, a shading density can still arise, and Phragmites dominate, because of the new rhizomes growing from the hinterland. In an equivalent hinterland, without this extra supply of shoots, Phragmites would remain sparse and subordinate.

Biotype is more important in mixed than in monodominant stands. In vegetation 1 m high, a Phragmites biotype 3 m high probably can shade and suppress other plants, while one 1 m high cannot.

Important characters in competitive balance are:
Shading ability,
Shade tolerance,
Litter mat formation,
Below-ground control,
Germination and establishment conditicns,
Growth form,
Growth rate,
Advancing or hinterland state of plant,
Historical accidents and interference.
(See Haslam 1970 a, 1971 c).

8. ECONOMIC IMPORTANCE

Cellulose

Cellulose production is possible from large reedbeds only, since large crops are needed for economic processing. The soils must be firm enough to take machines, and be dry enough to allow machine access in late winter or early spring. Hence the primary requirement is a suitable geographical area, and management merely aims to increase yield in minor ways.

The cellulose content of Phragmites is 27–69%. Mean fibre length is 0.9–2.0 mm, being longer in taller biotypes.

Most species used in fibre production have longer fibres. Phragmites used alone produces poor quality material, but good quality paper comes from 20% Phragmites and 80% better quality fibres. (See Rudescu et al. 1965).

Thatching

The primary requirement is again geographical, but small reedbeds are feasible, as useful quantities can be small. Somewhat softer soil is tolerable because harvesting can be manual or by small machines, but access in late winter or early spring is again required. Good management improves both quality and yield.

Good quality reed is usually 1–2 m high, the height being nearly uniform within each stand. It is hard and slow to decay, particularly at the cut end. Quality is often best in slightly brackish water.

Between biotypes, sclerification. hardness and breaking strength all vary (sometimes independently). Hardness appears to depend on biochemistry more than an anatomy. Some biotypes are too soft for thatching.

Within one biotype, quality increases with sclerification. Breaking strength increases, and flexibility decreases, with increasing diameter (Szczepański 1970).

Drainage

This is used mainly in the Netherlands. Fruits are sown in wet land. It is ploughed a few years later, when dry, and crops are sown. Fruits of high viability are needed.

Minor uses

These include litter, insulation, grazing, fencing, stuffing, and lining watercourses.

Eradication

Phragmites is a major nuisance in shallow drainage channels in flat alluvial plains. Treatment may be mechanical (cutting, dredging) or chemical (usually a dalapon, or dalapon-paraquat spray).

See Bittmann (1953), Hasiam (1969 b), and Rudescu et al. (1965) for fuller descriptions.

9. CONCLUSIONS

Phragmites is widespread as a dominant and a subordinate species, and is of economic use. It has an unusually wide habitat range, but is sensitive to competition and is limited as much by this as by the inorganic environment. Many biotypes exist. They vary in morphology, in growth cycle, and in response to temperature. They may also differ in response to other factors, but this has not been demonstrated. This variation, as Fiala (1970) suggests, undoubtedly contributes to its wide distribution. Growth cycle and temperature responses are related to climate. At least within Britain, physiological and morphological variation is not correlated.

Biotypes may differ genetically, but major differences can be caused by long-continued or drastic differences in habitat. Changes in biotype have been noted or suspected with nutrient additions (Björk 1967), burning, past cutting and burning, shading, salinity, and transplanting (also see Rudescu et al. 1965).

The clonal stands are very long-lived, but no one part is likely to live more than 8 years; a negligible proportion of the life of the clone. The rhizomes live longer than the aerial shoots, and provide the continuity from year to year and century to century.

Most of the plant is underground (2/3 underground, Szczepański 1969). The general performance is determined more by the habitat in the upper soil (that which affects the upper vertical rhizomes) than by other factors, apart from gross interference. Because of this, the behaviour of Phragmites may be expected to differ from species such as trees or annuals.

Variations between communities can be interpreted in terms of (a) population type, a medium-term habitat effect, (b) biotype, determined by genotype, long-term habitat effects and major shocks, and (c) the minor variations with short term fluctuations (e.g. in weather) and small-scale differences (e.g. in litter thickness).

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J. P. ONDOK

SOME BASIC CONCEPTS OF MODELLING FRESHWATER LITTORAL ECOSYSTEMS WITH RESPECT TO RADIATION REGIME OF A PURE PHRAGMITES STAND

Department of Hydrobotany, Institute of Botany, Czechoslovak Academy of Sciences, Třeboň, Czechoslovakia

ABSTRACT

Some fundamental concepts of the theory of modelling are explained, and its application in investigations on freshwater littoral ecosystems is described. The construction of a submodel of radiation regime in a pure Phragmites stand, which forms a part of a complete ecosystem model, is discussed in more details.

1. GENERAL CONCEPTS

Modelling has proved to be a useful method in ecosystem investigations. An ecosystem usually involves many elements and mutual relationships of causal or other character. The idea of a model as an abstraction of a real system has become a basis for mathematical modelling, the theory of which has been gradually elaborated during the last few years. Several kinds of models exist but in ecosystem investigations the "compartment models" are most widely used. A compartment model is an abstraction of a system whose variables can be conceived as describing the contents of various compartments (boxes) connected through flow of energy and/or material. From the mathematical point of view, a compartment model is any system of differential equations of the first order (Bledsoe 1969, Bledsoe, Van Dyne 1969, Swartzman 1971 and others); their solution by means of digital computers is preferred to the method of mathematical analysis.

Electrical analog models are another type used in studies of ecosystem functions (Odum 1960, 1962, Patter 1971): electrical analogs substitute biological energy circuits in these models which are more suitable for simulation than the compartment models. But even if an electrical analog model of an ecosystem is more complex than a set of equations constituting a compartment model, the latter is preferred in ecosystem investigations. This paper therefore deals with compartment models only.

A model is constructed either by successive steps from simpler (neglecting some elements and relationships) to more complex formulas, or by modelling certain subsystems first and then synthetizing all submodels into a general model. The level of abstraction given by the technical possibilities and interests of the investigator decides which elements and relationships are involved and what degree of "resolution" can be expected from the model. The process of constructing a model may be divided into 4 steps:

1. Construction of a hierarchical diagram, which is the graphic representation of the elements and their relationships selected for modelling.

2. Determination of all terms (variables) introduced into the model. Generally, 5 kinds of model variables are distinguished:

   a. Principal system variables — which are immediately related to the required information on an ecosystem, its structure and functioning (e. g. biomass, energy content, weight of dead material, mineral content).

   b. Intermediate system variables — which serve for determination of other variables (e.g. photosynthetic rates, respiration rates, translocation, mineral uptake, death rates).

   c. Driving variables — which are needed for specifying other variables, but the physical mechanisms on which they depend have no relevance for the model (e. g. incoming solar radiation, air temperature, precipitation).

   d. Parameters — which are all the constants or coefficients occurring in the model (compensation points, coefficients in regression equations, etc.).

   e. An independent variable — which is usually the time.

3. Formulation of the model from the hierarchical diagram. In a hierarchical diagram, relationships between individual boxes are described by differential equations or by any other functions of either deterministic or stochastic character. Such formulation is carried out on the basis of experimentation and theoretical considerations.

4. Verification and precision of the model. In an adequate model, the empirical data and those obtained by means of the model are consistent. When their consistency is not satisfactory, the model must be reformulated. More precision is attained by introducing more terms into the model or by refining its mathematical formulations. Compartment models can also be used for simulation, which, in this case, is a study of model "behaviour" under various conditions, even under such that may never occur in actual reality.

The construction of a model is a compromise between the requirement for a high degree of resolution on one hand and the technical possibilities of the investigator on the other. The two ways of model construction described above, i. e. gradual abstraction by simplifying the whole system, and the gradual synthesis of submodels, will be illustrated by some examples.

2. APPLICATION OF A COMPARTMENT MODEL TO A FRESHWATER LITTORAL ECOSYSTEM

A multitrophic model of energy flow through a freshwater littoral ecosystem is formulated, at the beginning, with a low degree of resolution. This is shown in Fig. 1, where producers and decomposers are involved, as well as 6 driving variables (climatic factors and stand geometry). The input and output to or from the consumers' level is represented by thick arrows marked with C. When considering the right part of Fig. 1 only (without driving variables), the hierarchical diagram describes energy flow as a time dependent process. Solar energy (PhAR) entering the ecosystem is partly reflected (albedo), partly converted into heat, and partly absorbed by plant tissues or by water. In the plants' photosynthesis, a certain fraction of PhAR is converted again

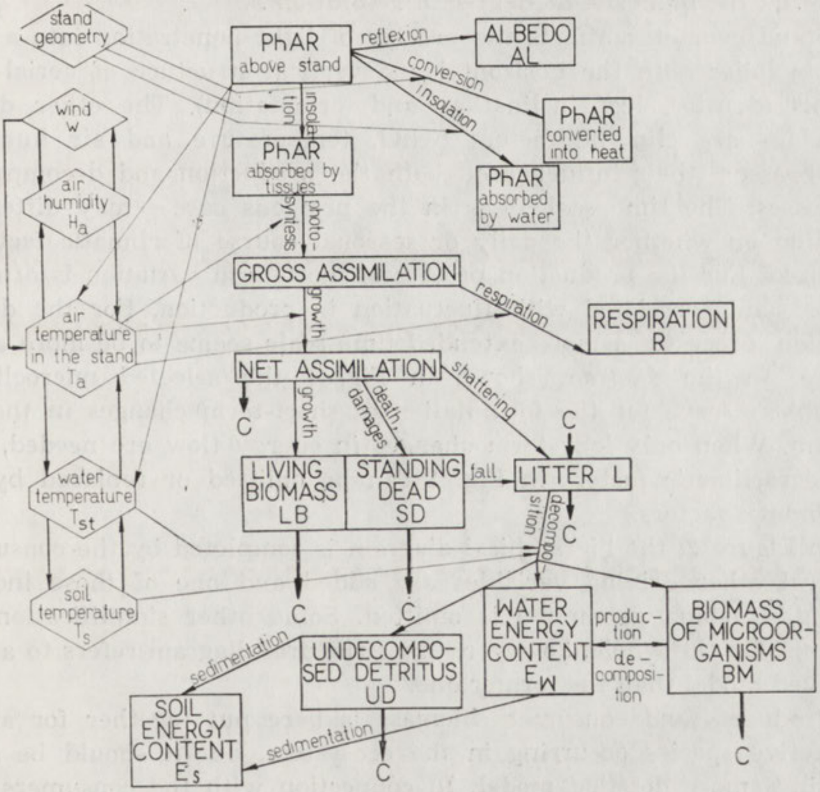

Fig. 1. Hierarchical diagram for construction of a model of energy flow in a littoral ecosystem. C — consumers

into potential chemical energy, a part of which is lost due to respiration. Assimilates used for growth create the living biomass, a fraction of which becomes "standing dead" material during the stand's development (all plants organs having died due to senescence, shading or mechanical damage). Most of the dead plant material, however, eventually forms the detritus layer on the bottom. The rate of decomposition — which is a further pathway of energy flow — is given in the hierarchical diagram by the contents of three boxes (amount of undecomposed detritus, energy content of the organic matter contained in the water and biomass of microorganisms. To complete the balance of energy flowing through the ecosystem, the energy content of the soil must be added, although its accumulation rate is difficult to estimate.

When considering the whole diagram, the energy flow is expressed as a process depending on environmental factors and thus its dynamics is not only "described" but also "explained" by causal interrelationships between the environmental factors and the changes which take place in the ecosystem under the influence of these factors. The more complete is the list of environmental factors significantly influencing the energy flow through the ecosystem, the more complete is the model (e. g., the higher is its degree of resolution).

Stand geometry affects the process of light penetration into a stand and includes both the horizontal and vertical structure of aerial plant organs (density, leaf inclination and orientation). The other driving variables are climatic factors (wind, temperature and air humidity) which assert their influence on both the production and decomposition processes. The time scale — as in the previous case — may differ, depending on whether the daily or seasonal course of climatic factors is required. For the production processes, short-term variation is often recorded and correlated with fluctuation in production. For the decomposition processes a more extended time scale seems to be more appropriate. In the diagram shown in Fig. 1 the selected microclimatic variables serve for the formulation of short-term changes in the ecosystem. When only long-term changes in energy flow are needed, some of microclimatic factors in Fig. 1 can be omitted or replaced by macroclimatic factors.

In Figure 2, the hierarchical diagram is completed by the consumers. Several other driving variables are added and one of those included in Fig. 1 (stand geometry) is omitted. Some other simplifications are obvious. On the whole, however, this structural diagram refers to a more resolved model than the former one.

Producers and consumers biomass is here put together for all the respective species occurring in the ecosystem, but it should be specified in a more detailed model. In connection with the consumers level being introduced into the model, some new intermediate system variables

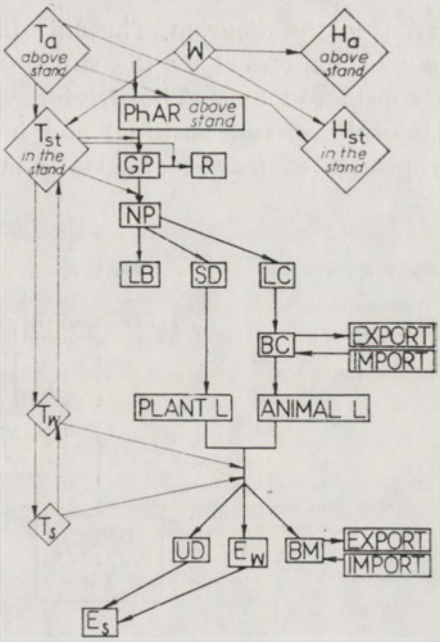

Fig. 2. Hierarchical diagram for the model of energy transfer in a littoral ecosystem. GP — gross plant production, NP — net plant production, LC — losses in plant biomass caused by consumers, BC — consumers biomass

appear in it, which should be determined when the model is formulated, e. g. birth and death rates, ingestion and food uptake rates. The boxes for export and import determine the changes in consumers biomass due to immigration and emigration of animals. The time scale may again differ, as in the two previous cases.

All the diagrams shown in Fig. 1 and 2 describe the energy flow through a freshwater littoral ecosystem. This presentation may appear oversimplified when compared with the real situation. But in a realistic model, all the data needed for filling the boxes of a structural diagram and for formulating the relationships among them, have to be obtained by the devices and means which are at the investigators' disposal. From this point of view, the diagrams in Fig. 1 and 2 represent a programme for experimental work.

3. SUBMODEL OF RADIATION REGIME IN A PURE PHRAGMITES STAND

The other way of building a model is the synthesis of submodels. One example of a submodel is that of radiation regime in a Phragmites stand. The complete hierarchical diagram of this model is given in Fig. 3. This diagram specifies in details the energy input shown in all diagrams in Fig. 1 and 2. The boxes with the thick and thin arrows represent the principal system variables and the driving variables, respectively. Intermediate system variables and parameters are not included because they apper in the formulation of the model which is based on the diagram. The only independent variable is the time which may be expressed by the sun position, if the daily course of variables is considered only. The driving variables can be divided into external (atmosphere, sun position) and internal ones (foliage geometry, optical properties of leaves, and stand structure which means the shoot density in this case), and they include a complex of factors having different importance; hence we may neglect some of the boxes or relationships. The working diagram is thus simplified (Fig. 4). The diffuse radiation from the sky and the radiation transmitted or reflected are put together in one box of "scattered radiation".

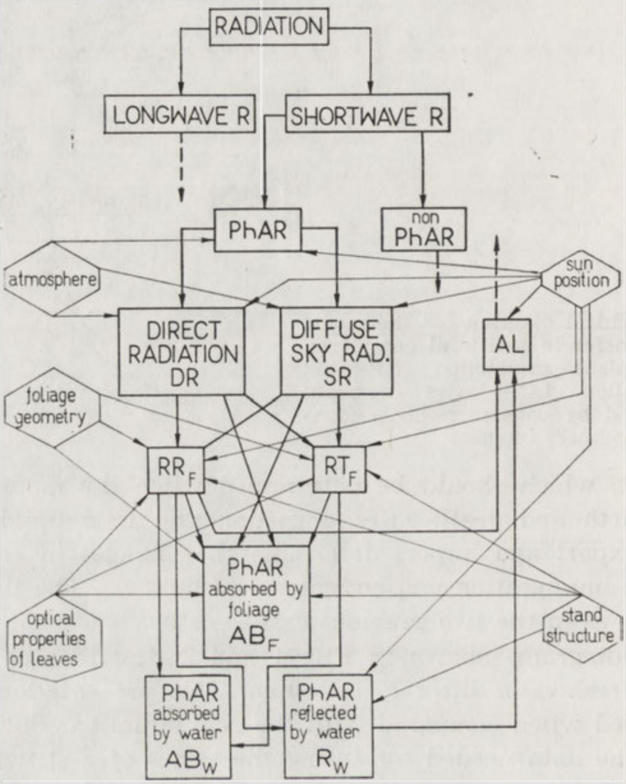

Fig. 3. Hierarchical diagram for a model radiation regime in littoral stand. RR_F — radiation (DR + SR) reflected by foliage, RT_F — radiation (DR + SR) transmitted by foliage

Some other assumptions and simplifications were made in formulating the model. The radiation once transmitted or reflected by a leaf is supposed to be fully absorbed if it reaches another leaf. The spectral distribution of energy in both the direct and diffuse radiation is considered for either clear sky or standard overcast sky. The dependence of the transmission and reflexion coefficients on the angle of incidence was neglected. The structural diagram specified in this way served as

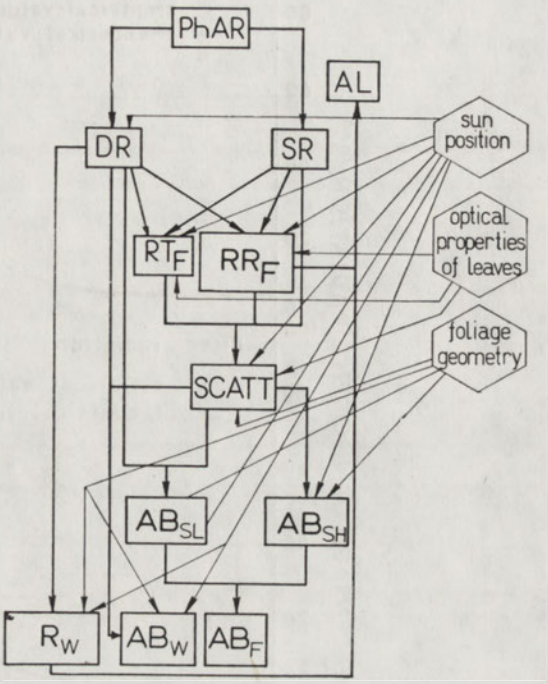

Fig. 4. Hierarchical diagram for model of radiation regime in a pure Phragmites stand. Model was formulated on the basis of measurements during 1970—1971 on Opatovický pond (South Bohemia). SCATT — scattered radiation (SR+ radiation transmitted or reflected by foliage), AB_{SL} absorbed by sunlit leaf area, AB_{SH} absorbed by shaded leaf area

a programme for sampling the experimental data during 1970–1971. From a model based on this diagram, the daily sums of radiation absorbed by the foliage, the extinction (or penetration) of the radiation and its seasonal trends were calculated. The example given in Fig. 5 illustrates the use of the model. For the penetration of PhAR, empirical values are compared with those derived from the model. All the experimental results and details of the model of radiation regime in a Phragmites stand (which, in fact, is only a submodel in a complete model of a particular littoral ecosystem) are being published (Ondok 1973 a, b).

Energy flow through an ecosystem is only one aspect of ecosystem functioning. Similarly, other ecosystem functions can be followed by means of modelling, e.g. the cycling of some ecosystem components: water, nutrients, etc., the dynamics of population development, interference among populations, the spatial organization and succession. Modelling was applied successfully in investigations on photosynthetic processes (Waggoner 1969, de Wit et al. 1970). Models referring to whole ecosystems are still rare. One of them, suggested by Bledsoe et al. (1971) for grasslands can serve as an example.

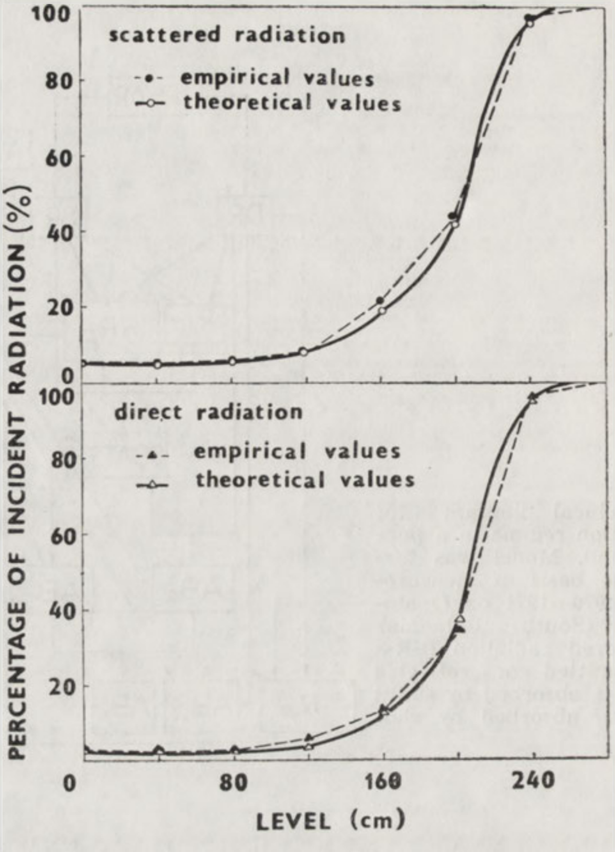

Fig. 5. Empirical and theoretical course of light extinction in a Phragmites stand (May 11, 12–12.30 p.m.). Theoretical values calculated from the formula: $R_i = k \ln (\sin \gamma)/F_i + a$, where R_i — fraction of PhAR incident on i-th level, γ — sun elevation, F_i — cumulative leaf area index above the i-th level, k, a — the constants of the equation

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D. DYKYJOVÁ and D. HRADECKÁ

PRODUCTIVITY OF REED-BED STANDS IN RELATION TO THE ECOTYPE, MICROCLIMATE AND TROPHIC CONDITIONS OF THE HABITAT

Department of Hydrobotany, Institute of Botany, Czechoslovak Academy of Sciences,
Dukelská 145 Třeboň, Czechoslovakia

ABSTRACT

Two Phragmites ecotypes growing in different habitats of the same fishpond littoral in the central European subatlantic climate of South Bohemia (Czechoslovakia) are described. Their productivity are related to water and soil chemistry and meso- and microclimatic conditions investigated during the growing season. The differences in morphological and productive characteristics and in the chemical composition of biomass of the both reed ecotypes are in a good relation with the content of mineral nutrients in the water and in the fishpond bottom, as well as with the changes in the soil, water and air temperatures during the growing season on both habitats.

1. INTRODUCTION

The productivity of each natural community is given: 1. genetically — by the ecotype of the population, 2. geographically — by such parameters as latitude and altitude of the site under investigation, and thus also by the photoperiodism, thermoperiodism and adaptation to the macroclimate, 3. by characteristics of the habitat, especially by the nutrient status of the soil (bottom) and water (in an aquatic environment), and by the meso- and microclimatic conditions.

From this point of view, the productivity of reed stands at two different biotopes in the littoral of the South Bohemian fishpond basin are investigated.

2. MATERIAL AND METHODS

DESCRIPTION OF THE BIOTOPES

Two different habitats in the eastern littoral and limoso-terrestrial (marsh) zone of the Opatovický pond (area 175 ha) were compared (Fig. 1). The "littoral" reed ecotype grows in the erosion zone of the fishpond littoral, with the water level varying from 10 to 120 cm, in dependence on the character of the growing season and on the fishpond management. The stands is exposed to the wind and wave erosion from the side of the open surface of the pond. The decomposition of the autochthonous litter is very rapid. The bottom is sandy with little accumulation of sapropel and reed drift, and with a blue-gray clay in the subsoil. The other "terrestrial" Phragmites ecotype develops a large monospecific stand in a marsh adjacent to the fishpond. It is never actually flooded. However, during the spring or autumnal elevation of the fishpond water level, the waste water from the channel going from nearly farm stable across the reed stand subflow

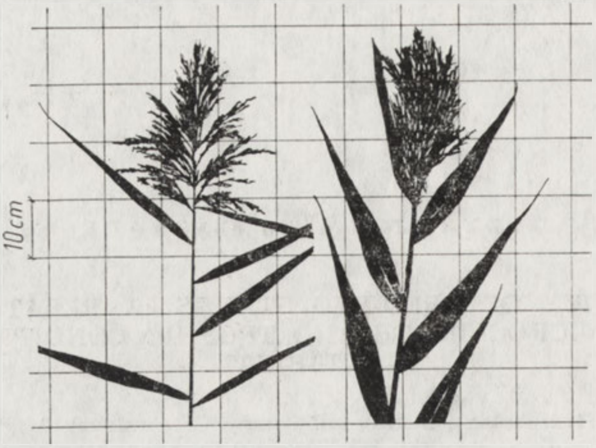

Fig. 1. Morphological differences between littoral (left) and terrestrial (right) ecotype of Phragmites

the whole stand area. The accumulated autochthonous organic material (litter) decomposes slowly and gives rise to a high layer of a black wet gyttja with typical features of anaerobic and saprobic marshes and with accumulation of certain nutrients. The differences between the two habitats are reflected in the different physiognomy, growth and production characteristics of both reed ecotypes.

ANALYSIS OF PRODUCTION

The shoot biomass is harvested at the time of maximum development of the aerial plant parts (i.e. at the time of flowering or shortly before it). In the invasion zone of the fully developed stand 4 or 5 samples were harvested from an area of 0.5 or 1.0 m^2, the shoots being cut at the ground level. The leaf area was measured with a photoelectric planimeter (12% of area were added as a correction for the surface of green parts of the culms). The below-ground biomass (rhizomes, tillers and roots) was estimated from monoliths excavated to the depth of about 1 m at the time when the fishpond was drained. The anual increments in below-ground biomass were estimated indirectly from the root/shoot ratio, found in hydroponic cultivations of several years old reed polycormones (see Dykyjová et al. 1971).

WATER, SOIL AND BIOMASS ANALYSES

The nutrient content of the fishpond bottom was determined in the oven-dried ground soil samples, using the common methods of chemical soil analyses (details of the methods used will be described in another paper). The analyses of the fishpond and waste water were made in the samples taken at different seasonal intervals, but only those corresponding with the date of biomass harvesting are used. The nutrients uptake by the stand (above and below-ground biomass) was estimated in the oven-dried and finely ground samples harvested at the time of maximum stand development.

CLIMATIC MEASUREMENTS

The characteristics of local mesoclimate were recorded in a mesoclimatological station in Algological Laboratory CzAS at Třeboň and the average values of 1955 to 1969 are presented in Table I. The daily totals of global radiation were recorded with a solarimeter (Kipp and Zonnen, type CM3). Air, water and soil temperatures in the biotopes were registered continuously. In some cases, daily courses of temperature were measured with standard station and soil thermometers. Relative air humidity was recorded with a thermohydrograph (Metra, type 859). The microclimatic data in both biotopes — air, water and soil temperatures — were registered continuously with the values of a nearly standard meteorological station (see also Dykyjová et al. 1971).

Table I. Climatic and geographic characteristics of the station at Třeboň (49°00′N, 430 m a.s.l., temperature, subhumide)

	Average for 1955—1969					
Mean annual precipitation	660—680 mm					
Mean annual temperature	7.5°C					
Mean annual sunshine duration (1965—1969)	1641 hr					
Length of growin season	April—Sept.					
Mean incident global radiation per season (1964—1970)	693,700 kcal/m²					
Maximum day length (June)	16 hr 15 min					
Mean daily temperature of the warmest month (July)	17.2°C					
Mean daily temperature of the coldest month (January)	—2.0°C					
Temperature of the warmest day	32.5°C					
Temperature of the coldest day	—22.4°C					
	1967					
	April	May	June	July	Aug.	Sept.
Mean air temperature (°C)	7.1	12.5	15.4	17.0	16.2	12.5
Mean day length (hr and min)	13.40	15.00	16.10	15.50	14.25	12.50
Mean totals of PhAR (kcal/m²/day)	1470	1908	1926	2183	1670	1161
Mean global irradiation (cal/cm²/day)	225	425	428	485	371	258
Total global irradiation per season (kcal/m²)	676,800					

3. RESULTS AND DISCUSSION

The evidence that shoot size and productivity of Phragmites stand depends on the supply of mineral nutrients is given by many authors, e.g. Gorham, Pearsall (1956), Allen, Pearsall (1963), Rudescu (1965, 1968), Björk (1967), and others. In habitats auxotrophicated through mineral and organic manuring (as it is in the case of the managed fishponds) the reed stand productivity may be limited by other factors than by the nutrient content of the substratum. It has been proved by Liubich, Arbuzova (1964) that reed takes up mineral nutrients not only via the roots penetrating into the bottom mud or the litter accumulated in the marshes but also via the adventive roots growing only in the water. The trophic conditions in both the water and the bottom thus control the inorganic nutrition of the reed stands. More nutrients are accumulated in the plant biomass in a highly eutrophic habitat than in an oligotrophic one. The decomposed autochthonous organic material in such a rich habitat is a good source of nutrients to be accumulated in the plant biomass, and this feedback mechanism is afforced if nutrients from a manured fishpond or waste waters are at disposal.

Figure 2 shows the trophic differences of both reed biotopes. The habitat of the terrestrial reed ecotype is characterized by a higher nutrient content in the accumulated organic material. Also the water from the waste channel has a higher nutrient content than the fishpond water and contributes to the nutrient accumulation in the substratum as well as in the plant biomass. On the other hand, the littoral reed biotope with a poor accumulation of organic sapropel on a sandy bottom produces a different reed ecotype with taller culms and narrower leaves, which is less productive and shows a poorer nutrient accumulation in the biomass.

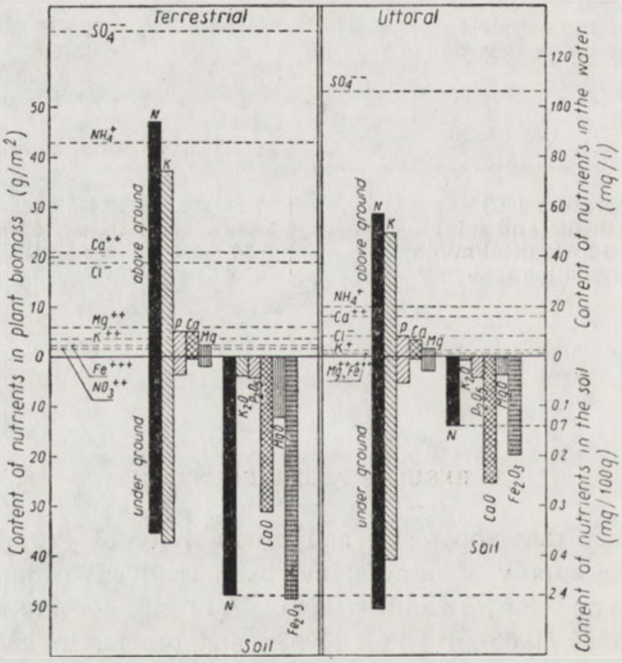

Fig. 2. Hydrochemical and pedochemical characteristics of the littoral (1) and terrestrial (2) habitats

The differences in trophic conditions are correlated with differences in the microclimatic conditions.

Some results of microclimatic measurements taken during three seasons are presented in Fig. 3—7. The more detailed analyses of mi-

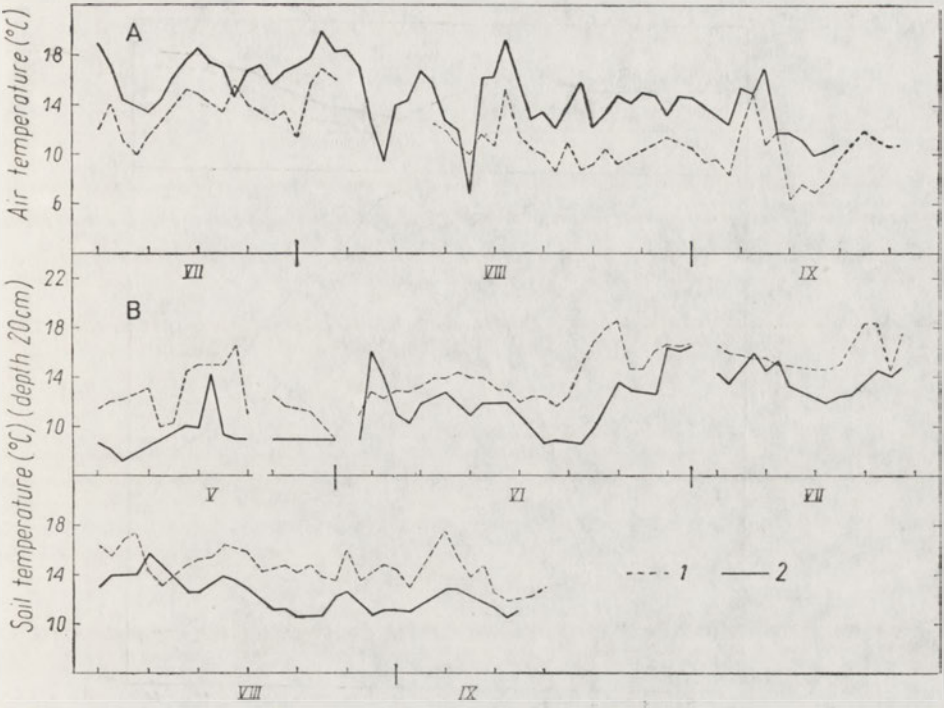

Fig. 3. Course of the mean daily temperature in stands of littoral (1) and terrestrial (2)biotope and in the standard meteorological screen (3) during the summer months of 1967. A — air (150 cm above ground), B — soil (depth 20 cm)

croclimatic conditions will be published in another paper. Figure 3 presents the course of the daily mean air and soil temperatures in the littoral and terrestrial stands during the growing season of 1967, in comparison with the course of mean temperature in a standard meteorological screen at the station. During the whole season, the daily mean air temperatures in the terrestrial stand are higher than in the littoral stand, which is more exposed to wind from the side of the open surface of the pond. The terrestrial biotope is sheltered and hence warmer, protected against wind by a high stand of a neighbouring forest and thus fully insolated from SE side. On the other hand, the swamp soil of the terrestrial biotope warms up very slowly. In this way the root system of the terrestrial reed ecotype is adapted to the absorption of nutrients under lower soil temperatures which is more suitable to the sorption of nutrients under anaerobic conditions, in a deep layer of gyttja.

Similarly, the daily course of air temperature (Fig. 4 and 5) shows higher values in the terrestrial stand during the summer months.

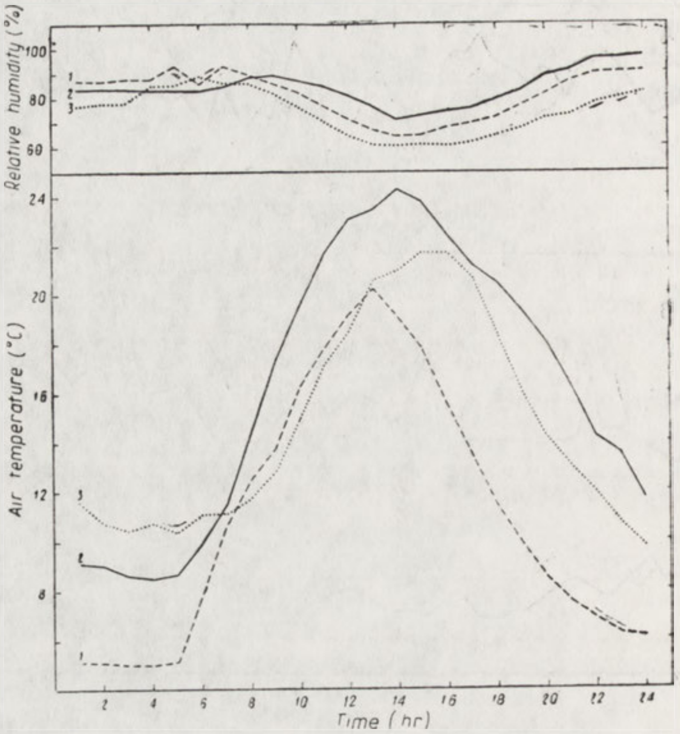

Fig. 4. Daily course of relative air humidity and air temperature (150 cm above ground) in the littoral (1) and terrestrial (2) biotope, and in a standard meteorological screen (3) in the mesoclimatological station at Třeboň

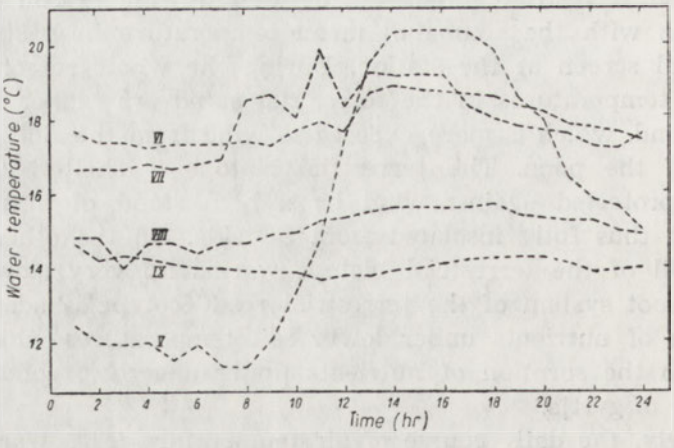

Fig. 5. Daily changes in water temperature (depth 10 cm) in the littoral habitat (August 1967)

The daily course of water temperature measured at the depth of 10 cm in the littoral biotope (Fig. 6) shows that the shallow water in the erosion zone warms up very easily and with the exception of the spring months (May), no large differences exist between the day and night temperatures.

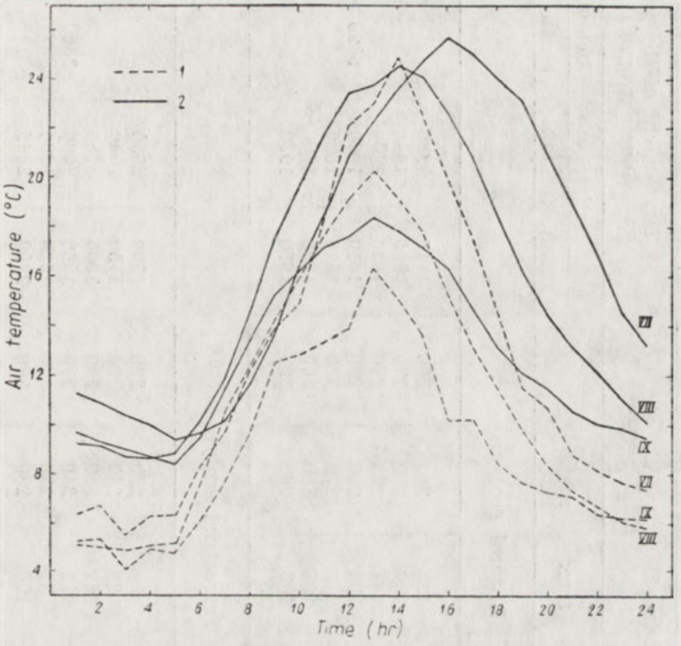

Fig. 6. Daily changes in air temperature (150 cm above ground) in the littoral (1) and terrestrial (2) habitat during the summer months of 1967

The soil temperatures measured at different depth in both biotopes are higher in the littoral biotope than they are in the swamp, during the whole season. Also the daily fluctuations are more pronounced in the littoral biotope especially in the summer months (Fig. 7). The

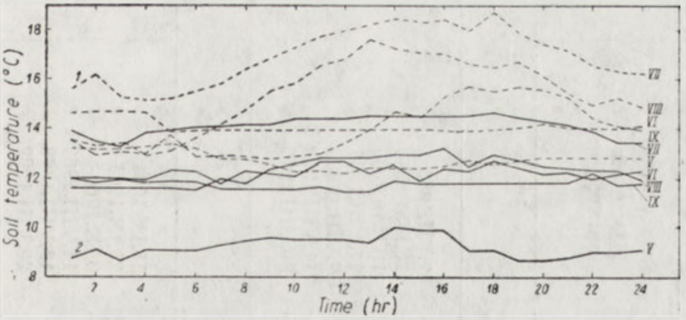

Fig. 7. Daily changes in soil temperature in the littoral (1) and terrestrial (2) habitats during the growing season of 1967 (depth 20 cm)

Table II. The dry matter production (standing crop) and some other production characteristics of the reed stands at the littoral and terrestrial habitats (1964—1970)

Date of harvesting	Length of growing season (successive day)	Number of shoots		Shoot height (cm)		Dry weight of the whole biomass (g/m²)				LAI*
						aerial		below-ground		
		mean	max	mean	max	mean	max	mean	max	
Littoral ecotype										
7.VII.1965	78	104	120	200	260	1110	1380			5.3
28.IX.1965	159	108	130	200	270	1535	1540			—
1.IX.1966	132	127	144	225	270	1920	2200			9.5
11.VIII.1967	112	92	108	220	260	1610	1800	5890	8560	6.2
7.VIII.1968	108	112	118	220	280	1370	1630			3.8
11.VIII.1969	112	80	101	250	300	1330	1600			7.8
20.VIII.1970	121	99	138	260	320	1650	1930			4.9
Terrestrial ecotype										
16.IX.1964	147			230	290	1990	2050			
28.IX.1965	159	83	88	240	320	1750	2040			
8.IX.1966	139	142	154	230	290	3000	3250			11.5
14.VIII.1967	115	103	112	240	270	1860	2000	3360	3700	6.9
15.VIII.1968	116	72	81	238	320	1520	1650			5.5
20.VIII.1969	121	106	106	230	280	2290	2335		5930	9.3

* Leaf Area Index, i. e. the whole leaf surface area per ground surface area.

temperature conditions in the swamp biotope are more stable which has many consequences for the onset of shoot sprouting, for nutrient uptake and for the growth and performance of the terrestrial Phragmites.

The production characteristics of the reed stands at the littoral and terrestrial biotope are presented in Table II.

Up to now we have little information on the relation between microclimate and productivity of reed stands. The data by Demidovskaya, Kirichenko (1964) from the arid climate of Kazakhstan cannot be compared with our results. Our results thus can contribute to a better understanding of the correlation between microclimatic factors and productivity of freshwater littoral communities.

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B. ÚLEHLOVÁ, Š. HUSÁK and J. DVOŘAK

MINERAL CYCLES IN REED STANDS OF NESYT FISHPOND IN SOUTHERN MORAVIA

Institute of Botany, Czechoslovak Academy of Sciences,
Stará 18, Brno, Czechoslovakia

ABSTRACT

Matter turnover and mineral cycles were studied in reed stands of the shoreline of Nesyt fishpond in southern Moravia, near the Lednice village. The following matters were discussed: chemical composition of water, sapropel and subsoil, annual primary production and chemical composition of plant matter, mineral composition of standing dead and litter, and internal cycles of N and P in water.

1. INTRODUCTION

Mineral cycles represent important characteristics of natural ecosystems. Comprehensive data on mineral cycles in woodland biomes have been published by Duvigneaud (1967) and Rapp (1971). A series of biomes ranging from tajga to steppes have been compared as regards the mineral constituents by Rodin, Basilevič (1968). A general discussion on the importance of bio- and geo-cycles, and on factors controlling the cycling of elements, can be found in Ovington 1968).

By the present study we intended to provide basic data concerning the matter turnover and mineral cycles in reed stands of the Nesyt fishpond in southern Moravia. The object of our study were six main compartments of the reed ecosystem shown in the model diagram in Fig. 1.

2. MATERIAL AND METHODS

The Nesyt fishpond, the size of which is about 300 ha and the water volume of about 4500,000 m^3, is situated near the Lednice village (48°48′N, 34°21′E, 175 m a.s.l.). About 30 ha, i.e. 10% of the fishpond area is covered with reed stands. From those about 50% are stands of pure *Phragmites communis*, 20% of pure *Typha angustifolia* and 30% of mixed stands.

Sapropels represent the end product of decomposition processes taking place in the fishpond. In 1969 to 1970 the chemical features of the sapropels, sediments and bottom soils were investigated at five selected sites. The sapropel layers are normally 15 to 25 cm thick, black, and smelling. The bottom soils were sampled from the depth of 25 to 40 cm; they were usually enriched with dark organic substances, and were sandy to clayey. The sapropels and underlying bottom soils were sampled at monthly intervals. Dry matter content was estimated on subsamples and the air-dried main samples were analysed for the contents of humus, nitrogen, calcium, magnesium, potasium, sodium, ammonium, nitrates and available phosphates, using methods described by Jackson (1962). Water samples from five different sites were analysed within 24 hr from sam-

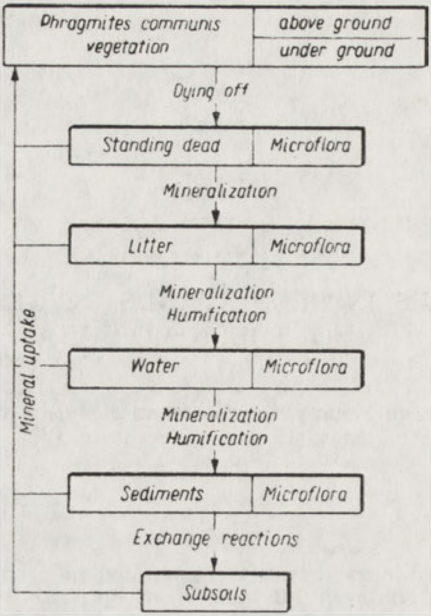

Fig. 1. A model of mineral cycles in reed stands ecosystems

pling at monthly intervals during 1969 and 1970. The contents of mineral substances and the pH were estimated by standard methods (Hofmann et al. 1965). In 1970 selected mineral constituents of Phragmites plant material were estimated at one month intervals during the vegetative period. The plant material sampled was air-dried, powdered and analysed essentially according to methods recommended by Koppová et al. (1955).

A more detailed insight on the internal cycles of phosphorus and nitrogen in the water in stands of Phragmites was attempted in 1971. The contents of a. total phosphorus and nitrogen, b. microbial phosphorus and nitrogen, and c. mineral forms of phosphorus (i.e. phosphates) and nitrogen (i.e. ammonium, nitrite, and nitrate nitrogen) were estimated periodically using filtration technique and methods described by Golterman, Clymo (1969). The contents of dissolved organic phosphorus and nitrogen were calculated from differences. The counts of microorganisms belonging to selected physiological groups were also estimated.

2. RESULTS AND DISCUSSION

The results of sapropel and bottom soil analyses are given in Table I. Contents of all the components estimated were lower in bottom soils than in sapropels, with the obvious exception of dry matter content. The data obtained for 1970 differ somewhat from those for 1969. This probably results from oxidative mineralization in sapropels and bottom soils, following the drainage of the fishpond and the harvest of fish crop, during the autumn and winter of 1969/1970. Most of the sampling sites differed from each other with respect to the

Table I. Composition of bottom soil and sapropels in reed stands of Nesyt fishpond

Contents		Bottom soil							Sapropel							
		1969	1970	Mean	Spatial variations (1970) Site				1969	1970	Mean	Spatial variations (1970) Site				
					1	2	4	5				1	2	3	4	5
Share of d. wt. in fresh wt. (%)		67.5	63.8	65.6	60.6	66.5	54.7	73.4	44.6	46.6	45.6	42.4	11.8	82.4	45.9	51.2
Organic matter in d. wt (%)		3.70	3.70	3.70	4.43	3.16	5.72	1.45	8.75	9.70	9.20	7.53	27.75	0.85	7.30	5.06
N total in d. wt. (%)		0.17	0.20	0.18	0.22	0.16	0.30	0.12	0.42	0.65	0.53	0.47	2.01	0.04	0.42	0.30
mg/100 g d. wt.	NH_4	3.0	6.2	4.6	6.6	7.3	6.1	5.0	6.8	11.0	8.9	11.1	23.8	5.1	7.9	7.1
	NO_3	1.7	1.3	1.5	1.3	1.4	1.3	1.2	2.30	5.87	4.10	4.9	18.1	1.6	1.9	2.8
	PO_4	2.5	—	—	—	—	—	—	3.6	—	—	—	—	—	—	—
	K	24.7	20.1	22.4	20.2	8.7	33.5	18.0	34.3	32.7	33.5	48.6	53.5	5.4	32.5	22.9
	Na	8.2	10.8	9.5	12.6	—	8.2	11.5	16.6	15.2	15.9	20.1	24.9	3.1	15.0	13.1
	Ca	307	257	282	288	162	308	269	435	330	382	339	472	221	342	279
	Mg	55.0	60.0	60.0	67.0	54.0	96.0	44.0	61.0	57.4	59.2	70.0	49.0	42.0	50.0	76.0

chemical composition of sapropels and the underlying bottom soils, to their zoning in the pond and to the texture of the bottom soil.

The results indicate that sapropels and the respective bottom soils are systems related by means of exchange reactions, diffusion, sorption processes, etc. Changes induced in sapropels by fishpond management are accompanied by concurrent changes of the bottom soil. Spatial variation of chemical properties of the sapropels and bottom soils appears to be considerably higher than the seasonal variation.

Many authors have discussed the specific character of the Nesyt fishpond from the biological point of view, and most of them suggested that it is controlled above all by the water chemistry.

Table II presents the results of water analyses. Differences between the two years are probably again due to the fishpond management, as was the case of sapropels and bottom soils. The spatial variation of water composition is much less than that observed in sapropels and bottom soils. The respective F data for spatial and seasonal variations are shown in Table III. In contrast to sapropels and bottom soils, the water displayed considerable seasonal variations of chemical composition.

Table II. Composition of water in reed stands of Nesyt fishpond

Contents (mg/l)	1969	1970	Mean	Spatial variations (1970). Site				
				1	2	3	4	5
NH_4	—	0.69	—	0.70	0.35	1.02	0.89	0.51
NO_3	0.46	3.25	1.85	4.70	2.07	2.52	4.99	1.97
PO_4	2.80	2.25	2.66	2.88	1.96	2.56	3.19	2.03
K	36.16	24.50	30.33	27.8	23.2	24.2	26.5	20.7
Na	77.3	56.1	66.7	56.9	54.2	53.8	56.2	59.3
Ca	89.74	73.00	81.37	98.8	64.7	57.3	83.9	60.5
Mg	39.56	58.90	49.23	51.2	62.3	63.3	56.2	61.7

Table IV is compiled according to Husák (1971). It gives the contents of mineral elements in plants of *Phragmites communis* during their onthogenesis and in different organs of the plants.

Young plants have the highest contents of most minerals. During onthogenesis, the mineral contents in plant tissues diminish, with the exceptions of Na and Ca. The greatest changes are recorded in potassium and nitrogen contents.

As suggested by the data given, the transfer of minerals between individual plant organs seems to be highly important. In all cases except sodium the concentration of minerals is higher in leaves than in stems.

Table III. Seasonal and spatial variations of chemical features of water in *Phragmites communis* habitats (F values for variance analyses)

	Spatial	Seasonal
pH	5.79 HS	11.08 HS
NH_4	1.85	9.68 HS
NO_3	1.12	10.49 HS
PO_4	0.87	5.44 HS
K	7.06 HS	7.80 HS
Na	3.14 S	28.32 HS
Ca	11.39 HS	5.68 HS
Mg	11.93 HS	188.63 HS
SO_4	2.48	3.74 S
Cl	2.16	5.99 HS
HCO_3	4.80 HS	8.03 HS

S — significant, HS — high significant

Table IV. Contents of minerals in plant tissues of *Phragmites communis* (according to Husák 1971)

Contents (mg/100g d. wt.)	Above-ground organs						Underground organs	
	Young plants		Ripe plants		Dying off plants			
	Stems	Leaves	Stems	Leaves	Stems	Leaves	Rhizomes	Roots
N	992	4410	808	3160	772	3013	919	992
P	293	353	172	309	180	231	406	309
K	1123	1060	509	840	325	499	709	459
Na	44	31	41	31	63	27	184	206
Ca	76	190	44	319	61	376	386	104
Mg	77	216	38	270	69	231	401	340

Distinct changes in mineral composition of plants take place during their dying off as expected. The greatest decrease has again been noticed in potassium content, and an important decrease also in nitrogen content. The concentrations of sodium, calcium and magnesium increase in stems of ageing plants. Underground organs (in comparison with aerial parts of the plant) are rich in phosphorus, sodium, calcium and — which is surprising — especially in magnesium.

The contents of mineral elements in individual structural units of reed-stand ecosystem per m^2 were calculated from Tables I, II, and IV, and are given in Table V. It shows the average chemical composition of the compartments under study and yields some informations about the specificity of cycles of individual mineral elements.

The input of mineral elements through rainfall is important with respect to Ca, Na, and N. The mineral contents in plant material is interesting because of specific distribution patterns of elements in both aerial and underground organs. Sodium, calcium and magnesium tend

Table V. Mineral cycles in *Phragmites communis* stand (g/m^2)

Specification			N	P	K	Na	Ca	Mg
Rainfall (acc. to Úlehlová, Ostry 1972)			0.8	0.06	0.8	1.0	3.8	—
Vegetation	aboveground	stems	11.14	2.47	7.02	0.56	0.60	0.52
		leaves	12.29	1.20	3.29	0.12	1.24	1.05
		total	23.44	3.67	10.28	0.68	1.84	1.57
	underground	rhizomes	19.06	8.45	14.71	3.81	8.01	8.32
		roots	2.86	0.92	1.37	0.61	3.11	1.01
		total	21.92	9.37	16.08	4.42	11.12	9.33
	Total		45.35	13.04	26.36	5.10	12.96	10.90
Standing dead	stems		11.33	2.74	4.77	0.92	0.89	1.01
	leaves		1.36	0.10	0.22	0.01	0.17	0.10
	total		12.69	2.84	4.99	0.93	1.06	1.11

	N	NH_4	NO_3	PO_4	K	Na	Ca	Mg
Water	—	0.21	0.55	0.79	9.01	20.00	24.38	14.77
Sapropel	583	9.79	4.50	3.96	36.85	17.49	421.0	65.00
Bottom soil	270	6.9	2.25	3.75	33.60	14.25	423.0	90.00

to be accumulated predominately by underground organs, while nitrogen, phosphorus and potassium are distributed more evenly. Such differences reflect different biochemical properties and physiological roles of the respective constituents. In connection with further data of the Table V they also reflect differences among the whole cycles of individual elements. Thus nitrogen and phosphorus appear to be competed for, as low quantities of available forms can be found in water, sapropel and bottom soil, while the bound forms are present in much higher amounts. On the other hand, both the monovalent and bivalent cations are available in higher quantities in the substrates.

A comparison of the amounts of minerals (in g per m^2) bound in mature and standing dead shoots of *Phragmites communis*, reveals that nitrogen, phosphorus and potassium are reexported from the ageing shoots, while sodium, magnesium and calcium accumulated to a considerable degree by the shoots, remain there, and in that way become disposed off by the plants.

Differences in the behaviour of potassium and sodium, known from other plant species, especially from cultured plants, are documented here, as regards the uptake and retranslocation by shoots, for Phragmites.

The results of the study of internal cycles of nitrogen and phosphorus in the water are presented in Fig. 2 and 3. There are distinct changes in microbial counts during the period of investigation. First small

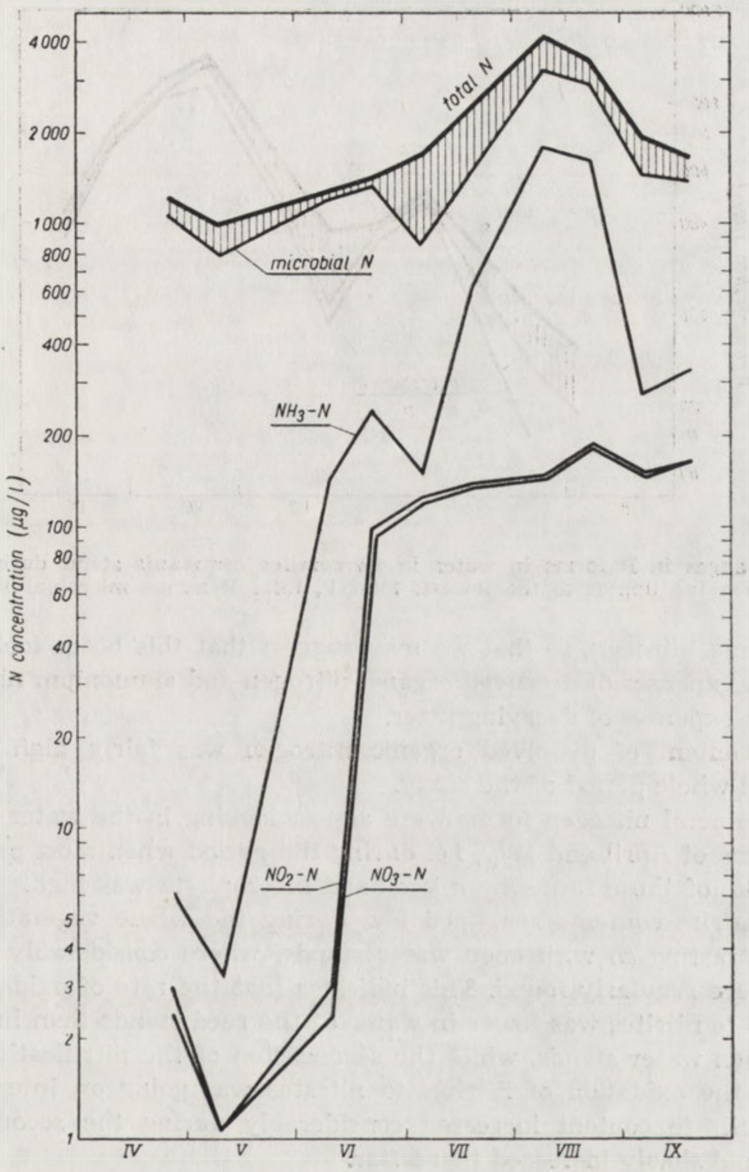

Fig. 2. Changes in different N forms in water in *Phragmites communis* stand during 1971. Curves from the uppest to the lowest: total N, total N minus microbial N, NH_3-N, NO_2-N, NO_3-N

increase in microbial population occurred in May, the second one, far more important, towards the end of June. The microbial counts and the microbial nitrogen remained high since the completion of the main growth period of the reed plants. The microbial explosion was accompanied by concurrent decrease of dissolved organic nitrogen and also

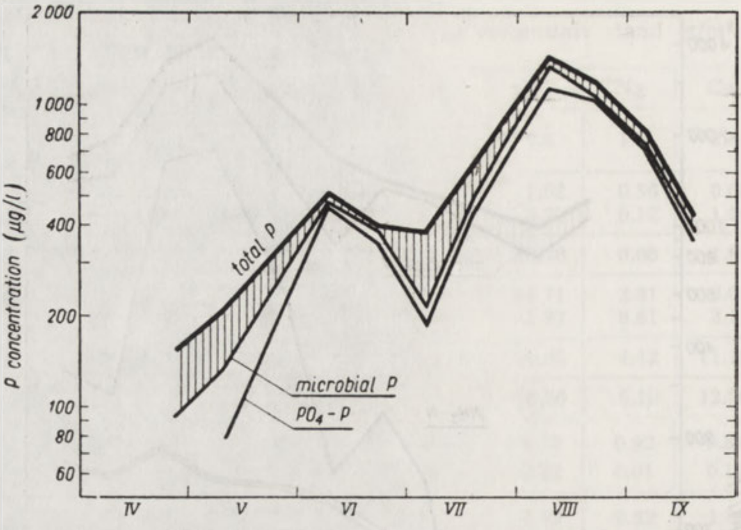

Fig. 3. Changes in P forms in water in *Phragmites communis* stand during 1971. Curves from the uppest to the lowest: total P, total P minus microbial P, PO_4-P

of ammonia nitrogen, so that we may suggest that this boom took place partly on expenses of dissolved organic nitrogen and ammonium nitrogen, partly on expenses of decaying litter.

The content of dissolved organic nitrogen was fairly high throughout the whole period of the study.

The mineral nitrogen forms were almost lacking in the water during the months of April and May, i.e. during the period when most probably the uptake of those forms by micro- and macrophyta was high.

The nitrite contents remained low during the whole vegetation period, contrasting so with open water stands, where considerably higher values were regularly found. This indicates that the rate of oxidation of ammonia to nitrites was lower in water of the reed stands than in water of the open water stands, while the second step of the nitrification process, i.e. the oxidation of nitrites to nitrates was going on intensively.

The nitrate content increased considerably during the second half of June and slowly increased thereafter.

The contents of ammonia nitrogen showed greatest changes during the vegetation period. The period with the high contents of ammonium nitrogen during August, reflect the high intensity of decomposition processes especially ammonification taking place in the reed stands. The delay in the increase of nitrate contents with respect to the increase of ammonia and the slow subsequent increase of nitrates indicate that besides ammonia concentration other factors participated in control of the level of nitrates.

We may conclude that the internal cycle of nitrogen in water of reed stands is a fairly complicated process with a number of different mutually more or less interrelated steps.

The internal cycle is rather different in the case of phosphorus: although the changes reflecting the microbial booms occurred in the same periods of the year as in nitrogen cycle. The concentration of dissolved organic phosphorus was very low. The initial increase in microbial counts as well as the main explosion were followed by an increase of total phosphorus and phosphate contents. The microbial boom is documented by a concurrent increase of microbial phosphorus and phosphate contents.

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	131—136	1973

F. KLÖTZLI and S. ZÜST

NITROGEN REGIME IN REED-BEDS

Institute of Geobotany, Swiss Federal Institute of Technology, Zürichbergstrasse 38,
8044 Zürich, Switzerland

ABSTRACT

Plant available nitrogen in fresh and incubated soil samples was determined in the main rhizome horizon of reed-beds in north-eastern Switzerland. Fresh soil samples show N values around 1–2 mg which is quite high compared to forest or meadow soils. In incubated samples the N values are around 2–3 mg, in extreme cases up to 10 mg/100 g dry soil (density around 1.2 kg/dm^3). Compared with total N in the same layer, these high values must probably be explained by additional uptake from lake detritus. There is no significant difference between samples of "reed-death" areas under highly eutrophic conditions and samples of well-growing reed-beds. Uncut highly productive stands show significantly higher nitrification. Suggestions are made as to the management of reed-beds considering the noxious influence of lake eutrophication.

1. INTRODUCTION

Estimating the factors which might cause "reed-death" (Klötzli 1973), special attention was given to the eutrophication of the lakes of the Swiss Midlands. Nitrogen (nitrate and ammonium), being one of the factors causing reduction of sclerenchymatic tissues in higher concentrations, was thought to be, together with phosphate, one of the chief indicators of potential and actual reed-death areas.

According to the investigations of Ellenberg (1964), León (1968), Williams (1968) and Klötzli (1969) on N turnover on wet sites, our main work in the whole scale of mineral turnover in reed-beds was concentrated on N regime, plant-available nitrogen being one of the decisive factors controlling productivity of terrestrial ecosystems.

Especially the influence of man and his activities, e.g. harvesting practices, on N regime was assessed (see preliminary report of Züst, in press). Furthermore it was of interest to investigate if that phenomenon called "reed-death" was connected with a special nutrient turnover. Finally the question was examined if the general eutrophication of the lake shores turned out to raise the amount of nitrate significantly compared with other investigations on other wet sites.

Complete balances of N turnover and turnover of the other elements will be treated later.

2. METHODS AND MATERIAL

Methods of N analysis (incubation method) were described in detail recently by Gigon (1968). Mixed soil samples were taken with an auger from the main rhizome horizon (15–25 cm under the surface) particularly in March till May and in September till December.

Nitrate was analysed by the 2,4-xylenol method, NH_3 by the Conway method. The special area including exclosures is the same as in Klötzli (1973) and is divided into 12 divisions (4 management practises, 3 repetitions).

3. RESULTS

Seasonal fluctuations

Obviously the characteristics of the site mark definite seasonal fluctuations (Fig. 1). During low water (December till March) winter frost inhibits nitrification and high water in summer (June till August) has a similar effect (formation of NH_4^+ only). During the summer months a considerable amount of lake detritus is deposited (5 to 15 kg/m² of fresh material in the drift zone). This material is partly mineralized in the first warmer month (March) and together with the action of frost explains the high nitrification values in spring and the generally elevated values towards autumn (N_{mom}). Incubated samples give values which are about twice as high. Comparable values result from autumn samples. 1971, with exceedingly low water, gave the opportunity to analyse samples the whole year over (except for one summer month). These values mount up to 10 mg N_{acc}/100 g dry soil ($\approx$120 mg N/dcm³) and are higher than other measurements so far assessed on wet sites. (Detailed graphs for N, water, pH in concluding paper).

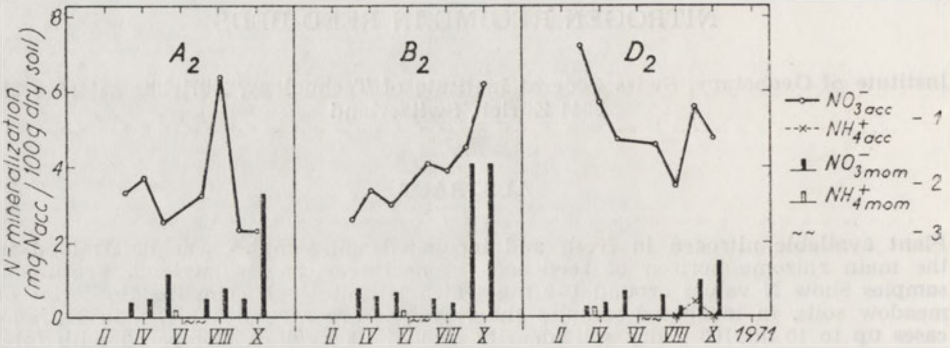

Fig. 1. N-mineralization during the dry growing season 1971. 1 — accumulated plant available nitrogen during 6 weeks incubation time, 25°C, 95% air humidity, 2 — momentary available nitrogen, 3 — inundation period

Effects of management and reed-death

Analogous to the effect of mulch on a meadow, uncut areas and cut, but mulched areas show a marked increase in nitrification (Fig. 2, see also Fig. 5 in Klötzli in press; Table I). Uncut areas can be characterized by remarkably thick stems, rather low density but highest average productivity in the special investigation area. Their nitrification is about twice as high. But also stands of low vitality (high density, low productivity) still show normal values and even stands with no living stem have sometimes nitrification values going on an average as high as 7 mg N_{acc}/100 g dry soil; on the other hand bare former reed stands can also have very low values. Reed-death therefore does not inhibit or accelerate significantly normal N-cycling of reed soil.

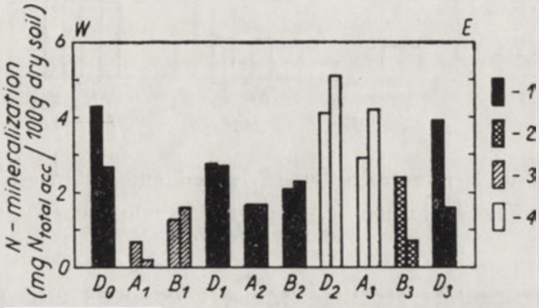

Fig. 2. Toposequence (West–East) of mean N-mineralization (without C-divisions) in 1967–1971. Vitality of stand: 1 — high, 2 — medium, 3 — low, 4 — gap

Table I. Accumulation of plant-available nitrogen (N_{acc}) and nitrogen in fresh samples (N_{mom})

Year	Division	N (mg/100 g dry soil)
		accumulated
1968—1971	A, B, D,	2—3
1970 (wet autumn)	A, B, D,	<0.5
1971 (dry autumn)	A, B, D,	2—10
		momentary
1968—1971	A	0.5—1 (extreme 10)
	B	0.5—1 (extreme 3)
	B fenced	2—3
	D	1—2 (extreme 5)

Management: A — mowing+removal of litter, B — mowing, no removal, D — no mowing.

Effects of exclosures

The exclosure prevents algae-mats from driving in and has therefore a beneficial effect on the development of reed-belts (compare Klötzli in press). Such stands show normally a higher productivity than the surrounding division under the same management (Fig. 3). Uncut stands especially have also higher N values than the unfenced parts of the same division (average up to 4.6 mg N_{acc}/100 g dry soil), in cut stands these values are lower (around 2 mg).

The construction of the exclosure gave the opportunity to analyse the effects of birds (sea-gulls) on nitrification; they sit on the enclosu-

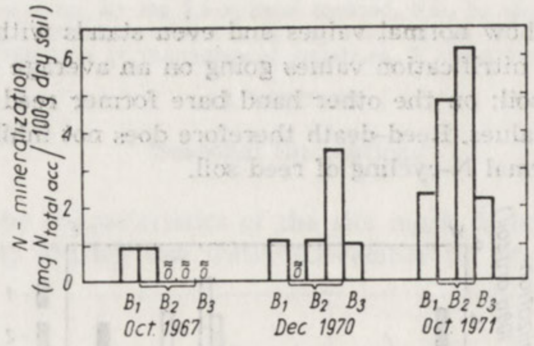

Fig. 3. Comparison of N-mineralization in fenced and unfenced areas (B-divisions). o. — open (uncovered) exclosure, c. — covered exclosure, 0 — values close to $\overset{\approx}{0}$ (denitrification)

res and their droppings fertilize these reed-beds and stimulate nitrification in a way that the N_{acc} values are doubled on an average (N_{acc} up to 6 mg, normal in incovered fence 2 mg). The same local eutrophication induces thick stems but with underdeveloped sclerenchymatic tissues.

4. DISCUSSION AND CONCLUSION

Comparing the results of total nitrogen accumulation (on a volumina basis) on wet sites — moist forests (Ellenberg 1964, Klötzli 1969) and moist meadows (León 1968, Williams 1968, Yerly 1971) — our results (2—3 mg/100 cm³) seem to be quite high compared with the results of Hürlimann (1951): 0.1 mg NO_3 — N, but are on an average only half as high as those obtained from reed-belts in the inundation area of the River Elbe near Hamburg, both being highly eutrophicated areas (Meyer 1957): 5—5.5 mg/100 cm³, density being around 120 g/ /100 cm³ of dry soil (Table II). This sounds rather astonishing considering that extremely eutrophe lake detritus furnishes the top soil layer of these sites with surplus nitrogen after every summer inundation, an action which according to Meyer (1957) would be to the benefit of the activity of nitrification. Regarding the role of nitrogen in the system

Table II. Comparison of plant-available nitrogen in reed zones and moist forests

Habitat	N (mg/100 g dry soil)		Yearly accumulation (g/dm³ dry soil)	Density (g/dm³)
	momentary in fresh samples	accumulated in incubated samples		
Reed zone	1—3	3—5 (extreme 19)	0.1—0.2*	1.2
Deciduous forest	<1 (extreme 3)	5	0.1	1.8
Carr forest	2—5	10—25	0.05—0.1	0.15

* Calculated for 3—4 months.

plant-soil it would thus not matter that — unlike other nutrients — nitrogen is not taken from sub-soil water (compare Björk 1967, for cations), for, according to Björk's investigations, a short time increase in nutrient supply, as given by lake detritus, can have prolonged effects, as nutrients are then preserved in the rhizomes to the benefit of a plant internal N-cycle (compare León 1968). So it would not matter either that our main rhizome horizon is far less N-eutroph (average value 0.4% N_{tot}) compared with the results of e.g. Burrichter (1969): around 3% N_{tot} of sites eutrophicated by sea-gulls.

Our lower accumulation values can be explained by the fact that our main rhizomatous soil horizon from where probably most nutrients derive directly (Buttery, Lambert 1965) is very likely on an average less well aerated, in a way that denitrification is high: water content averages 100 (max. 180) g water /100 g dry soil. Particularly in the wet year 1970 values were extremely low. Only in drier periods values go up to more than 10 mg/100 cm³ (for N_{acc}), the fine-sandy, somewhat silty top-soil being then well aerated. Values are attained which are only beaten (natural middle European habitats) by some birchcarrs in summer months (Klötzli 1969). Even in dry spring months high values are attained, the top soil being warmed up very quickly after the beneficial action of the frost (Mayer 1957).

After "reed-death" has eliminated any living Phragmites stem, eutrophe rather rare plant communities with *Ranunculus sceleratus* and *Catabrosa aquatica* take advantage of the remarkable N supply.

The influence of birds is merely local (exclosures). The quantities of N and P coming from lake detritus are higher. This is in accordance with results obtained from investigations on fens (*Carex elata*) near Zürich (Ellenburg, Klötzli 1967, Klötzli 1967). Even on mesotrophe fens raised sea-gull populations are found, the extremely eutrophe fens having developed under the influence of ditches bringing rather eutrophe water from villages and purification plants. To the contrary Burrichter (1969) was able to trace a quick eutrophication by sea-gulls on the Zwillbrocker Venn.

Suggestions for management of reed-beds under abnormal conditions coming also from our work on N mineralization aim to lessen eutrophication of reed stands (see Klötzli 1973). Still well-growing stands should therefore be cut and litter removed. Nitrification is then reduced to about 65%; the stems grow sturdier and denser and thus can stand the action of mechanical factors much better.

The old practise of cutting reed-belts in winter was therefore indirectly a means to maintain optimal productivity and densely growing stands with solid stems and little gap formation under less eutrophe conditions.

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J. KVĚT

MINERAL NUTRIENTS IN SHOOTS OF REED (*PHRAGMITES COMMUNIS* TRIN.)

Institute of Botany, Czechoslovak Academy of Sciences, Brno, Czechoslovakia

ABSTRACT

Seasonal changes in percentages and contents per m^2 of N, P, K, Ca, Mg, Na, total and "residual" (mainly SiO_2) ash were followed in an eutrophic fishpond littoral invasion Phragmites stand. Generally, leaf blades and young parts of stems with leaf sheaths (stems) were mineral-richer, but the contents per m^2 were higher in stems, whose biomass was higher than that of leaf blades. "Residual ash" increased from 1/6 of total ash in spring to 5/6 in autumn. The content of all other mineral constituents was highest when biomass was highest.

1. MATERIAL AND METHODS

The seasonal changes in the percentages of total ash, N, P, K, Ca, Mg and Na in the dry matter, and the seasonal courses of their content (defined as the amount of a mineral component contained in the stand per unit ground area) were estimated in a littoral (water level at about 40 cm) invasion stand of *Phragmites communis*. The samples were harvested in a stratified manner (by 40 cm layers) on 6 successive dates during the 1966 growing season. The stand was situated at the northern shore of the Nesyt fishpond (for its characteristics see Fiala, Květ 1970 and Květ 1973). For the sampling technique and data on the growth, production, leaf area index (LAI) and seasonal development of the vertical stand structure see Květ et al. (1969). The dried plant material was ground and analysed according to modified recommendations by Koppová et al. (1955): N after Kjehldahl, P — colorimetrically with molybdenum blue, K, Na — by flame photometry, Ca, Mg — complexometrically, residual ash (containing mainly SiO_2 and some SO_4) as the difference of P+K+Ca+Mg+Na from total ash, total ash — by ignition. The analyses were performed at the laboratories of the Institute of Forestry Research, Station Opočno.

2. RESULTS AND DISCUSSION

The growth curves of biomass and LAI in the stand are given in Fig. 1. Figure 2 shows the seasonal course of both the percentage of N in dry weight and content of N (g/m^2). Figure 3 shows the same, with the shoots stratified by 40 cm horizontal layers. The content of total N reflects that of protein-rich tissues: the N percentage is therefore higher in the leaves than in the stems (which also include

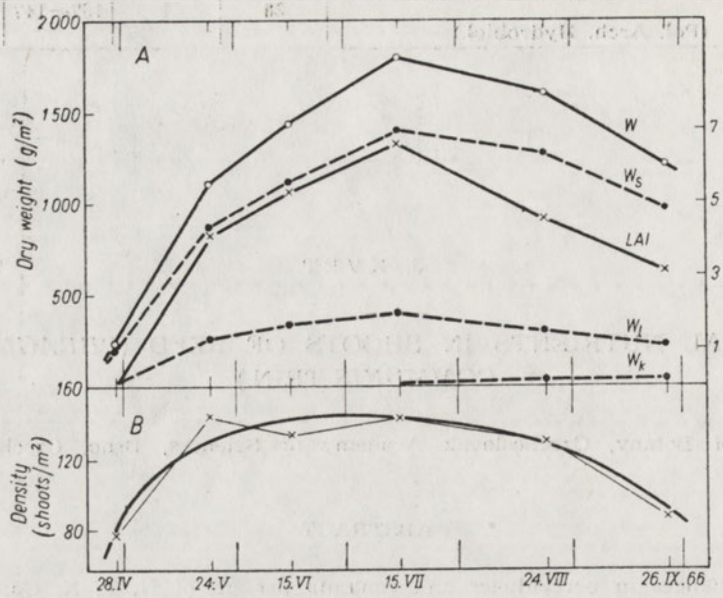

Fig. 1. Invasion stand of *Phragmites communis* at the northern shore of Nesyt in 1966. A — seasonal changes in the dry weight (ordinate) of: total shoot biomass (W), stems with leaf sheaths (W_s), leaf blades (W_l), panicles (W_k), and of the leaf area index (LAI, leaf blades only, ordinate); B — seasonal changes in stand density (from Květ et al. 1969)

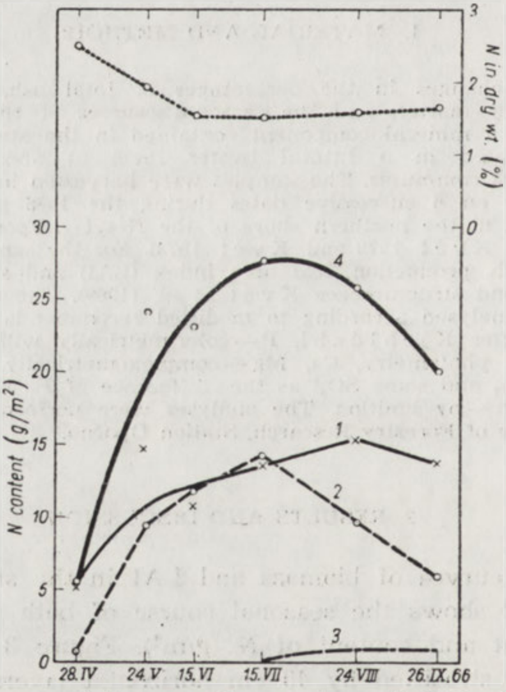

Fig. 2. Seasonal course of the overall percentage of N in dry weight and of the N content (g/m²), in the stems (1), leaves (2) and panicles (3), and the whole Phragmites stand (4)

the leaf sheaths); because of the higher dry weight of the stems, their total content of N per 1 m² is about the same as that in the leaves. The increase in N content in the lower stand layers before the end of the growing season is due to the emergence of new young shoots. On 15 June to 15 July, the stand contained 25 to 28 g N/m² (Fig. 2); much of it was in the canopy layers situated higher than 200 cm above the bottom level. Large amounts of N are therefore rapidly returned to the environment if the stand is cut in summer and the cut-off shoots are left to decompose in the water, which is a common practice used in fishpond management, in order to control the width of the reed-belt.

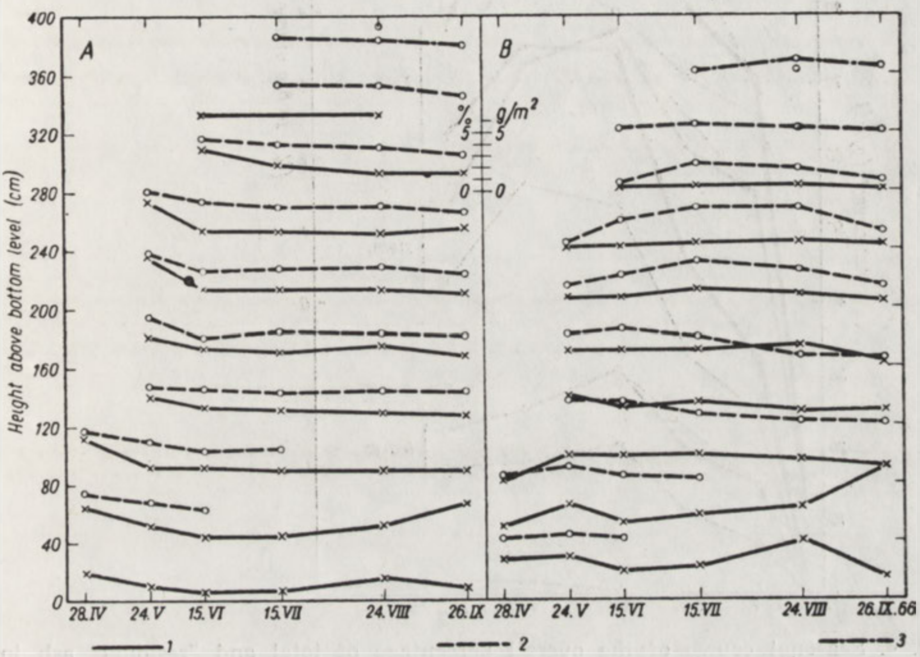

Fig. 3. Seasonal course of: A — the percentage of N in dry weight (%) and B — the N content (g/m²) in 1 — stems, 2 — leaves, 3 — panicles; stratified by 40 cm horizontal layers, in the Phragmites stand

Figure 4 shows the seasonal course of the percentages of total and residual ash in the biomass of the whole shoots, and the course of their content per m², in the different shoot components. The highest content of total ash, recorded on July 15, was 110 g/m², i.e. about 6% of the total seasonal maximum biomass (1.8 kg/m², of which leaves about 0.4 kg/m², LAI 6.5). The percentage of the physiologically inactive residual ash increased from about 1% in the spring to about 5% in the autumn. Both the percentages and amounts of the principal mineral elements contained in the ash exhibited the following seasonal changes:

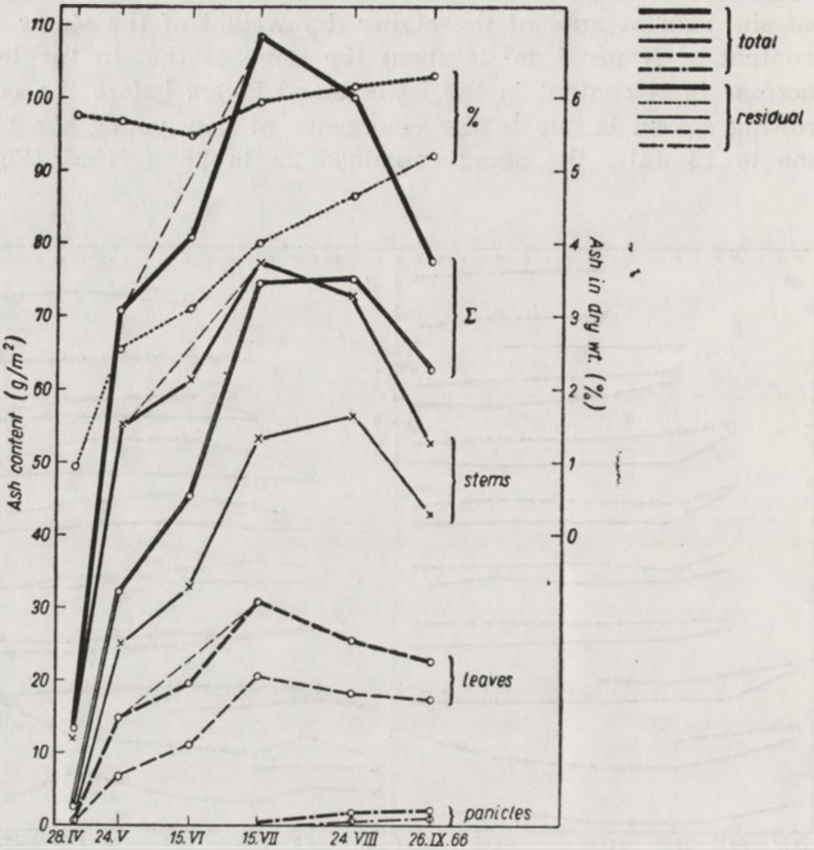

Fig. 4. Seasonal course of the overall percentage of total and "residual" ash in total biomass and of the content of both total ash and "residual" ash in the stems, leaves, panicles and the whole Phragmites stand (Σ)

P (Fig. 5). The P percentage fell from 0.24% on April 28 to 0.07% on Aug. 24, and rose insignificantly on Sept. 26, due to the emergence of new shoots. The P content was rather evenly distributed, but relatively more P persisted in the leaves towards the end of the growing season. The P content in the panicles was relatively high: 0.1 g/m^2. On the whole, the P content rather closely corresponds with the physiological activity of the plant parts concerned.

K (Fig. 6). The K percentage fell from 4 to 0.9% during the growing season; the highest content of nearly 32 g/m^2 (of which 25 g/m^2 in the stems) was recorded on July 15. After this date, the content of K rapidly decreased.

Ca (Fig. 7). The Ca percentage increased from about 0.11% on April 28 to 0.35% on July 15. On Sept. 26, it was only 0.21%. The highest content was recorded on July 15: 6.3 g/m^2, with 4.0 and 2.3 g/m^2 in the stems and leaves, respectively. On Sept. 26, however, the stems contained only 0.9 g/m^2 whereas the leaves did 1.7 g/m^2.

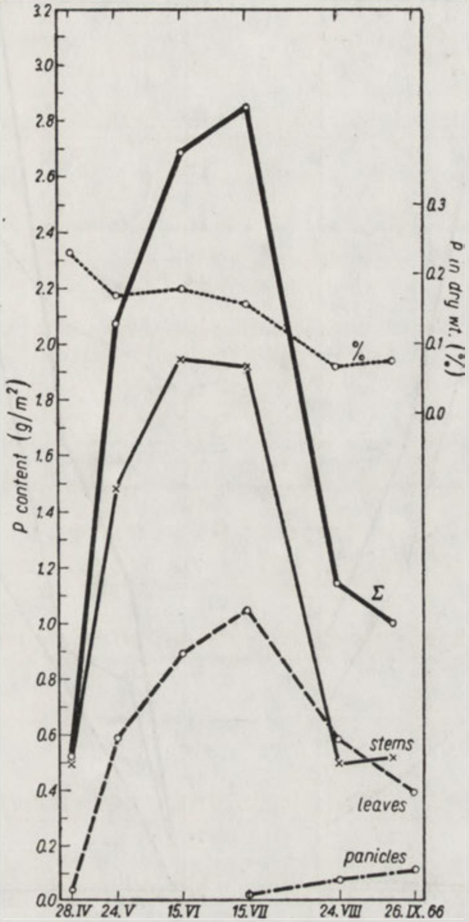

Fig. 5. Seasonal course of the overall percentage of P (dotted lines), and of its content (other lines) in the stems, leaves, panicles, and in the whole Phragmites stand (Σ)

Mg (Fig. 8). Mg was contained mainly in the leaves (chlorophyll), between 0.07 and 0.14%. The stems contained only 0.04 to 0.05%. The highest content of 1.2 g/m² (of which 0.5 g/m² in the leaves) was recorded on July 15. The emergence of new shoots slowed down the fall in Mg uptake at the end of the growing season.

Na (Fig. 9). Na is interesting to follow in the slightly saline habitats of South Moravia. The Na percentage fell from 0.9 % on April 28 to 0.4% on Aug. 24. After this date, it rose to about 0.5%, probably due to the emergence of new young shoots. The maximum Na content of nearly 9.0 g/m² was recorded on May 24; most of the Na was present in the stems.

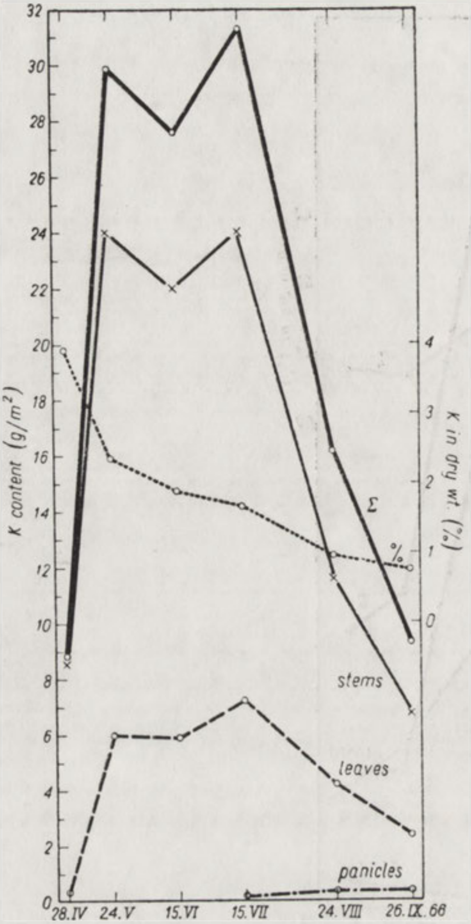

Fig. 6. Seasonal course of the overall percentage and content of K in the Phragmites stand (explanations as in Fig. 5)

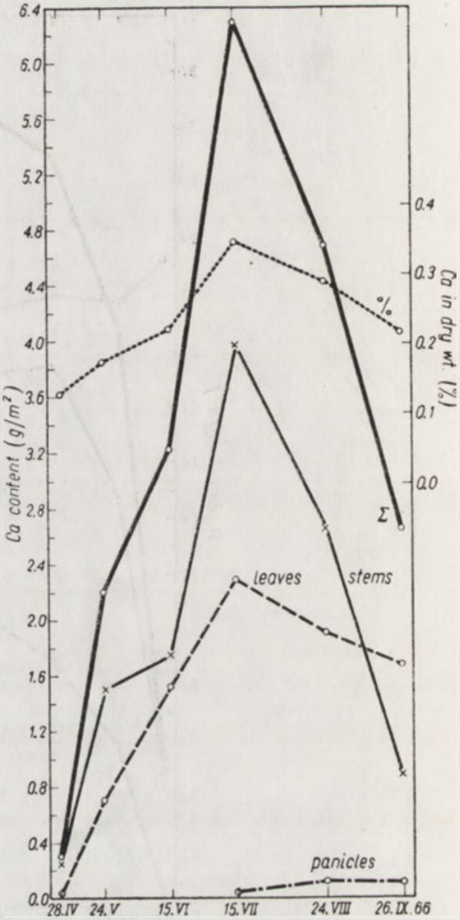

Fig. 7. Seasonal course of the overall percentage and content of Ca in the Phragmites stand (explanations as in Fig. 5)

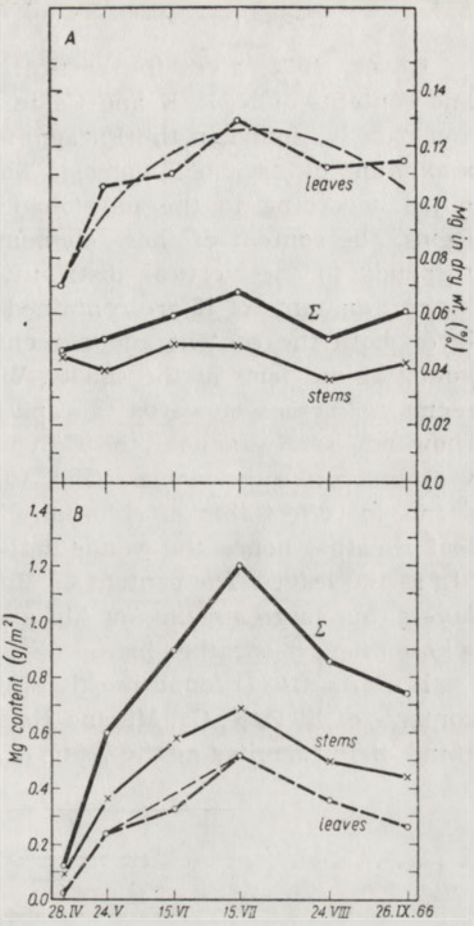

Fig. 8. Seasonal course of A — the percentage and B — content of Mg in the Phragmites stand (explanations as in Fig. 5)

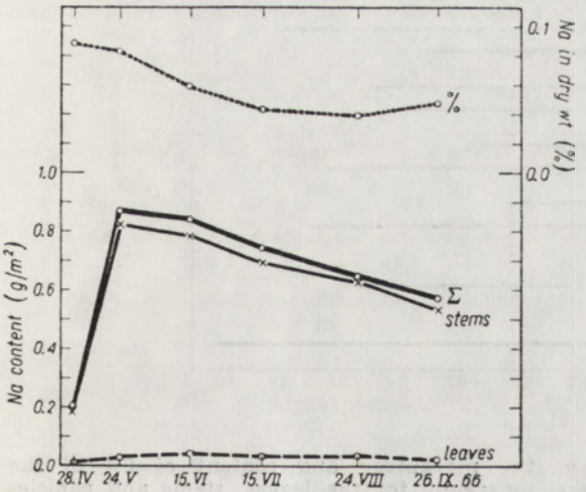

Fig. 9. Seasonal course of the overall percentage and content of Na in the Phragmites stand (explanations as in Fig. 5)

Květ (1971) gives the vertical distribution of both the percentages and contents of N, P, K and Ca in the leaves, stems (with leaf sheaths) and panicles found in the Phragmites stand investigated, at the seasonal maximum of its shoot biomass. The percentage of N and P is distributed according to the physiological activity of both the leaves and stems, the content of these elements by individual layers roughly corresponds to the vertical distribution of leaf and stem biomass. The highest amounts of K are contained in the basal stem parts above water level; both the content and percentage of K are relatively low in the young apical parts of the shoots. While the Ca percentage in the stems seems to increase towards the apical parts, that in the leaves does not show any such gradient; the Ca content per m² is vertically distributed very much like the biomass (Fig. 10). The distribution of the Mg content seems to reflect that of chlorophyll in both the leaves and stems with leaf sheaths: hence the young upper stem parts are about as rich in Mg as the leaves. The content of Mg is highest in the leaf-richest canopy layers, but large amounts of Mg are also stored in the basal stem parts whose biomass is rather high.

Husák (1971) found mostly slightly lower both the percentages and contents of N, P, K, Ca, Mg and Na in the dry matter of another invasion stand of Phragmites at the Nesyt fishpond, in a somewhat less favoura-

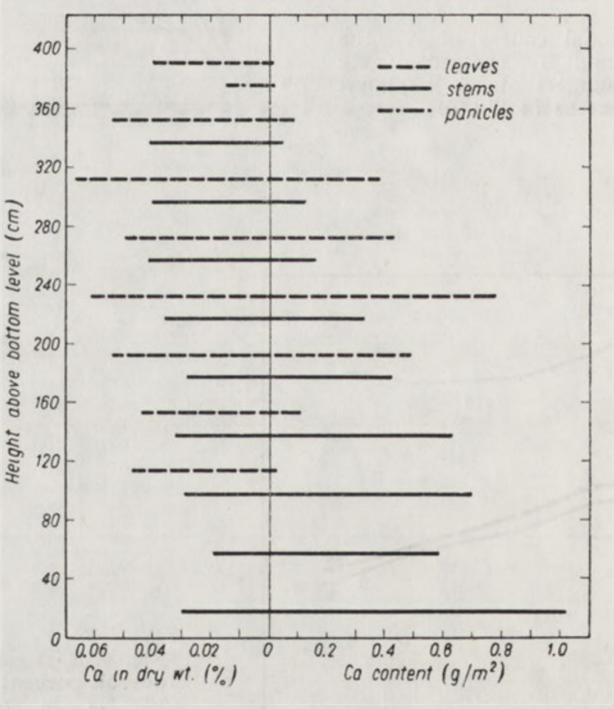

Fig. 10. Vertical distribution of the percentage and content of Ca in the Phragmites stand, by 40 cm layers, separately for the leaves, stems and panicles

ble habitat. The content of these elements per m^2 was lower, also because of the smaller total shoot biomass. In the summer of 1968, Květ, Dykyjová and their collaborators (unpublished) estimated the seasonal maximum shoot biomass, leaf area index (LAI) and mineral content in the shoots in a number of invasion stands of Phragmites occurring in the fishpond littorals in South Bohemia and South Moravia. Their sampling methods followed the Project Phragmites (1969) recommendations, the plant material was analysed chemically in the same way as the Phragmites from Nesyt in 1966. The LAI ranged from 3.5 to 6.3 m^2/m^2. The ranges for the values of both the content and percentage of individual mineral elements are shown in Table I. The differences may be ascribed to various factors: habitat, phenological stage of stand development and damage by stem-boring insects will probably be the most important ones. The values presented in this paper fairly agree with those quoted by Bernatowicz, Wolny (1969). All the mineral nutrients contained in the shoots cannot be assumed to originate from the soil or water as considerable transport apparently takes place both ways between the shoots and rhizomes. The mineral composition of *Typha angustifolia,* which is the other principal dominant in South Moravian reedswamps (Fiala, Květ 1970), is somewhat different and will be discussed elsewhere. When the percentages of N, P, K, Ca and

Table I. Highest and lowest values of percentage in dry weight and content per 1 m^2 of N, P, K, Ca, Mg and Na, found in the shoots of 14 littoral invasion stands of *Phragmites communis,* harvested at the peak of the growing season (late July to mid-August 1968) in 14 fishponds in South Bohemia and South Moravia

Element	Content				
	% dry wt. in		g/m^2		
	leaves	stems*	leaves	stems*	whole shoots
N	5.10	2.34	19.69	17.56	34.67
	3.35	1.12	6.63	9.57	18.81
P	0.240	0.185	1.05	1.62	2.67
	0.152	0.084	0.30	0.58	1.06
K	2.07	1.39	6.92	14.90	21.30
	1.21	0.55	3.29	4.34	8.29
Ca	0.651	0.129	2.92	1.67	3.98
	0.245	0.062	0.49	0.57	1.42
Mg	0.209	0.060	0.85	0.64	1.32
	0.120	0.030	0.36	0.23	0.61
Na	0.080	0.130	0.24	0.96	1.35
	0.035	0.045	0.09	0.39	0.46
Average biomass values (dry weight) (4—5 samples from 1 m^2)			198—470	563—1072	824—1511

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* Including leaf sheaths and panicles.

Mg recorded in our Phragmites stand in July are multiplied by the estimated average seasonal maximum biomass of the reed stands at the Nesyt fishpond (about 1.5 kg/m^2) the resulting estimates of their maximum content per ha, and in the whole reed-belt of Nesyt (estimated area 30 ha) are as follows: N — 200 kg/ha and 6 t, P — 20 and 0.6, K — 230 and 7, Ca — 42 and 1.2, Mg — 8 and 0.25. These values are lower when they are estimated either before or after the seasonal maximum of shoot biomass. For a more complete understanding of mineral cycling in reedswamp ecosystems, the knowledge of the seasonal changes in mineral content in the dominant plants is indispensable.

Acknowledgements

The author wishes to thank sincerely Mr. J. Svoboda and Mr J. Vacek for their assistance in preparing the samples for chemical analyses and for the accomplishment of the analyses, respectively.

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	147—150	1973

J. KVĚT, B. ÚLEHLOVÁ and J. PELIKÁN*

STRUCTURE OF THE REED-BELT ECOSYSTEM OF THE NESYT FISHPOND[1]

Institute of Botany, Czechoslovak Academy of Sciences, Brno, Czechoslovakia
*Institute of Vertebrate Zoology, Czechoslovak Academy of Sciences, Brno, Czechoslovakia

ABSTRACT

An outline is given of the main structural elements and of their functioning in reedswamps colonizing the shores of a large (320 ha) eutrophic and slightly saline (about 0.1%) fishpond situated in the Pannonian region of Central Europe. The main primary producers are Phragmites and Typha with their understorey synusia the composition of which differs according to the position of the water level. Most of the primary production (some 15 t/ha/year, on an average) is used up by various decomposers forming the detritus food chain, but direct consumers (water-fowl, small mammals, stem-boring insects, aphids, etc.) also fulfill several functions the importance of which perhaps exceeds that of their role in energy flow through the ecosystem.

The reed-belts occurring along the shores of managed fishponds develop into specific ecosystems, with their own long-term homoeostasis and with characteristic types of short-term response to different management measures. The reed-belt of the Nesyt fishpond covers about 10% (30 ha) of the total fishpond's area of about 320 ha. It functions under a set of environmental conditions typical of the eutrophic and slightly saline stagnant waters situated in the Pannonian lowlands in the SE of Central Europe. Both the structure and functioning of the reed-belt ecosystem are largely controlled by the position of the water level and by its fluctuations during both the current and the past growing seasons. The position of the water level is partly controlled artificially, and partly depends on the balance between rainfall and evaporation in the fishpond's catchment area. According to the actual position of the water level, three zones are distinguished in the reed-belt: terrestrial, limosal and littoral, with the water level below, at, and above ground level, respectively. Shallow open water, especially its enclosures ("lagoons") situated within the reed-belt, represents a different type of the

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[1] A summary. The full paper: Pelikán, J., Květ, J., Úlehlová, B. 1973. Principal constituents and relationships in the reed-belt ecosystem at the Nesyt fishpond. In: Květ, J. [Ed.] *Littoral of the Nesyt fishpond.* Studie ČSAV Praha, Academia.

fishpond's littoral, and so do unstabilized reedswamps along Nesyt's wind- and wave-eroded steeper shores as well as the fishpond bottom free of perennial helophytes which emerges in some years.

In the established reedswamps forming the reed-belt, the principal producers are the helophytes, particularly *Phragmites communis* and *Typha angustifolia*. Across the three zones, the production of this dominant synusium increases from land towards water: the structural arrangement of this synusium is best developed in the littoral zone. The undergrowth synusia, containing most of the other primary producers, show a distinct zonation: a number of higher-plant species occur here in the terrestrial zone; *Carex riparia* prevails in the limosal zone; *Lemna gibba, Riccia rhenana*, filamentous algae (e. g. Cladophora) and periphyton prevail in the littoral undergrowth. Some of the primary production is harvested by man: every winter, reed and reedmace are cut on an area of some 10 ha. The winter cutting follows an irregular pattern: some parts of the reed-belt are cut nearly every winter while others are practically never cut and become "degraded".

Only 1/5 to 1/6 of the primary production of the reed-belt is destroyed by herbivores, and only a part of this matter and energy passes through the richly differentiated grazing-predatory food chain. A great deal of the herbivore-destroyed plant material is not consumed, and is readily decomposed by detritophagous organisms and microorganisms. The herbivores are represented by molluscs, a great number of insect species, especially by stem-borers of the genus Lipara, mining dipterous larvae, noctuid larvae of Nonagria, Leucania and Tapinostola, larvae of Tineidae, Pyralidae and Tortricidae, by aphids (mostly *Hyalopterus pruni*), thripses (Chirothrips, Iridothrips) and phytophagous Coleoptera (mostly Chrysomelidae and Curculionidae). Certain birds, especially the grey-lag geese (*Anser anser*) and phytophagous ducks, also have a great direct impact on the plants. The muskrat (*Ondatra zibethica*) is another important consumer and destroyer of Typha and Phragmites. Young sprouts of littoral and limosal Phragmites are damaged by *Arvicola terrestris*; *Microtus arvalis* and *Clethrionomys glareolus* act in much the same way in the terrestrial zone.

The next trophic level comprises a wide selection of carnivores: spiders, predatory Coleoptera (Carabidae, Staphylinidae, Dytiscidae) and Hemiptera, and a large set of Odonata. About 6 species of frogs and 2 lizard species prey upon insects, and so do several species of reed warblers and other birds, and 4 species of shrews (genera Sorex, Neomys, Crocidura). The black-headed gull, *Larus ridibundus*, nesting mainly in Typha stands, is important as predator for the whole fishpond community. Trampling of the plants and eutrophication of the water by the guano is an important side effect of the rich bird life at Nesyt, for which this as well as other fishponds in the area (Lednice Fishponds) were declared a State Nature Reserve in 1953. With much of the birds' food originating from outside the fishpond area, the birds act as vectors of large amounts of materials into the reed-belt. This also holds for the large flocks of starlings and swallows roosting in the reeds at night during the autumn migration. The duck farm, situated opposite the widest part of the reed-belt, represents a great input of guano directly into the open water. In the reed-belt, the top carnivores are *Natrix natrix*, the grey heron (*Ardea cinerea*), marsh harrier (*Circus aeruginosus*) and several visiting predatory mammals (Vulpes, Putorius, Mustella, Felis). In the water, the main terminal producers are the fish — the carp (*Cyprinus carpio*) is the principal species cultivated in the fishpond.

Most of the net primary production of the reed-belt constitutes a source of energy and matter for a bulky detritus food chain. Some of the dead plant material is consumed by larvae of Diptera (Tipulidae, some Chironomidae). It also supports, together with planktonic organisms, a huge number of larvae of Culicidae. Imaginal stages of all these insects are preyed upon by reed warblers. Part of the energy originating from the dead plant material is thus transferred to the grazing-predatory food chain. The largest proportion of the dead organic matter is eventually consumed by the microflora participating in its humification and mineralization. These processes take place in all structural units of the reed-belt ecosystem, but predominantly in the litter and detritus both above and below the ground, in the water and in the organic sediments. The qualitative and quantitative composition of the microbial synusia depends above all on the surrounding medium which may change from water to air. Different metabolic pathways are in operation under conditions varying, within the reed-belt, from complete anaerobiosis to aerobiosis. Typical seasonal variations exist in the rates of different microbial processes. The most important environmental factors controlling the development and functioning of the microflora in the reed-belt are the fluctuations of the water level, trophic status of the habitat, and temperature.

On an average, the primary production by the reed-belt is estimated to vary between 1.5 and 3.0 kg/m^2 of dry weight per year (mean value about 2.0 kg/m^2). Man's harvest removes, where performed, about 0.6 kg/m^2 per year, and about 0.7 kg/m^2 per year is the estimated amount of organic matter decomposed by microorganisms in the reed-belt.

For more detailes about the reed-belt of the Nesyt fishpond see Květ (1973) and Fiala, Květ (1971).

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	151—156	1973

H. SIEGHARDT

UTILIZATION OF SOLAR ENERGY AND ENERGY CONTENT OF DIFFERENT ORGANS OF *PHRAGMITES COMMUNIS* TRIN.

Pflanzenphysiologisches Institut der Universität Wien, Dr. Karl Lueger Ring 1, A-1010 Wien, Austria

ABSTRACT

The energy content of different organs of *Phragmites communis* was determined using an adiabatic oxygen bomb calorimeter. The ecological efficiency of solar energy conversion and the alterations of energy content during growing season was investigated in relation to ecological environment. In June the utilization of incoming irradiation was the highest. The energy content of above- and underground parts alterates with season and its course is obviously contrary. The leaves show the highest (in spring) and the lowest (in autumn) calorific values of all investigated organs. In autumn, the energy content of stems appears to be even higher than that of rhizomes. In winter, the rhizomes come up to their maximum amount of energy, on the contrary they obtain relative low calorific values in summer.

1. MATERIAL AND METHODS

Calorimetric investigations of dry matter production of Phragmites were carried out on the material from growing season 1970. The samples were collected in the dense reed stand at the western shore of lake Neusiedler See (Rust am See). For avoiding substance losses after the harvest, the samples were immediately oven-dried in the laboratory at 85°C and divided into the different organs (leaves, leaf-sheaths, stems, rhizomes, and roots). The dry material was ground (Culatti--Schlagmühle) and combusted as pills, respectively as dissolute powder (these results were partly better reproducable) in an adiabatic (Janke & Kunkel) oxygen bomb calorimeter at 20 atm. The ash content was substracted for calculating the combustion values in kcal per gram ash-free dry matter (methodical details see Brzóska 1971, Sieghardt 1973). The samples dating from Hübl (1967) and Burian (1966) were examined quite similar.

2. RESULTS

ECOLOGICAL EFFICIENCY (CALCULATED ON ABOVEGROUND BIOMASS)

The ecological efficiency can be calculated using two different ways: one related to total irradiation and the other in relation to photosynthetic active part (PhAR 400—700 nm). In the following investigations last mentioned reference was supposed to be 45% of total irradiation (see

Lieth 1965, Dykyjová 1971). Utilization is given by following ratio:

$$N = \frac{F \cdot 100}{\mathrm{PhAR}}$$

Formula according to Dykyjová et al. (1971), where F — energy content of organic dry matter per area unit of stand and per harvest interval. F and PhAR in kcal/m$^2 \cdot$ t. For calculation of ecological efficiency the energy content of above-ground parts of Phragmites (leaves, leaf-sheaths, and stems) was determined.

Considering the utilization of solar energy figured in Table I, a parallelism to global irradiation or PhAR can be observed. The increase of irradiation sums per area unit induces an ascent of utilization (exception 1967, see Table I). If the timing of harvest is in early summer, the utilization ranges relatively high (highest values in June). With continuance of growing season and increase of total irradiation per area unit from the beginning of vegetation period on, the utilization decreases gradually. In three compared years, it attains the relative lowest values in July. Comparing the average energy stores from 1966 till 1970, as figured in Table I, in all three investigation periods by chance in June an obvious decrease of calorific content from 6923 kcal (1966) to 4463 kcal (1970) can be observed. In June 1967 the average energy store was about 1500 kcal below that of 1966 at the same time. In spite of this fact, the ecological efficiency of about 5.1% appears to be quite the same. On the other hand in June 1970 the utilization of solar irradiation of about 3.3% was essentially smaller than at the same time in 1966 and 1967.

Table I. Utilization of solar energy and energy store of Phragmites per 1 m^2 area unit (aboveground biomass). 1 cal=4.186 Joule

Period	Mean energy store of dry matter (ash-free)		Intensity of incident radiation (kcal/m^2/month)		Utilization (%)	
	kcal	kJ	total	PhAR	total	PhAR
1966 May	4215.8	17,650.711	142,150	63,968	2.3	5.0
June	6923.2	28,986.054	142,370	64,067	2.3	5.1
July	6366.3	26,654.425	132,080	59,436	1.4	3.0
1967 May	2182.5	9,137.691	134,500	60,525	1.7	3.7
June	5561.6	23,285.307	154,470	69,512	2.3	5.1
July	4083.7	17,097.635	159,620	71,829	1.0	2.3
1970 May	1677.3	7,022.520	136,790	61,555	1.3	2.9
June	4463.1	18,686.107	142,660	64,197	1.5	3.3
July	5282.9	22,118.446	137,560	61,902	1.1	2.5

ENERGY CONTENT OF DIFFERENT ORGANS

Table II figures the average energy amounts of the particular organs. The variability of calorific values occurring in the different stalk parts are significant. In average the dispersion of values was about 13 gcal. Obviously the energy distribution between above- and underground parts depends on season. In spring the young leaves obtain the highest calorific values. The high energy content of leaves during spring results from high energetic compounds in form of storaged carbon hydrates in the underground parts. On the contrary the leaves themselves occur to be the synthesizers of high energetic compounds. Vice versa in summer the leaves' calorific values decrease. Certainly a dislocation of high energetic compounds into other organs (stems and rhizomes) takes place, on the other hand the age of leaves has to be taken into consideration. Actually in autumn the leaves show the lowest calorific values of all investigated organs.

Unfavourable meteorological conditions (as low temperatures etc.) assimilates dislocation, high content of inorganic compounds (silicates etc.) and chemical decomposition in leaves lead to a rapid energy decrease.

In the course of vegetation period no obvious differences of energy content of stems can be observed. In spring the energy content of stems is about 160 cal below that of leaves. The autumnal decrease of calorific values appears to be not so distinct as that of leaves. The energy ratio between underground and aboveground parts shows a negative correlation. In winter the maximum amount of energy store appears in rhizomes. In the single case calorific values up to 4.3 kcal

Table II. Energy content of leaves, stems and rhizomes of Phragmites during growing season 1971 (average values from 30—35 single measurements). 1 cal=4.186 Joule

	Period	Energy content		Ash content(%)
		kcal/g d.wt.	kJ/g d.wt.	
Leaves	Spring	4.306	18.025	3.4
	Summer	4.153	17.384	6.5
	Autumn	4.072	17.045	9.5
Stems	Spring	4.139	17.326	3.0
	Summer	4.266	17.857	3.5
	Autumn	4.212	17.631	4.1
Rhizomes	Spring	4.150	17.372	3.0
	Summer	4.100	17.163	3.0
	Autumn	4.144	17.347	3.0
	Winter	4.255	17.811	4.0

per gram dry weight are obtained. Krejci (1972) points out that during winter a relative large amount of starch can be found in the rhizomes. The starchpool appears to be preserved with just small alterations up to the next spring, there exist just symptoms that in the rhizomes energetic displacements take place, which lead to a considerable increase of high energetic compounds. Just in May the starch content of rhizomes obtains a minimum amount. A part of the assimilates synthesized in the leaves is retransported into the rhizomes at a moment of highest photosynthetical activity (May/June, see Burian 1972). In summer the energy content of rhizomes occurs to be the lowest, just in autumn the energy pool is refilled. Nevertheless a part of energy is invested for formation of new shoots, which almost are developed in October and November. (The high energy content of new formed shoots implies a high compatibility against stress situation in winter). The ash content of aboveground organs increases considerably from spring till autumn. In autumn the ash content of leaves attains twice the values of the stems (10% and more). On the other hand it seems to be striking that the ash content of underground parts shows only small alterations and during the whole vegetation period remains relatively constant at an value of 3% (see Table III).

Table III. Mean calorific values and ash content of aboveground dry matter. 1 cal=4.186 Joule

Year	Calorific values		Ash content (%)
	kcal/g d. wt.	KJ/g d. wt.	
1966	4.464	18.686	7.0
1967	4.465	18.690	6.3
1970	4.468	18.703	5.8
1971	4.450	18.628	5.5

3. DISCUSSION

The ecological efficiency and energy distribution within the particular organs of *Phragmites communis* alterate during growing season. In the three investigation periods the utilization of solar energy was the highest in June at a time of high photosynthetical activity of the stand (see Table I). For reed banks, Dykyjová et al. (1970) figure a quite similar course of ecological efficiency of solar irradiation. The maximum amount of irradiation and utilization is obtained in June. In another paper Dykyjová et al. (1971) compare the ecological efficiency of cultivated plants with energy conversion in a natural habitat. In cultural environment Phragmites obtains an efficiency of more than 12% PhAR, at the natural habitat values of about 5.39 and 5.92% are gained.

In spite of different sums of irradiation per area unit and year and considerable differences of energy store of the whole dry matter, the same ecological efficiency can be observed. This references to, that besides absolute value of irradiation, photosynthetical activity (assimilate budget) and ecological efficiency depend on temperature as well (see Tuschl 1970, Burian 1969, 1973). Considering the energy content of different organs in spring the leaves attain the highest calorific values of about 4.3 kcal per g d. wt. Likewise for comparable graminees Golley (1961) describes values of about 4.3 kcal per g d. wt.

Hunt (1966) figures values for different grasses (kcal/g d. wt.):

	Young leaves	Mature leaves	Sheaths
Cynosurus cristatus	4.230	4.240	3.9
Lolium perenne	4.425	4.235	3.8
Festuca arundinacea	4 490	4.260	3.9

In autumn in the leaves no high energetic compound occurs, thus in comparison with all other investigated organs the energy content is the lowest (4.072 kcal). In winter the rhizomes attain their highest calorific values (4.3 kcal per g d. wt.), but they never obtain such high amounts as the leaves in spring. For underground organs of different graminees, Golley (1961) specifies energetic contents of about 4.7 kcal per g d. wt. Gorham, Sanger (1967), Straškraba (1968) give some calorific values for aquatic macrophytes. Thus the energy content of Potamogeton is about 4.28 kcal per g d. wt. (ash-free), *Myriophyllum sp.* attains values of about 4.59 and 5.20, and *Typha sp.* 4.20–4.52 (compare Table I and III). The ash content of the total aboveground dry matter ranges quite twice as high as the values of underground parts.

As to its energy content of the particular organs, their alterations during growing season and its ecophysiological efficiency Phragmites is quite comparable with other graminees (like middle european wild grasses and cultivated grasses).

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	157—158	1973

F. SZAJNOWSKI

THE RELATION BETWEEN THE LEAF AREA AND PRODUCTION OF THE ABOVEGROUND PARTS OF COMMON REED *(PHRAGMITES COMMUNIS* TRIN.) [1]

Department of Applied Limnology, Institute of Ecology, Polish Academy of Sciences, Świerczewskiego 14, 11-730 Mikołajki near Mrągowo, Poland

ABSTRACT

In studies on production and morphometry of common reed, biomass of the aboveground parts of reed per surface unit of the reed stand, the length of plants, and green area of leaves were determined. A statistically significant relation between the area of green leaves and production of aboveground parts of reed was found: the production value and leaf area increased almost identically. The ratio of plant biomass to leaves biomass decreased with the increase of leaves production. Moreover, the negative influence of forests on reed production was observed.

This paper presents the studies on production and morphometry of common reed. The investigations were carried out according to the methodical suggestions recommended in the Project Phragmites.

The investigations were carried out from August 15 to September 15, 1969 (during the period of maximum biomass of reeds — Szczepański unpubl.). The samples were collected at 19 sampling sites on 10 lakes in the Mazurian Lakeland. The following factors were determined: biomass of the above ground parts of reed per surface unit of the reed stand, the length of plants, and green area of leaves.

The following dependences were observed. The leaf area of reed from all examined sites was on the average 227 dcm²/m² of the reed-belt. It was slightly lower than that found by Björk (1967) in Sweden and Zealand (238 dcm²/m²). The reed-belts situated near the lake shores with coniferous forests were lower than the other reed-belts (208 dcm²/m² as compared with 242 dcm²/m²).

The reed leaves production was on the average 167 g/m², and it varied from 18 to 513 g dry weight/m². This value was also lower near the shores with coniferous forests (144 g/m²) than on other sites (186 g/m²).

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[1] A summary. The full paper will be printed in *Pol. Arch. Hydrobiol.*, 1973, 20.

The average value of production of aboveground parts of reeds was 759 g dry weight/m² for all examined sites and varied from 58 to 1998 g/m². Also in this case it was observed that the average values on sites near coniferous forests were lower (659 g/m²) than the average values on other sites (838 g/m²). The reed production was more differentiated near the shores covered with forests, and the variability index for this group of sites was 0.46, while for all other sites 0.42. The lowest production value was observed at the site with the smallest area of reed leaves.

A statistical analysis of the obtained results showed a significant relation between the area of green leaves and production of aboveground parts of common reed. The correlation index $r=0.85+0.04$. The production value increased almost identically as the increase of leaf area. This relation was less visible for sites near the shores overgrown with forests. The highest index of production to leaf area was found for the reed-belts with low production and small leaf area. It was found that the ratio of plant biomass to leaves biomass decreased with the increase of leaves production.

The reed production in small eutrophic lakes located in forests was relatively low (457 g/m²). Small lakes in the open area had production nearly twice higher (846 g/m²). The latter value is similar to the one of the reed-belts in large holomictic eutrophic water bodies (786 g/m²).

The above observations suggest the negative influence of forests on reed production, which is in agreement with Bittman's (1953) data. This author found that the trees growing on the shores limit the quantity of light necessary for reed development. In the present investigations, reed-belts located near the forests were probably in bad nutrient conditions, as forests in Poland grow on poor soil.

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M. ZAX

DIE TEMPERATURRESISTENZ VON *PHRAGMITES COMMUNIS* TRIN.

Pflanzenphysiologisches Institut der Universität Wien, Dr. Karl Lueger Ring 1,
A-1010 Wien, Austria

ABSTRACT

Phragmites zeigt eine weitgespannte Breite seiner potentiellen Temperaturverträglichkeit. Innerhalb dieser schwankt die aktuelle Temperaturresistenz auf Grund der Wirkung steuernder Faktoren wie Wasserbilanz, Temperatur, Lichtintensität, Photoperiode und stoffwechselphysiologische Aktivität. Die Absolutwerte der Hitzeresistenz liegen im Vergleich zu anderen Gramineen extrem hoch. Es zeigt sich im Jahresgang eine positive Korrelation zwischen hoher Temperaturresistenz, erschwerter Wasserbilanz, hohen Lichtintensitäten und Karztag. Bei Vertikaldiagrammen der Temperaturresistenz ist ein Zusammenhang zwischen der Insertionshöhe der Blätter am Halm und damit ihrer stoffwechselphysiologischen Aktivität und ihrer Temperaturverträglichkeit zu erkennen.

1. EINFÜHRUNG

Stocker (1967) weist darauf hin, dass unter den krautigen Typen allein der monokotyle Grastyp weiträumig geschlossene Vegetationsformen zu bilden imstande ist. Unter Streßbedingungen (wie Wasserstreß, kurze Produktionszeiten und nicht zuletzt Hitzestreβ) vermögen die Gramineen jenen ökologischen Raum zu besiedeln, in dem sie auf Grund ihrer Widerstandskraft anderen Konkurrenten, vor allen holzigen Gewächsen, überlegen sind. Das Schilf, das am Neusiedler See unter submersen Bedingungen, an glykischen und halophilen Trockenstandorten vorkommt, ist ein Beispiel.

2. MATERIAL UND METHODEN

Zur Erstellung der Jahresgänge der Temperaturresistenz wurden Proben verschiedener Organe von *Phragmites communis* (Blätter, Blattscheiden, Halme, Rhizome und Wurzeln) von unterschiedlichen Standorten am Westufer des Neusiedler Sees (Österreich) in monatlichen Abständen untersucht. Bei der Hitzeresistenzbestimmung betrug die Einwirkungszeit der gewünschten Endtemperatur 30 Minuten (Temperaturstufung 1°C), bei der Kälteresistenzbestimmung 2 Stunden (Temperaturstufung 2°C). Die angegebenen Expositionszeiten beziehen sich auf die tatsächlich im jeweiligen Objekt erreichte Endtemperatur, die mit Hilfe von Thermoelementen und einem Kompensationsschreiber laufend registriert wurde. Die Überlebensrate wurde direkt nach Ende der Expositionszeit und ein zweites mal nach einer Nachkulturphase unter konstanten Bedingungen (7 Tage) bestimmt. Als Vitalitätskriterien wurden die makroskopische Schadensbeurteilung und die Vitalfärbung zahlreicher Schnitte des jeweiligen untersuchten Gewebes mit Neutralrot verwendet. Überschritt die Schädigung 40% oder regenerierten die Pflanzen nicht mehr, so wurde das Objekt als tot eingestuft (Methodik vgl. Rottenburg 1967, Maier 1969 und Zax 1972).

3. ERGEBNISSE UND DISKUSSION

JAHRESGÄNGE DER TEMPERATURRESISTENZ

Abb. 1 zeigt Jahresgänge der Temperaturresistenz halbsubmersen Schilfs für die Vegetationsperioden 1970 und 1971. Bei den angegebenen Werten handelt es sich um Mittelwerte aus allen untersuchten Geweben, wobei sowohl unter-als auch oberirdische Anteile berücksichtigt sind. In den beiden Jahren war der Kurvenverlauf annährend parrallel, die Absolutwerte zeigen jedoch beträchtliche Unterschiede. Der Jahresgang der Hitzeresistenz ist deutlich zweigipfelig: Im Vorfrühling steigt auf Grund hoher Lichtintensitäten (Maier 1971) und steigender Temperaturen, trotz zunehmender Tageslänge, die Hitzeresistenz von Minimalwerten aus kontinuierlich zum ersten Maximum im Juli an; daran schließt sich ein Abfall im August (abnehmendeLichtintensitäten). Im Anschluss daran steigt die Hitzeverträglichkeit zu einem zweiten, herbstlichen Maximum an, wobei hier sicher der Kurztageffekt zur Auswirkung gelangt, der im Frühjahr durch die hohen Einstrahlungen und die ansteigenden Temperaturen überlagert war (Biebl, Maier 1969). Das erreichte Maximum wird über die Wintermonate hin beibehalten.

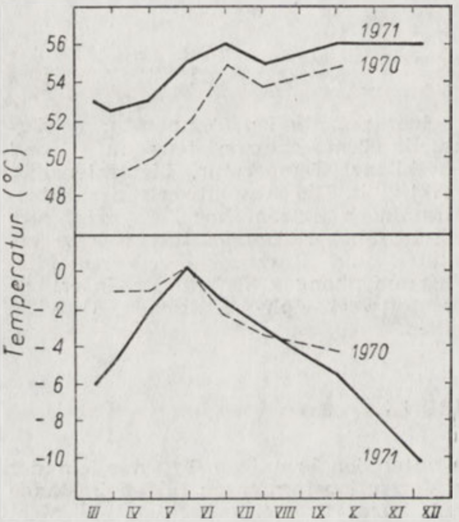

Abb. 1. Jahresgänge der Temperaturresistenz von *Phragmites communis* an einem halbsubmersen Standort für die Vegetationsperioden 1970 und 1971 (Mittelwerte für die ganze Pflanze)

Der Verlauf der Kälteresistenz im Frühjahr und Sommer geht negativ zu dem der Hitzeresistenz. Auffallend ist, daβ das Minimum im Mai/Juni zeitlich eng begrenzt bleibt, und ab diesem Zeitpunkt ein kontinuierlicher Anstieg der Kälteverträglichkeit erflogt; im September wird die Pflanze bereits wieder echt frostresistent, es wird der Kurtzteffekt wirksam, während im Sommer trotz hoher Lichtintensitäten keine echte Frostresistenz erreicht wird. Hier dürften die tiefen Temperaturen zum Erlangen der Härte fehlen. Der Verlauf ist abweichend vom dem anderer Gramineen. Obwohl auch beim Schilf während der Sommermonate keine Frostresistenz, also Eisresistenz, erreicht wird, scheint es doch bemerkenswert, daβ der Bereich minimaler Kälteresistenz extrem schmal ist, und die Pflanze während des Sommers eine hohe Verträglichkeit gegen tiefe Temperaturen ohne Eisbildung besitzt. Sicher spielen hier noch nicht abzusehende Schwankungen im Assimilathaushalt (Kohlenhydrate) eine entscheidende Rolle.

Die absoluten Unterschiede der Temperaturresistenz in den beiden Vegetationsperioden korrelieren mit Unterschieden der Globalstrahlung. Höhere Lichtintensitäten und Temperaturen, wie sie 1971 im Vergleich zu 1970 auftraten, bedingen eine erhöhte Temperaturverträglichkeit (vgl. Tab. I).

Table I. Monatsmittel der Lufttemperatur und der Globalstrahlung in Rust am Neusiedler See

Mittlere Lufttemperaturen (°C)		Monate	Globalstrahlung (cal/h) (Monatsmittel)	
1970	1971		1970	1971
3,8		März	186,1	
10,2	12,0	April	218,6	(452,0)
14,0	17,0	Mai	278,6	486,6
19,7	17,3	Juni	292,3	457,8
19,5	20,4	Juli	288,98	456,2
19,7	21,4	August	273,72	435,3
15,4	14,0	September	139,78	256,9
9,1	9,1	Oktober	74,45	
7,2		November		
0,2		Dezember		

Betrachtet man die Unterschiede der Temperaturverträglichkeit ober- -und unterirdischer Pflanzenteile (Abb. 2), so wird deutlich, daβ auch die unterirdischen Anteile eine Amplitude ihrer Temperaturresistenz afweisen, obwohl sie nicht direkt und in so groβem Maβe Schwankungen der meteorologischen Faktoren ausgesetzt sind wie die oberirdischen. Das ist ein klares Indiz, daβ Veränderungen des Assimilathaushaltes, bedingt durch Abbau und Verlagerung der Reservestoffe, resistenzbeinflussend wirken. Allerdings kann dieser Mechanismus je nach Exposition des Organs der Pflanze und je nach Jahreszeit durch meteorologisch bedingte Resistenzveränderungen überlagert werden. Bei unterschiedlichen edaphischen-und Wasserversorgungsverhältnissen zeigt sich (Abb. 3), daβ das Schilf am glykischen Trockenstandort die höchsten Werte der Temperaturverträglichkeit erreicht, während jene des halbsubmersen Schilfs darunter liegen. Parallel dazu, jedoch auf Grund der hohen Salzbelastung weit niedriger, trotz erschwerter Wasserbilanz, liegen die Werte für den Salzstandort. Die absolute Höhe der Hitzeresistenz von Phragmites übertrifft die aller übrigen untersuchten Gramineen bei weitem, diese Pflanze besitzt also eine weitgespannte potentielle Temperaturresistenzbreite, sie liegt bei Werten, die z. B. von Succulenten erreicht werden. Aus den vorliegenden Ergebnissen wird die Fähigkeit der Pflanze offenbar, ihre Resistenz den Umweltfaktoren anzupassen (Resistenzadaptation). Nicht nur die negative Korrelation zwischen Wasserversorgung und Resistenzhöhe geht aus den vorliegenden Daten hervor (vgl. Levitt 1956), sondern es kann darüber hinaus eine positive Korrelation zwischen Resistenzhöhe und Photosyntheseraten beobachtet werden. Burian

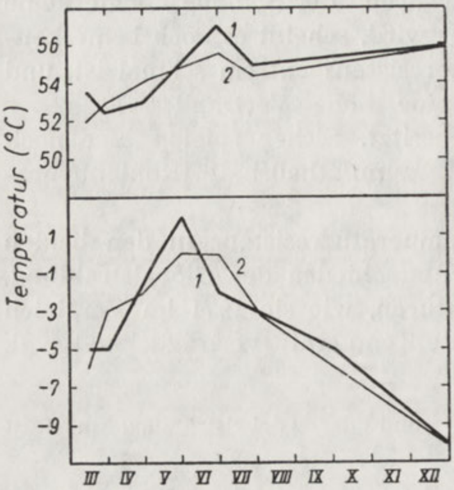

Abb. 2. Jahresgang der Temperaturresistenz oberirdischer (1) und unterirdischer (2) Organe von *Phragmites communis* für die Vegetationsperiode 1971

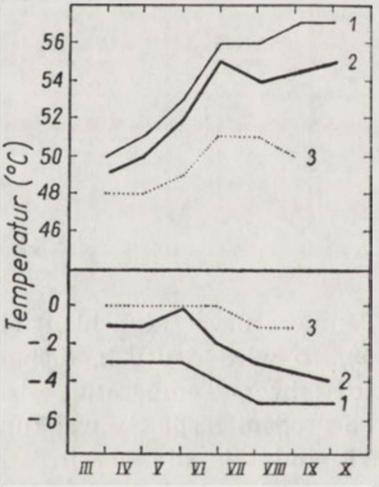

Abb. 3. Jahresgänge der Temperaturresistenz von *Phragmites communis* an verschiedenen Standorten für die Vegetationsperiode 1970. 1 — glykischer Landstandort, 2 — halbsubmerser Standort, 3 — halophiler Landstandort

(1973) konnte feststellen, daß beim halbsubmersen Schilf die höchsten Photosyntheseraten auftreten, während sie beim Trockenschilf nur ein Fünftel betrugen.

VERTIKALDIAGRAMME DER TEMPERATURRESISTENZ

In der Vertikale sind am Halm ebenfalls Unterschiede der Temperaturresistenzhöhe der Blätter zu erkennen. Entsprechend der Insertionshöhe treten Schwankungen der Hitze- und Kälteverträglichkeit auf. Das Spitzenblatt und die mittlere Halmzone zeigen jeweils die geringste Temperaturresistenz (Abb. 4), während obere und unterste Zone höhere Werte erreichen. Blätter in unterschiedlicher Insertionshöhe besitzen unterschiedlichen Entwicklungs- und Aktivitätszustand. Rychnovská (1967) weist darauf hin, daß die mittelere Halmzone jene mit der maximalen Photosynthesekapazität ist, Tuschl (1970) konnte beobachten, daß gerade in diesem Halmbereich die stärkste Transpiration zu verzeichnen ist. Auf Grund der hohen stoffwechselphysiologischen Aktivität tritt gerade hier die geringste Temperaturresistenz auf, da Pflanzen mit regem Metabolismus meist eine geringe Temperaturverträglichkeit aufweisen. Aus diesem Zusammenhang wird auch die höhere Temperaturresistenz der untersten, ältesten, nicht mehr aktiven Blätter verständlich. Auf Grund der Stabilität der Wasserversorgung und des Auftretens relativ geringer Wassersättigungsdefizite ist keine Relation zwischen Wassergehalt und Härte zu bemerken. Auch das Mikroklima (Lufttemperatur in der mittleren Halmzone fast immer maximal, relative Luftfeuchte am geringsten — Burian 1966, 1969) wirkte nicht erhöhend auf die Temperaturverträglichkeit. Vielmehr ist ein deutlicher Zusammenhang zwischen Höhe der Temperaturresistenz und der Stoffvechselaktivität zu konstatieren.

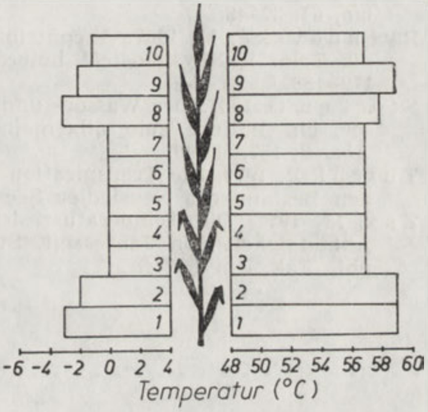

Abb. 4. Vertikaldiagramme der Temperaturverträglichkeit von *Phragmites communis* an einem halbsubmersen Standort (23.VI.1971). 1–10 — untersuchte Halmabschnitte

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G. IMHOF

ASPECTS OF ENERGY FLOW BY DIFFERENT FOOD CHAINS IN A REED-BED. A REVIEW

II Zoologisches Institut der Universität Wien, Dr. Karl Lueger Ring 1,
A-1010 Wien 1, Austria

ABSTRACT

In the reed-belt of Lake Neusiedlersee (Austria), investigations on productivity and food conversion of dominant phytophagous and detritophagous animals were carried out, which lead to an approach to the quantitative role of different food chains: The phytophages are more important by preventing than consuming primary production. Only a few percentage of the energy bound in plant material is ingested by phytophages, whereas at least the tenfold is converted by detritophages after the break-down. The major part, however, remains to direct microbial decomposition. It is supposed that part of the energy flow is intercepted by sedimentation due to insufficient microbial activity in deeper mud layers.

There are two ways of dealing with the flow of energy bound by primary production: one is from the point of view of the plant material itself, observing decomposition and losses caused by several factors; the other one is from the point of view of organisms involved in these processes making use of plant materials.

The second one has been the scope of the working group of zoologists participating in the Austrian IBP Wetland Project in the extended reed beds of Lake Neusiedlersee. Whereas there are only a few dominant species of primary producers in a reed bed, so that comprehensive data are already available on different parameters of primary productivity, zoologists had to face a considerable variety of animals involved in different food chains. Investigations on energy budgets had therefore to be restricted to species or ecological types which hold some "key-position" in the ecosystem. Due to personal and technical facilities most work has been done until now on "big invertebrates". A general survey of the present state of research in the reed-belt project is given elsewhere (Imhof, Burian 1972). In this paper submitted here some considerations are to be communicated contributing to the problem how to assess the share of different food chains by means of only fragmentary data.

1. Within the trophic level of phytophages dependent on *Phragmites communis* several feeding types were found (Waitzbauer 1972):

Gall-formers: *Lipara lucens* (Diptera Chloropidae), *Perrisia inclusa* (Diptera Cecidomyidae);

Stem-miners: *Thomasiella flexuosa* (Diptera Cecidomyiidae), *Phragmataecia castanea* (Lepidoptera Cossidae) and several species of Pyralidae;

Stalk-suckers: *Chaetococcus phragmitidis* (Homoptera Coccidae);

Leaf-suckers: *Hyalopterus pruni* (Homoptera Aphididae).

It may be pointed out that there are nearly no leaf-feeders on helophytes in the reed bed (apart from occasionally grazing grey geese), a fact which is considered characteristic of Phragmites and Carex. Other organs of the Phragmites plant are ingested, however, by some vertebrates: young shoots by the muskrat *Ondatra zibethica* and seeds by the titmouse *Panurus biarmicus.*

The role of the phytophagous insects on productivity relationships can be quite different. Whereas, for example, the stem-borer *Phragmataecia castanea,* intaking 1500 cal/stem/year (Pruscha 1972) causes no visible affection to the plant's growth, the gall-former *Lipara lucens,* intaking only 60 cal/stem/year (Waitzbauer 1969), inhibits growth remarkably and prevents blooming. Also muskrats are more effective by mechanical damage than by feeding. Regarding the ecology of the other species involved it must be stated that phytophages on Phragmites are more important by preventing than by consuming primary production.

2. An attempt was made to assess the total share of the phytophagous food chain in the ecosystem (i.e. in the central reed zone which is permanently submerged and not influenced by turbid water of the open lake). Whereas data on the total energy budget are available only of a few dominant species of the main feeding types, an approximation is possible for the remaining species by using the known active biomasses and the assumption of similar energetic regimes for species of closely related ecology. The lower the biomasses of these remaining species are in comparison to those of respective dominant species, the better this approximation will be. At present the amount of energy intake by all phytophagous insects on Phragmites is estimated to about 40 to 60 Kcal/ /m^2/year. Regarding the net primary production of Phragmites amounting to about 15 000 Kcal/m^2/year, this means only less than 1%. Though muskrats (and barbed titmice) are more effective feeders on the reed, their intake (which is not known until now) cannot alter this percentage essentially because of their relatively sparse occurrence.

There is little knowledge on the losses of submersed plants (*Utricularia vulgaris*) and algae caused by phytophages; but they must assumed to be much higher than those of Phragmites. Different energy flow regimes in the aquatic food chain, however, cannot shift remarkably the total energy flow ratio in the ecosystem. This is illustrated by the comparison of the net production of Utricularia estimated at 100 to 200 and of phytoplankton at several hundred Kcal/m²/year (see also papers of Dokulil 1973, Meier 1973 in this proceedings volume), with that of Phragmites at 15 000 Kcal/m²/year; even the rather important production of periphythic algae not investigated until now will probably not exceed 1000 Kcal/m²/year. These considerations confirm the conclusion that a predominant part of primary production breaks down before being consumed.

3. The trophic relationship of detritophages (which cannot be separated clearly from microphages) are much more complicated. Due to lack of sufficient staff for establishing complete energy budgets, the most urgent step was felt to investigate actual population dynamics, which is the most ecosystem-bound element of the population energy budget and which permits a primary approximation to the role of populations in the energy flow of the ecosystem.

Most emphasis was and is laid on water snails, water sow bugs (*Asellus aquaticus*) and several groups of Nematocera. Other important detritophages are represented by Trichoptera and Oligochaeta. Especially the census of Nematocera required considerable efforts and the application of different methods (Imhof 1972) aiming at an assessment of productivity derived from emergence rates. A combined series of census of big Chironomidae (Endochironomus, Camptochironomus and Chironomus spp.) in 1971 resulted in about 700 larvae/m² before pupation, whereas 100 of which have emerged as imagines (Imhof, Burian 1972). Regarding losses in earlier larval stages, a rule of thumb can be stated that production of Chironomids amount to at least ten times the biomass of emerged imagines.

Total net production of some of the most important detritophages mentioned above are estimated as follows (Kcal/m²/year): water snails 30, *Asellus aquaticus* 10, Chironomidae 10 (for comparison phytophagous insects: 15). An imagination of the share of the detritophagous food chain may be achieved when considering the *P/C* ratio, which is commonly much less in detritophages — e.g. 5% in *Asellus aquaticus* (Prus 1972) — than in phytophages — exceeding in gall-formers to more than 60% (Waitzbauer 1969). On the other hand there are uncertainties caused by the part of microorganisms in the food intake of "detritophages", as well as by the fact that part of the material ingested passes more than one gut in a decomposing chain. The factor by which the energy flowing through the detritophagous food chain exceeds that through the phytophagous food chain, nevertheless seems likely to amount between 10 and 20. That means, however, that even by both food chains, the phytophagous and the detritophagous together, only a minority of the produced plant material is decomposed. **The major part of primary production goes directly into microbial decomposing processes.**

4. Facing the predominant importance of microbial decomposition of reeds, another question is still arising: Is primary production in a reed bed reduced completely, anyhow? Is the microbial activity sufficient to accomplish remineralization of all the organic material accumulating in water and mud, particularly under the prevailing anaerobic conditions? Indeed, some indications are available from mud analysis and tests of microbial capacity (Farahat, Nopp 1966) that organic substances accumulate in deeper layers of the muddy sediment, what means an interception of flowing energy. Little is known about the extent of this withdrawal of organic material, the processes involved and factors by which they are governed. Further investigations on these questions seem desirable, the more so as this phenomenon may be possibly a characteristic feature of the energy flow system of wetlands in general.

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	169-174	1973

R. MAIER

ASPECTS OF PRODUCTION OF *UTRICULARIA VULGARIS* L. IN SOME VEGETATION TYPES IN THE REED-BELT OF LAKE NEUSIEDLERSEE

Pflanzenphysiologisches Institut der Universität Wien, Dr. Karl Lueger Ring 1,
A-1010 Wien, Austria

ABSTRACT

The presence of *Utricularia vulgaris* L. in the reed-belt of Lake Neusiedlersee is quantified according to a sociological classification. The dry matter development in the *Scirpo-Phragmitetum utricularietosum*, a well developed natural stand, is compared with that in the *Scirpo-Phragmitetum utriculariosum*, a reed-tree lacune. Seperately the paper deals with those reed banks, which are harvested in winter. In the landsides situated *Caricetum acutiformis-ripariae*, Utricularia attains to a lightpoor zone and simultaneously to the reach of yearly periodical alternation of water gauge. During the following year the resettlement is partly brought into relation to high drought resistance of turios (winter buds); the growing conditions in this zone are discribed.

The main part of the reed-belt at the Lake Neusiedlersee can be classified to the *Scirpo-Phragmitetum utricularietosum*, lakewards it alterates with a *Scirpo-Phragmitetum phragmitosum* (plain reed stand) and occurs to be a reed bank, which is signified by infiltration of *Utricularia vulgaris*. Mixed with *Typha angustifolia* L. and *Potamogeton pectinatus* L., possibly small extented stands or border associations of lacunes and chanals can be formed (mainly in anthropogen disturbed zones, Weisser 1970).

Utricularia vulgaris, a submerged rootless plant, which during its growing season has to put up with considerable light damage, being shadowed by reed, gains an adventage being more or less not exposed to breaking of waves. On account of these conditions dislocation of plants can be avoided, which on the other hand occurs at the free surface. Of course with regards to the growing conditions for Utricularia two different spheres within the *Scirpo-Phragmitetum utricularietosum* can be distinguished: 1. natural reed stands, which at last are not influenced by harvesting of reed, 2. reed banks, which are cut for economical purposes. On account of widespread harvesting the wind influence becomes more effective. By that, the turios of Utricularia are displaced and accumulated at distinct places (see Maier 1973). On account of the higher biomass at the very beginning of growing season, at those habitats the biomass per area unit occurs to be higher than within the reed. In addition to that fact, apart from complete irradiation penetrating to water surface at the beginning of growing season, the cut stands gain more light (relative light-use on 6.VIII.1971 11.1%). Only 6.23% of total irradiation penetrates through to the water-surface at the same time, after foliation of reed (from May on) in a well developed, natural reed stand.

Tóth, Szabó (1961) characterized the *Scirpo-Phragmitetum utriculariosum* in the Hungarian part of the lake to be a swampy pool-zone, which is protected from breaking of waves and is signified by crowded vegetation of Utricularia. The plant forms distinct stands, where smaller, open water areas alterate with reed banks. In these loosened, light penetrated reed stands, Utricularia develops quite better. In comparison with an uncut stand the better light conditions in a cut one are able to increase the standing crop not just absolutely but also relatively (Fig. 1).

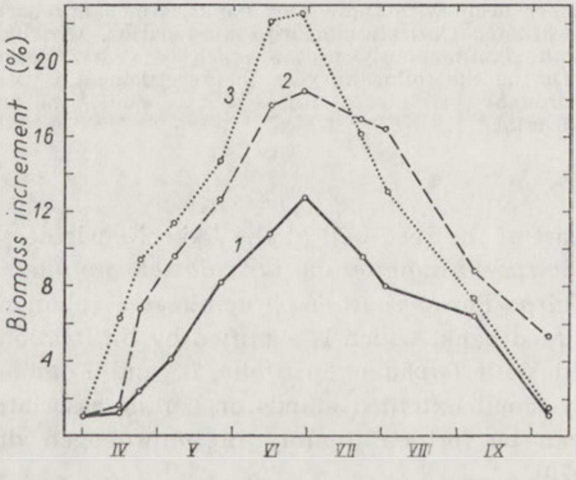

Fig. 1. Relative development of biomass of *Utricularia vulgaris* (1971). 1 — in a natural reed habitat, 2 — in an adjoining cut stand, 3 — in a reed-free lacune

If the reed stands are loosened up in that way that reed-free spheres of natural or anthropogen origin are scattered in the reed-belt, a plain stand of Utricularia can be formed — the *Scirpo-Pragmitetum utriculariosum* (Weisser 1970). The stubble-lacunes („die Stoppellacken"), those spots which are reedless during the whole year, and occur in consequence of harvesting injuries, are settled with the Utricularia vegetation of the formal *Scirpo-Phragmitetum utricularietosum*. Of course there is no possibility for the plants to anchor, if not by decreasing of water depth the old reed stalks are situated near water surface; the plants are floating to the border of the lacunes and partly into the reed stand. The lacunes are settled only to a small extent. Just if the reedfree spots are small the effect of wind is eliminated (mainly in natural lacunes). Just in every case the growth conditions are obviously different from those in the reed stand. Besides the mentioned wind effect, the more widespread temperature amplitudes, the altered exchange of water with the atmosphere and mainly the changing light conditions, quantitative and qualitative ones, have to be taken into considerations. Here Utricularia, which normally grows under inferior light conditions, is confrontated with high light intensities. In the dense stand no algae layer on the plants can be observed, vice versa mostly in the lacunes the plants show thick layers of algae (mainly Diatomeae and near ground Cyanophyceae) and of suspended particles. By that, they become weighty and the basal part of the shoots sinks downwards. These seem to be processes, which surely have an importance for Utricularia's light climate. The high light loss, which the plant is concerned within the reed, is ceased here. By that in spite of mean settlement density there results a rationally high maximum amount of standing crop at the end of June (Table I). The energy profit by higher irradiations is shown off in the calorific values. During the time of maximal standing crop full light plants compound 2812 cal/g d. wt., on the other hand plants in the stand just 2617 cal/g d. wt. (Imhof, Burian 1972).

Table I. Biomass of *Utricularia vulgaris* in reed stands and open lacune in 1971 (int = interpolated values)

Type		Biomass (g d. wt./m^2)			
		31.III	5.V	29.VI	21.VII
Scirpo-Phragmitetum utricularietosum	natural	1.10	4.48	14.06	10.60
	harvested	2.35	22.65	43.46	39.68
Scirpo-Phragmitetum utriculariosum		1.74	19.83	38.91	28.10
Caricetum acutiformis-ripariae		2.42 (26.III)	32.50	23.80 (int)	15.60 (int)

Relatively, relating dry weight to starting weight (d. wt. of turios/ /area — Fig. 1), up to the maximum the plants in the open lacunes occur to be the most productive. In the natural reed habitat just on account of the light decrease the plants do not come up to that amount. At the beginning of development the complete irradiation and later on the improved light conditions in the cut stand as well, guarantee favourable growth. But in relation to dry matter production of lacune plants they cannot obtain such high values. After exceeding of maximal standing crop the relative dry weight decrease is lower (according to the reduced decomposition — Maier 1973) than that of lacune plants. But absolutely during the whole growing season in the cut stands the highest amounts of biomass per area are obtained (Fig. 1). As mentioned already this is because of the accumulation of turios in this habitat.

Landsides the *Scirpo-Phragmitetum utricularietosum* is followed by a *Caricetum acutiformis-ripariae*. According to Weisser (1970) one can confirm, that those stands, mixed with reed, also can be appointed to the Scirpo-Phragmitetum. In comparison to the widespread amplitude of reed the more narrow amplitude of the great rushes gives insurance for classification of these stands rich of rushs as a Magnocaricion society.

The raising of water gauge by means of slowing down the drain by the "Einserkanal" had its consequence in innundation of large areas of the *Caricetum acutiformis-ripariae* (1965). By and by during the years a settlement of *Utricularia vulgaris* took place. By that the plants get in the reach of that zone, in which besides of Phragmites large *Carex riparia* stands become effective light competitors as well. In those uncut stands only 2.3% of total irradiation (6.VIII.1971) penetrates to water surface. Only at the beginning of growing season, whereby certainly also the faster warming of the shallow water improves development, than better light conditions the matter production can be sustained. But at the beginning of May the maximum amount of biomass is obtained (Table I). Just in July numerous turios are formed. By the large extension and the shallowness of the lake the zone in between the highest and the lowest water level is far extended. With beginning of September (1971) the stand dries by retiring of water.

The yearly resettlement of this stand after the return of water cannot be arranged just only by water drift. Examinations in the laboratory have confirmed that also under extreme conditions (about 30% relative air humidity) the drying turios are able to survive at least two months. But only turios investigated in autumn are so drought-resistant. Just before sprouting (February) the turios occur to be very sensitive against drought. The cause of this high drought resistance — the turios dry up to a water content of about 6% d.wt. — seems to be the morphological structure by which water output respectively the water input after remoisting is retarded. On the other hand this is caused by the mucilage which the new formed turios are rich of (in contrary to the turios in February, which have less mucilage content). When drying this mucilage solidifies and covers crustlike the turios surface. Thuswise at remoisting, the mucilage has to swell first, the stiff crust has to be mollified. By that the central part of turio is slowly moistured, a process which improves the surviving chance of plasm. According to Iljin (1935) the plasm is distroyed mechanically by quick water input of cells at remoisting. Besides these physical effective components, doutless the cause of such high drought resistance has to be a plasmatic property (Höfler 1943). Turios are storage organs; possibly the drought resistance of cells is effective by means of these substances (Maier in prep.) Nevertheless the drying up is connected with losses. To certainly occurring deficiencies by drought injuries bacteria decomposition of turios has to be added. Mainly the effective infection by caterpillars of *Nymphula sp.* and during winter season climatical conditions are damaging as well. Also in astatic pools, where drought injuries are excluded, the climatical conditions are more extreme than in the inundated part of the reed-belt. If the resettlement is caused only by drifting, the turios would advance as far as the water. But this does not take place, a zone in the inundated region occurs to be free of turios also at high gauge.

In connection with different light climate, in the particular vegetation types, a characteristical development of habitus of *Utricularia vulgaris* can be observed. A racial character of this plant is the extinction of the basal part of the shoot, although the top still grows. It is commonly said that the dying parts of plants are significantly shorter in the reed than in the open lacunes. Weisser (1970) connects there higher rates of extinction with the organic layer, which reduces the light, and limits also the surface exchange. For figuring the length development, extreme habitats were choosen as to their light climate, simultaneously the leaves' development during growing season at these two habitats is shown (Fig. 2). The standing crop of Utricularia in the natural Magnocaricion gains its highest amount at the very beginning of May and coincides with maximal development of leaves. In spite of continuing length development the dry weight decreases (Table I, Fig. 2). The leaves

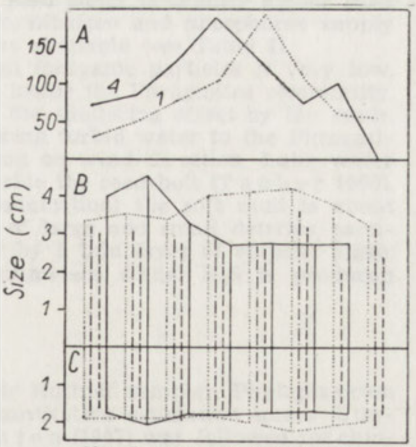

Fig. 2. Leaf sizes in comparison to shoot length of *Utricularia vulgaris* (1971). A — average length of shoots, B — leaf length (middle region of shoot), C — average leaf breadth. 1 — ligth exposed lacune, 2 — cut reed stand, 3 — well developed natural reed habitat, 4 — lightpoor silting zone

become smaller and the utricles are reduced (see Maier 1972). Vice versa in the reed-free lacunes the leaves are rich with utricles and attain just in summer the maximal size, maximal length coincides with maximal amount of dry matter.

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	175—180	1973

M. DOKULIL

PLANKTONIC PRIMARY PRODUCTION WITHIN THE PHRAGMITES COMMUNITY OF LAKE NEUSIEDLERSEE (AUSTRIA)

Limnologische Lehrkanzel der Universität Wien, Bergg. 18/19, A-1090 Wien, Austria

ABSTRACT

Planktonic primary production within the Phragmites community of Lake Neusiedlersee was measured using the ^{14}C method. Values were at or below 20 mg $C/m^3 \cdot hr$ which is only 35% of that for the open lake. The main controlling factor is the intensity of underwater illumination which is reduced by shading effects of the Phragmites and through absorption by the strongly coloured water. Benthic and epiphytic algae are often a dominant component of the biomass; a typical phytoplankton community being encountered only at depths of 0.5 m or more.

1. INTRODUCTION

Since the limnological characterization of Lake Neusiedlersee as a whole has been presented in several papers (Ruttner-Kolisko, Ruttner 1959, Schiemer et al. 1969, Weisser 1970, a.o.), only brief comments relating to the situation within the Phragmites stand need to be given here.

Reed covers nearly 58% of the whole lake area (Kopf 1967 cit. acc. to Weisser 1970). Water depth inside the reed-belt varies from 0 to 1.1 m. According to Neuhuber (1971) the ionic concentration of the reed water is slightly higher than the water of the open lake, the pH value is lower, nitrogen and phosphorus supply is better but sodium, chloride and sulphate are less available (see Table I).

In contrast to the open lake, turbidity through inorganic particles is very low, but there exists always a marked brownish colour inside the Phragmites community. Wind influences are seldom detectable because of the sheltering effect by the reeds. On the other hand, horizontal water movements bring turbid water to the Phragmites belt or clear water out into the lake depending on wind direction. Lake water losses its turbidity rapidly due to sedimentation inside the reed-belt (Tauber 1959). According to Löffler (1971 and personal communication) the soft mud is about 1 m thick, its surface being covered by 0.5–5 cm of large and small detritus particles (Tauber, Wieden 1959) and held together by a thin layer of epipelic algae. No oxygen is detectable below the top few centimeters whilst H_2S is produced (Schiemer, Farahat 1966).

2. METHODS

Samples were taken with a one litre non-toxic Ruttner sampler. Phytoplankton was fixed with lugols-acetic acid solution for quantitative estimation under Utermöhls inverted microscope. The method of Lorenzen (1967) was followed for chlorophyll estimation corrected for degradation products. Millipore filters (Membranfiltergesellschaft Göttingen) pore size 3 μ were used for the gravimetric analysis of turbidity. Measurements of productivity were done by the normal ^{14}C light and dark bottle technique according to Steeman-Nielsen (1952), the bottles being suspended in situ at the depth of maximal production for a 4 hr period around noon [1].

Light penetration was measured by aid of a photo-cell with Schott filters RG_2, VG_9 and BG_{12}. Colour was characterized by means of the extinction-value at 430 nm (1 cm path length).

Samples were taken on the northern shore near Neusiedl where the average water depth is about 0.3 m and on the western shore near Rust at a depth of 0.6 m.

Table I. Comparative data for the two stations within the Phragmites community of Lake Neusiedlersee and for the Station Seemitte in the open lake

Parameter		Reed-belt		Open lake Seemitte Station
		Neusiedl	Rust	
Water depth z (m)		0.3	0.6	1.5
Extinction ε (ln/m)	Range	0.70—2.00	0.78—2.74	3.60—5.00
	Mean	1.4	1.72	4.3
Depth of euphotic layer z_{eu}(m)	Range	to bottom	to bottom	0.1—2.0
	Mean			0.85
Irradiance I_z (%)		35—40	30	$\ll$1—10
Light penetration mainly influenced by		colour	colour	turbidity
Turbidity (mg/l)		0.5—8	3—12	10—500
Colour (E/cm)		0.010—0.036	0.015—0.045	0.0—0.01
Biomass B (mg chl-A/m^3)		1—4	2—5	1—23
Production P (mg C/mg chl-A $\cdot$ hr)		0.69—2.06	0.60—2.78	4.36—6.55
Production nP (mg C/m^3 $\cdot$ hr) max.		22.0	14.5	109.09
Gross photosynthetic rate A/h (g C/m^2 $\cdot$ hr) max.		0.007	0.0073	0.163
Gross photosynthetic rate A/d (g C/m^2 $\cdot$ day)	max.	0.084	0.0876	1.95
	mean.	0.050	0.060	0.182
pH		7.7—8.7	7.5—8.2	8—10
Ions$_{tot}$ (mval/l)		18.3	—	17.41
P_{tot} (μg/l)		5—40	—	10—50
P_{dis} (μg/l)		5—20	—	1—5
NO_2^- (μg N/l)		1.25	—	<1
NH_3 (mg N/l)		0.28	—	0.16

3. RESULTS

Phytoplankton at Station Neusiedl develops very rapidly after ice break and reaches its peak in summer around July. Durig spring and early summer small Chlorococcales and Cryptomonas are most abundant. Later in the year diatoms become more and more dominant. Desmids and euglenophytes are present during the year in different amounts.

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[1] The standarized ampoulles are from the "International Agency for ^{14}C-Determination", Charlottenlund, Denmark. Counts and calculations were done at this Institute by Miss Ann-Mari Bresta.

The latter have a maximum in August and September. Only one blue-green algal bloom was recorded, this occurred in August 1969 (Fig. 1).

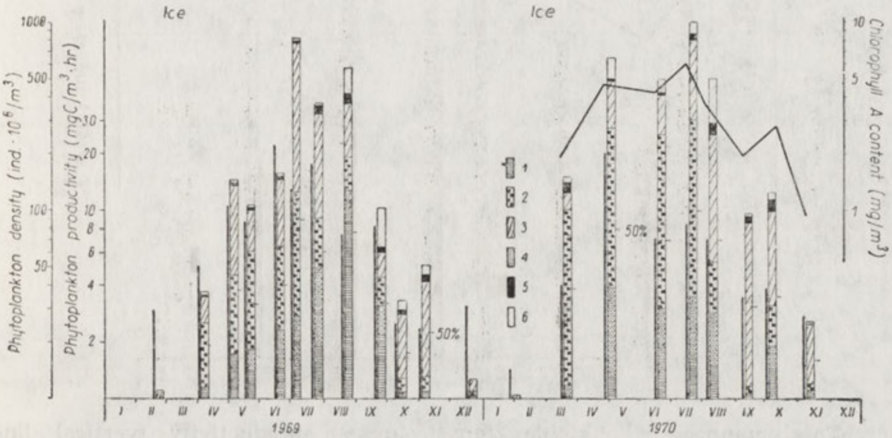
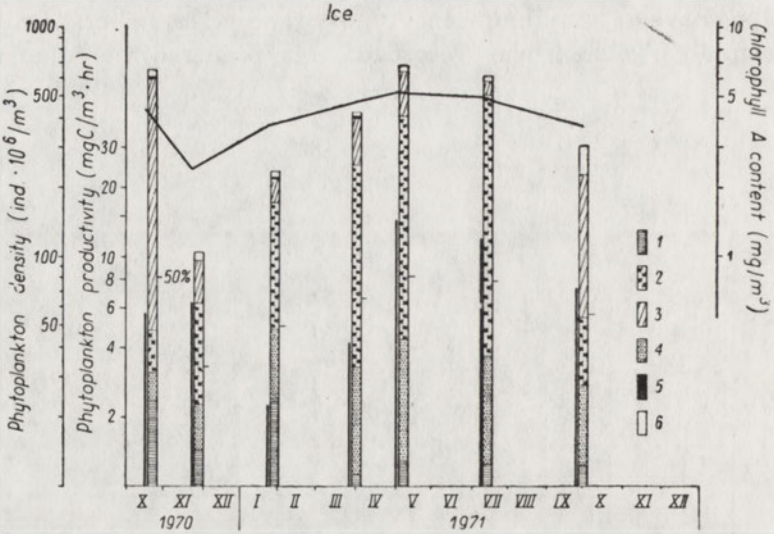


Fig. 1. Total numbers of phytoplankton individuals (columns), productivity (vertical lines) and chlorophyll content (curve) for Station Neusiedl within the Phragmites community at Lake Neusiedlersee for 1969–1970 (semi-log graph; algal groups are given in per cent of total number). 1 — blue-green algae, 2 — Cryptophytes, 3 — Chlorophytes, 4 — Diatoms, 5 — Desmids, 6 — Euglenophytes

Great species diversity occurs because epiphytic and epipelic algae often contribute considerably to the plankton community. These are mainly diatoms, desmids and euglenophytes, while the Chlorococcales and Cryptomonas species are typical planktonic organisms. A colourless blue-green algae, *Lampropedia hyalina*, is common at this station, too (Dokulil 1971).

Productivity, with a maximum of 20 mg C/m^3 · hr, appears to be very low, but is slightly higher than at Station Rust. In winter, primary production falls to bearly detectable values and sometimes it is impossible to take samples, because of freezing to the bottom. Biomass in terms of chlorophyll A shows great variations between 0.8 and 6 mg/m^3.

As is seen from Fig. 2, biomass changes are much smaller at Station Rust varying between 2 and 5 mg of chlorophyll A per m^3. There is more typical plankton: *Ankistrodesmus falcatus* together with different species of Cryptomonas can constitute up to 80% of the total biomass, in contrast to Station Neusiedl where a mixture of green algae exists. In autumn small diatoms, like Cyclotella, Nitzschia and Navicula, become dominant. Productivity is in the same order of magnitude as it was at Neusiedl. During the winter season, primary production is higher than at Neusiedl, because of a more stabilized phytoplankton community and better light conditions.



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4. COMPARISONS

Comparison of these two stations with values from the open lake (Table I) shows that biomass is much lower within the reed-belt and productivity is on the average 35% of that of the lake. Light is the main controlling factor of primary production.

Penetrating light is reduced in the open lake by absorption and scattering in the turbid water. Inside the reed stand, total irradiance is first reduced by Phragmites and second by absorption in the humic coloured water. The vertical extinction coefficient of the green and red part of the spectrum is lower for the reed water and is nearly the same whereas out in the lake green is the most penetrating spectral region (Fig. 3).

Finally some remarks to the stirring mechanisms should be given. For the open lake wind is the main factor influencing primary production, affecting turbidity and therefore regulating the underwater light climate as was outlined by Dokulil (1972). Planktonic primary production is partially regulated by the shadow effect created by the surrounding reed stems whose presence effectively curtails the day length at the water surface by screening it from horizontal illumination at low solar elevations. Other factors are the colour of the reed water and influences of dissolved gases released from the bottom sediment. Figure 4 gives a preliminary scheme of the controlling factors ignoring nutrients to keep it simple.

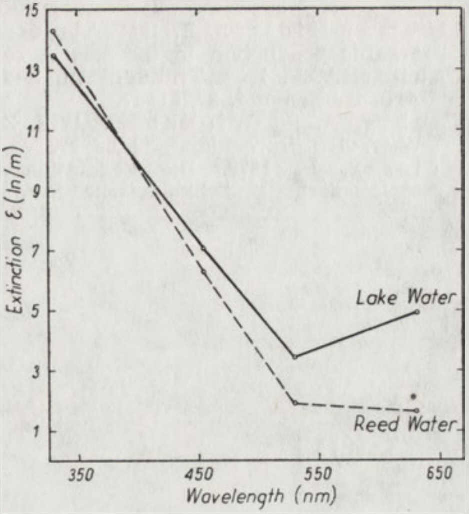

Fig. 3. Vertical extinction coefficient for different spectral regions for lake and reed water

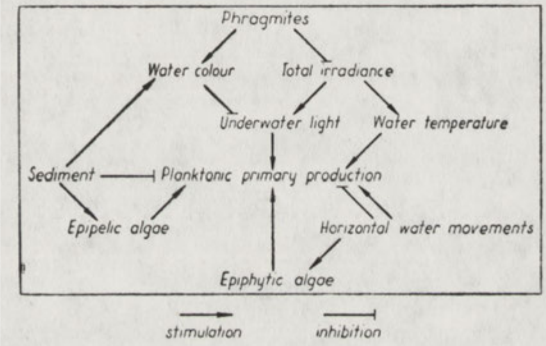

Fig. 4. Scheme of factors effecting planktonic primary production within the Phragmites community of Lake Neusiedlersee. Nutrients are excluded to keep the scheme simple

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	181—184	1973

H. ETTL

CYTOLOGICAL INVESTIGATION METHODS FOR THE GROWTH OF *CLADOPHORA GLOMERATA*

Department of Hydrobotany, Institute of Botany, Academy of Sciences, Brno, Czechoslovakia

ABSTRACT

Two cytological investigation methods for studying the growth and differentiation of the cells in the thalli of *Cladophora glomerata* are mentioned. The first one, using glass tubes, makes it possible to determine the increase of the cell number and the differentiation in the thalli. The other one, based on periodical sampling and staining of parts of the thalli from natural populations, aims at determining the growth rate and the diurnal changes of the single cells.

Various methods for studying the primary production in littoral algae have been applied (Sládečková 1963, Pieczyńska 1968, 1971, Vollenweider 1969), but none of them has been universally employed. Only the actual gross primary production of the whole littoral community can be estimated by those methods. To get more information about this complicated process we have to know also the life cycles of the species in the community, especially of the dominant ones (the kind of reproduction, the differentiation of cells in the thallus and the cell division ability) as well as the growth characteristics of the species with regard to their diurnal rhytmus. For this reason it was necessary to elaborate methods which clarify cell division and differentiation in the thallus of littoral algae. During 1971 the most important species of the littoral algae in the Nesyt fishpond (near Lednice in Southern Moravia) was *Cladophora glomerata*, building large areas of periphyton on stones and on *Typha angustifolia* in the surf-zone. The mass production of this alga has made it possible to try two cytological methods (Ettl et al. 1973) in studying of growth and diurnal rhytms as follows.

Method 1. The growth of the thallus and the differentiation of cells of *Cladophora glomerata* can be studied only in containers under natural conditions. This container has to allow streaming of the surrounding natural water and to prevent the entrance of animals and other algae. Parts of fresh grown thalli were therefore put into small glass tubes with a length about 8 cm and diameter of 1 cm (Fig. 1).

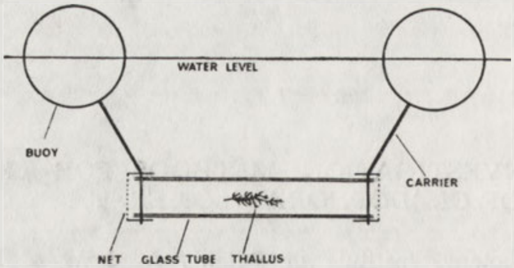

Fig. 1. Diagram of the glass tube for investigation of growth of *Cladophora glomerata*

Just before insertion of the thallus into the glass tube the number of cells was counted under low magnification (× 60) in a drop of natural water without a cover slip. After the thallus was put in, both ends of the tube were closed with fine net to exclude the above mentioned disturbing factors. The whole manipulation has to be done in the natural water, so that the alga does not come into contact with air. After closing with nets the tubes were placed in the water at the place of natural occurrence of this alga. After an exposure of 48 hr the increase of the cell number was found out in six parallel experiments which are demonstrated on Table I. The calculated values are very similar to each other and show that the growth of the thalli is continued after isolation from the cluster. The doubling time can be derived by assuming the validity of the exponential growth. Simultaneously the differentiation of the cells (especially of the terminal cells — terminal growth of Cladcphora) in the thallus can be studied. This can be facilitated by employing microphotographs of the thalli before and after the exposure. This method makes it possible to find out not only the increase of the cell number (the growth of the thalli) but also cells capable of further growth or reproduction (the differentiation in

Table I. Growth of *Cladophora glomerata* cells in glass tubes during two-day experiment

	Glass tube					
	1	2	3	4	5	6
Initial number of cells (20.VII.1971)	113	77	62	86	61	117
Final number of cells 22.VII.1971)	579	314	310	425	295	354

the thallus). However, the growth rate of single cells may differ substantially according to their location in the thallus and according to their vitality. These differences can be determined by another method as described below.

Method 2. This method is based on the periodical sampling of terminal parts of the thalli of *Cladophora glomerata* from natural algal populations, aimed at finding out the growth rate and the diurnal changes of the single cells, especially of the terminal and subterminal ones. The samples were taken at the same time as the above mentioned experiments were running. At regular intervals throughout a two day period samples were taken and were immediately fixed with Carnoy solution and stained with aceto-carmine according to the method of Geitler (1940). The average number of nuclei per cell as well as frequencies of the mitotic nuclei in the total number of nuclei in the single cells (mitotic index) were determined. The last was calculated as the ratio of mitotic nuclei to the number of interphasic nuclei in the cells:

$$MI = \frac{M}{I} \cdot 1000$$

where *MI* means the mitotic index, *M* indicates the number of the mitotic nuclei and *I* the number of the interphasic nuclei. Simultaneously the changes of plasma volume belonging to one nucleus and the length of the terminal cells were noted. In every sampling 30 cells from the terminal part of the thallus were evaluated. The mitotic index, the

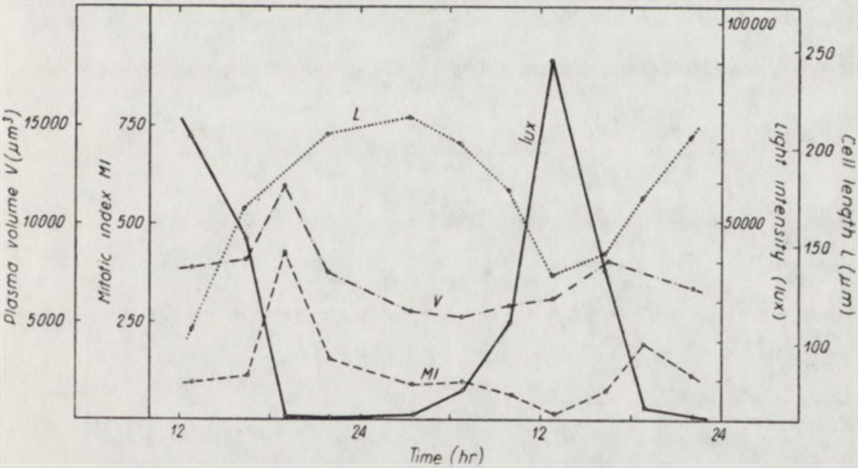

Fig. 2. Diurnal changes of average plasma volume belonging to one nucleus, of the mitotic index and of the length of the terminal cells in relation to light-darkness periodicity in the terminal parts of *Cladophora glomerata* thalli

plasma volume and the length of the terminal cells reach their maxima early after the onset of darkness, whereas the minima appear at noon (Fig. 2). This method demonstrates both, the most actively growing cells and how the growth rate of the single cells differs according to their location in the thallus. In order to follow the growth rate of the cells, only one sampling after the onset of darkness is sufficient.

Both of these methods for the cytological investigation of the growth and differentiation of cells in the thalli of *Cladophora glomerata* make more precise the methods for studying of primary production. All results about the primary production of the littoral algae are incomplete if there is no mention of cell division and differentiation in the thalli. Only a complete knowledge of the activity of the cells, not only from the physiological but also from the cytological and morphological point of view, makes it possible to understand the complicated process of primary production in littoral algae.

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	185—188	1973

R. BOHR

PHYTOSOCIOLOGY OF PERIPHYTON

Institute of Biology, University of Nicholas Copernicus, Toruń, Poland

ABSTRACT

Phytosociology has become a very useful research method; it has been used for macrophytes so far, but can be used for microphytes, as well. Algae in the periphyton form associations, connected with limnological type of a lake, and can be a suitable basic unit for studying periphyton. The detailed procedure in question is given.

The periphyton presents a very wide range of problems for investigation. In the first place it is necessary to find an adequate unit as a basis for studying and described it. Such unit must accomplish the following requirements:

1. It must adequately reflect nature.
2. It must be: recurrent and comparable; as easy as possible to determine; useful for several kinds of research and practical ends.

After a long period of trials and experience, botanists and ecologists have achieved some results in the use of phytosociological methods. They successfully use the concept of "plant association" as a basic unit for vegetation.

It is my belief that phytosociology as separated from botany no longer exists, but it has now become a very useful research method. There are a lot of examples of application of phytosociology and its results to various purposes, both theoretical and practical. Today, when ecologists all over the world focus their attention on productivity and other functions of ecosystems, it is of particular importance to have a reliable unit for making syntheses and comparisons of different results.

If we draw a parallel between an ecosystem and an individual organism, we see that the question of energy and matter flow is at the physiological level of study; on the other hand we know that for a proper understanding of some physiological processes, a good knowledge of anatomy and morphology of the object is indispensable. For communities it is the list of constituent species, their quantitative dependences and their structural distribution in space that constitute their anatomy and morphology.

There are many phytosociological schools, which use different definitions of "plant association" as well as different methods. One of the best known in Western and Central Europe is the so-called Swiss-French phytosociological school, founded by Braun-Blanquet. This school has carried out the largest number of experiments and has been very successful in devising its own classification and systematics of all, or almost all, vascular plant communities.

Is it possible to adapt phytosociological methods used for macrophytes to the study of microphytes? Many authors have already tried to do this with varying success, but it is true that phytosociology has never been widespread in algology.

In my opinion, phytosociological methods for periphyton investigation are the only ones which can be used for describing a particular algal community. Further, more detailed investigation, like production measurement, population analyses etc., can be carried out by means of the „plant association" concept, and then generalizations and syntheses can be made.

In my two publications (Bohr 1962, 1967) I tried to describe algal associations of the periphyton, using phytosociological methods of the Swiss-French school. I proposed there some modifications and adaptations to the needs of algology. I believe that the final effect of my attempt has been rather positive. I have stated that algae in the periphyton really do form associations. Each of them is connected with one particular limnological type of the lake and they fulfil the conditions mentioned at the beginning.

Here is a brief statement of the procedure by which an algal association can be best determined:

1. Collecting the samples from the lake (with part of substratum); beside all general recommendations, one must remember to take the samples from a uniform station, that is, to keep a uniform phytocenose.
2. In a laboratory, the material for microscopic investigation is prepared in the following way: the periphyton is scraped off carefully from a 2 cm^2 surface, which is enough (i. e. "minimum area") to find all species of algae; after a very thorough dispersion of the samples, slides are prepared.
3. The most important and at the same time the most difficult stage of the investigation is to determine all the species, but it cannot be neglected. I am afraid that at this stage of investigation a man will never be neglected by even the best computer.
4. Then it is necessary to establish the quantitative relations of several components of the community. I think that for phytosociolo-

gical purposes a relative estimation is enough, using two parameters: the number and the size of the algae, as shown in Table I.

Table I. The scheme of classification of periphyton for phytosociological purposes

Size class	Mean size (μ^2)	Cover size (%)					
		5 75-100	4 50-75	3 25-50	2 10-25	1 1-10	0 1
		Mean number of specimes counted in 3 stripes of 3 slides					
3	$<$ 100,000	100	75—100	50—75	10—50	10	r
2	10,000—100,000	200	100—200	75 -100	50—75	10—50	r
1	1000—10,000	2000	1000—2000	750—1000	500—750	100—500	10
0	$>$ 1000	10,000	5000—10,000	2500—5000	1000—2500	100—1000	100

As size criterion, the surface area of thallus was taken (i. e. "projection of shadow"). The following algae belong to particular size classes: 0 — Chroococcales, many of Protococcales, same Desmidiales and small Bacillariophyceae, 1 — most of the Bacillariophyceae, Desmidiales, smaller Cyanophyta, Chlorophyceae, 2 — colonial Cyanophyta, Chlorophyceae and Bacillariophyceae, 3 — macroscopical algae.

My own experience shows that this way of estimation of abundancy is easy to use and express the real quantitative relations between several algal populations.

5. It is necessary to know the structure of the spatial distribution of the components of a community. The structure of the periphyton is often very complicated and in this connection I have some proposals for simplifying it. Algae are phototrophic organisms and their distribution results from their light requirements, and therefore I suppose that it is possible to apply, by analogy to macrophytes, a division into several "layers". These "layers" correspond not only to the "topography", but also to the ecological character of the species. They form euharmonic biological groups, which can be consider as "vital forms". They are:

1. Filamentous algae, branched or not, permanently attached to the substratum. They play an enormous role because they constitute the main part of the whole structure. This is layer A.

2. Filamentous algae, most of them unbranched, not attached to the substratum. They wind up around the algae of the former "layer" and they form layer A_1.

3. Colonial attached algae, lamelliform, globullose etc. These algae are able to settle quickly on a new substratum and in a mature community they constitute layer B.

4. Colonial non-attached algae which form long belts and, like the algae in A_1, wind up around other algae, but are very easily breakable. They belong to layer A_1.

5. Epiphyties attached to the substratum by a long mucilagineous stylus.

6. Epiphyties attached directly to the porophyt.

7. Facultative epiphyties.

The last three groups belong to layer C.

8. Free-living algae but biologically connected with the periphyton (possibly by chemical or others factors). These algae are classed to layer D.

All the above mentioned information serves to set the „phytosociological records", which becomes the main document for further interpretations.

Using these methods I and my collaborators have examined the periphyton of more than 40 lakes. We have found that:

1. Periphytonic algae form associations marked by fixed structures and constant floristic compositions.

2. In such associations several biological groups can be distinguished.

3. The periphyton associations are closely dependent on the limnological type of the lake.

4. So far we have determined two associations of the periphyton:

1. *Oedogonio-Epithemietum littorale*, occurring in eutrophic lakes of hard water. It occurs in several varieties, e. g. in lakes of great transparency a variety characterized by the absence of Cladophora and the domination of some species of Zygnemales. The variety with *Symploca sp.* occurs in vast shallow lakes and the variety of Cladophora develops in the lakes of very low transparency etc.

2. *Hapalosiphono-Tabellarietum calcifobum* occurring in lakes of soft water (low level of Ca^{++}). In dystrophic lakes, a variety of this association develops, in which the sphagnophilic (acidophilic) species of algae participate.

It is, therefore, of essential importance to get an exact picture of periphytonic communities, particularly of their specific composition, their quantitative and biocenotic relations etc. The determination of periphytonic associations as basic units will permit in future for wider syntheses and generalizations regarding ecology, biology, productivity, as well as the practical importance of the plant periphyton in the lakes.

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	189—193	1973

R. BOHR and M. REJEWSKI

SCOLOCHLOA FESTUCACEA (WILLD.) LK. IN LAKE JEZIORAK (POLAND)

Institute of Biology, University of Nicholas Copernicus, Toruń, Poland

ABSTRACT

The trial is made to explain the reasons of expansion of *Scolochloa festucacea*, the species alien to Lake Jeziorak till 1960. The possible reason is damage of the littoral parts of shores, caused by intensified wave action created by motorboats, the number of which has been still increasing during the last decade. This phenomenon is connected with the total change in the floral community, previously existing in the Lake Jeziorak.

1. INTRODUCTION

A rather rare species of Polish flora is the *Scolochloa festucacea* (Willd.) Lk. In Poland, it has about thirty localities of which the majority is concentrated in the region of Eastern Pomerania (Bock 1908, Müller 1911, Szafer 1919, Abromeit et al. 1940). Outside of Poland it is known in Brandenburg and Mecklenburg where it reaches the western limit of its area in Europe (Hermann 1956, Rothmaler 1962). There are also some localities of it in the south-east of Sweden and in the south of Finland (Hulten 1950). The main centre of its occurrence are the European territories of the U. S. S. R. (excluding the northern and south-western parts) and also the near Ural and south-western part of Siberia. Further on, eastward, its occurrence is largely dispersed up to the middle part of the Lena River. After a break off it appears again on the North American continent, mainly in the central territories of the Great Lowlands in the central-western part of North America (Meusel et al. 1965).

In Polish flora, Scolochloa represents a boreal element which arrived here from the near Ural part of Siberia (Kulczyński 1927). Its steril stems remind of short stems of reed, and the flowering ones look like *Glyceria aquatica* owing to its large, scattered panicle. It may be easily overlooked because it grows in habitats and in the company of the above named species.

In Lake Jeziorak *Scolochloa festucacea* was found for the first time in 1960 (Bohr 1965). It grew then at one locality involving hardly several square meters. During some further investigations regarding the distribution of macrophytes in this lake in 1971, more than 30 stands of this plant could be found. During the time of 10 years between both dates, there has occurred a remarkable expansion of that species, growing in Lake Jeziorak near south-western limit of its area. This paper is an attempt to explain the causes of that phenomenon.

2. ECOLOGICAL CHARACTERISTICS

The occurrence of Scolochloa in Lake Jeziorak has been, as yet, limited to the southern part of the lake (Fig. 1). All the found localities involving areas of from several up to some thousands of square meters have three common features:

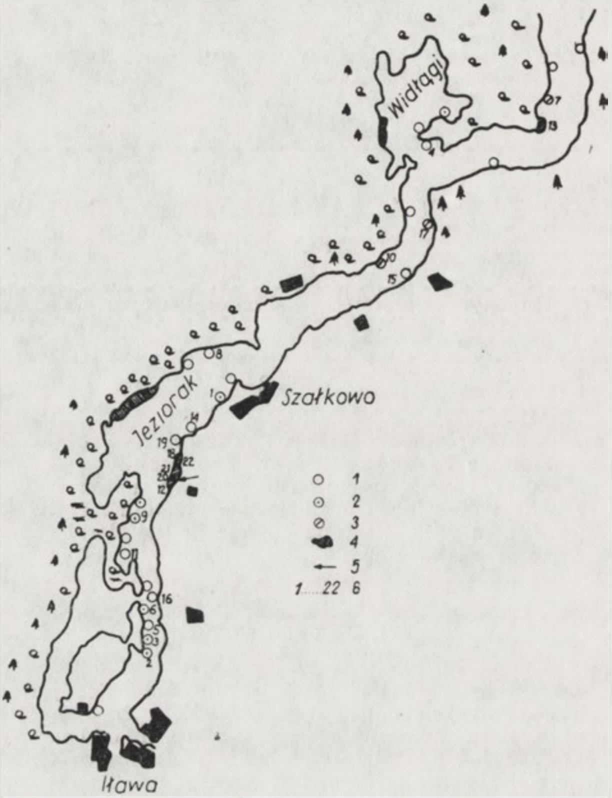

Fig. 1. Distribution of the localities of *Scolochloa festucacea* in the southern part of Lake Jeziorak. Surface of localities: 1 — to 50 m², 2 — 50–100 m², 3 — 100–250 m², 4 — more than 250 m²; 5 — the first locality in 1960, 6 — numbers of the fitosociological records

1. There are placed at the bottom softly inclined into the depth,
2. The bottom is hard, sandy, sometimes gravely and stony,
3. The depth of water in the stands at which Scolochloa grows does not exceed 90–100 cm, the mean is 20–60 cm (in only one case it grew at the depth of about 120 cm).

The spreading of *Scolochloa festucacea* in Lake Jeziorak to a new locality is connected with a retreat of the species which had grown there previously, and with the establishing of an arrangement close to the one presented in Fig. 2. Reeds retreat the most rapidly which is shown by well preserved fragments of reed rhizome at the localities most recently taken over by the Scolochloa. Relatively slowly space is given up by the *Heleocharis palustris* which coexists now at almost all the places with Scolochloa. It is also possible that both these plants enter into the new habitat at the same time. The cause of the sudden extension of the Scolochloa in the southern part of Lake Jeziorak cannot be of any climatic-hydrological nature. During the last ten years neither the climate nor the aquatic conditions of the lake or its neighbourhood have changed in any way. However, a factor which might be called the "wave-creative" one has changed entirely. It is the sudden development of the motor-aquatic sports on Lake Jeziorak. The neighbouring town Iława, destroyed during the war, has developed since 1960 into a first class tourists' centre with various types of motorboats circulating on the lake. Waves and whirlpooles caused by the boats break with great force at the shores of the lake, most strongly where the lake is most narrow. The sketch showing the distribution of the Scolochloa localities shows at once the distinct correlation between its frequency and the narrowness of the lake.

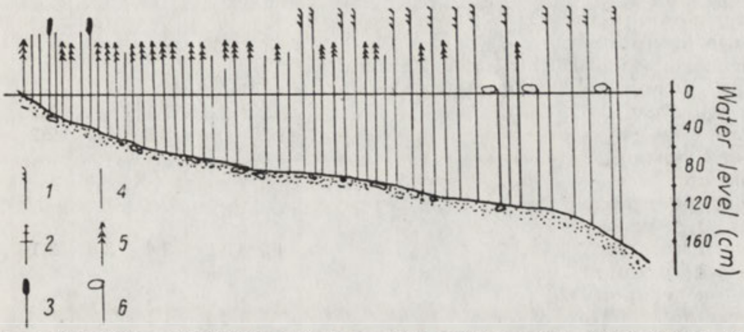

Fig. 2. The schematic structure of the community with *Scolochloa festucacea*. 1 — *Phragmites communis*, 2 — *Glyceria aquatica*, 3 — *Typha angustifolia*, 4 — *Heleocharis palustris*, 5 — *Scolochloa festucacea*, 6 — *Nuphar luteum*

The meridian arrangement of the lake with a majority of western or eastern winds is not favourable for bringing up any larger wind waves. Therefore, the wave action caused by the circulation of motorboats brought into being a new environmental element in the southern part of Lake Jeziorak. It limits the growth of some species and favours some other ones owing to the mechanical damages caused to rhizomes and young stems by the waves whirling up sands and tiny gravels. This characteristic process undoubtedly affects the shape of the bottom of some parts of the littoral.

There is also no doubt about the fact that the Scolochloa obtains its new localities by taking adventage of a defined ecologic recess in the littoral. In the southern part of Lake Jeziorak there has been an anthropogenic factor responsible for the recess. It may be assumed that an accidental transfer of seeds (by aquatic birds) to this part of the lake, coinciding in time with the development of aquatic sports, has been the cause of the sudden and strong development of the Scolochloa. In the southern part of Lake Jeziorak a natural factor is the strong wave action of winds bringing into being, at some sections of the

Table I. Community with *Scolochloa*

	Number						
	1	2	3	4	5	6	7
Mean depth (cm)	30	35	30	30	40	40	25
Cover (%)	85	70	80	50	70	50	70
Surface of record (m^2)	100	100	60	30	20	50	100
Characteristic species of the aliance Phragmition							
Glyceria aquatica	.	2.2	2.2	2.2	3.4	3.3	1.1
Schoenoplectus lacustris	.	2.1	1.2	1.1	1.1	1.1	+
Typha angustifolia	.	.	.	.	.	+	2.1
Phragmites communis	.	.	.	.	.	.	.
Sparganium ramosum	.	.	.	.	.	.	+
Characteristic species of the order Phragmitetalia and of the class Phragmitetea							
Heleocharis palustris	2.2	2.3	1.1	.	1.1	+	1.2
Acorus calamus	1.2	+	3.3	1.2	2.2	+	.
Equisetum limosum	.	+	+	.	.	.	+
Carex rostrata	.	.	.	.	.	.	.
Lysimachia thyrsiflora	.	.	.	.	.	.	.
Accompanying species							
Scolochloa festucacea	4.5	3.2	3.4	3.3	2.1	3.2	3.1
Polygonum amphibium	.	+	.	.	.	.	1.2
Potamogeton perfoliatus	.	.	.	.	.	.	.
Nuphar luteum	.	2.1	1.1	.	.	.	.
Potamogeton lucens	.	.	.	.	.	.	.
Potamogeton natans	.	.	.	.	.	.	.

shoreline in the north-eastern part of the lake, some fragments of a large lake littoral. During the next years we can expect the appearance and the development of the Scolochloa here.

3. SOME NOTES ON PHYTOSOCIOLOGY

The above described phenomenon of the spreading of a new, rare species of flora has some interesting phytosociological aspects. There comes into being a new floral community (Table I) of a compound unidentical to any other hitherto known one. It develops in the habitat of Scirpo-Phragmitetum, however, absent are those species which are characteristic for this association. The presence of several species which are characteristic for the alliance Phragmition, order Phragmitetalia and of the class Phragmitetea qualifies it to be included into the above named units of a higher level, and consequently to accept it as an equal to the Scirpo-Phragmitetum.

The presently developing community with the Scolochloa has a substitutive and anthropogenic character. In the nearest future it may, however, occupy the habitats coming into being by the activity of natural factors, taking advantage of the ecologic recess of the large lake littoral. Further observations of the role and the behaviour of the *festucacea* (records on 7—8.IX.1971)

of record															Con-stan-cy
8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
60	25	45	35	40	45	30	40	30	40	40	30	50	55	40	
80	70	70	40	60	50	50	50	70	70	50	50	75	60	80	
100	100	100	20	100	100	20	100	40	100	100	20	100	100	100	
.	1.2	3.3	1.1	.	1.2	2.3	2.1	3.2	3.2	2.1	2.2	.	.	0.2	IV
1.1	1.1	1.1	1.1	.	.	.	.	.	.	.	.	.	.	.	III
1.2	1.1	2.2	1.2	1.1	1.2	2.1	.	.	.	.	.	.	.	.	III
.	3.2	.	2.2	.	.	.	+	1.1	2.2	.	.	.	.	.	II
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I
2.1	+	1.1	.	2.1	2.2	1.1	1.1	1.1	1.1	1.2	1.1	1.1	+	1.1	V
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II
+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I
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.	.	.	.	0.2	.	.	.	.	.	.	.	.	.	.	
4.4	3.3	3.3	3.3	4.3	3.3	2.3	2.1	3.3	3.3	3.3	3.4	4.4	4.3	5.4	V
1.1	+	.	.	0.2	1.2	.	.	.	.	1.2	.	.	.	.	III
.	.	.	.	1.1	.	+	.	.	.	1.1	+	1.1	1.1	.	II
.	+	.	.	.	.	.	1.2	.	.	0.2	.	.	.	.	II
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.	.	.	.	.	.	.	3.2	.	.	.	.	.	.	.	I

Scolochloa in our water basins may provide a lot of new materials permitting to verify and explain the processes of eutrophication and the overgrowing with aquatic plants of some types of lakes.

The establishing of the final rank of the newly described community should be also postponed up to that time.

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M. DE GEUS-KRUYT and S. SEGAL

NOTES ON THE PRODUCTIVITY OF *STRATIOTES ALOIDES* IN TWO LAKES IN THE NETHERLANDS[1]

Hugo de Vries-Laboratory, University of Amsterdam, Sarphatistraat 221,
Amsterdam, Holland

ABSTRACT

The productivity of *Stratiotes aloides* was measured during 1967 in two Dutch lakes. The net productivity was very high: about 112 kg/ha/day in Lake Achterweiden and 210 kg/ha/day in Lake Venematen, with maxima of 300 and 460 kg/ha/day, respectively. The specific gravity changes during the growing season in a different way in each of the zones (submerged, emergent and that of Hydrocharis) which shift in the direction of the lake centre during the season. The periodicity of the vegetation is discussed. The phosphate content of the total Stratiotes vegetation in Lake Venematen is at least 12 times greater than in the water body, the nitrogen content — 16 times greater. Potassium might be a limiting factor if Stratiotes were to cover a much larger part of the lake.

1. INTRODUCTION

The north-western part of the province of Overijsel in the Netherlands is a marshy fen region. It forms a part of the phytogeographical district which is known as the "Haf district" (i.e. Haff or Lagoon district) (Van Soest 1970). The Haf district covers large parts of the western and northern Netherlands, and the adjacent parts of Belgian and French Flanders and north-western Germany. North-eastern Germany, northern parts of Poland and parts of the Baltic states are closely connected in a phytogeographical sense, and the landscape shows some similarity. The polders, which lie partly below sea level, are typical of large parts of the Dutch Haf district, but the region from which the research on *Stratiotes aloides*, the water soldier, is described here, is not a polderland.

Large parts of the north-western part of Overijsel were peat bogs, but the peat was mostly removed by the end of the Middle Ages. The region now consists of a lot of lakes of all sizes. These were formed in two ways:

1. When the peat was dug out, drying strips were left above the level of the water, but the strips being relatively narrow, were destroyed by waves.
2. Some larger lakes were formed by flood water after the dam of the former Zuiderzee had burst in several places.

The region lies between higher diluvial areas, and the differences in water level cause seepage phenomena in the lower parts, especially in the transition areas.

The lakes show a characteristic zonation. Generally this zonation consists of submerged vegetation in the centre of the lakes, helophyte vegetation in the shore region, and floating-leaved vegetation in between. In certain conditions, described elsewhere, this type of zonation becomes much more complicated (Segal

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1965, 1971). Stratiotes can settle, and the zonation may then approximately be described as follows:

elodeids → nymphaeids + elodeids → submerged stratiotids + nymphaeids + elodeids → emergent stratiotids + hydrocharids + lemnids + ricciellids + ceratophyllids → floating islands with helophytes → helophytes → terrestrial vegetation.

This type of zonation may be expected where wave action has not been strong, the water depth is no more than about 2 m, and sapropel is formed or deposited.

Stratiotes grows very quickly and has a high productivity. Smaller lakes may soon be completely covered after the establishment of Stratiotes. This type of zonation is found commonly in the western and southern parts of the lakes, due to the prevailing westerly and southwesterly winds. This causes an undercurrent in the opposite direction, carrying small particles to the windward side. Thus the accumulation of sapropel is relatively high in the sheltered places near these shores. Stratiotes production is greater in shallower waters, so that sapropel accumulation may reach an even higher level. Thereupon the vegetation markedly reduces the size of waves.

Our research on Stratiotes communities has been undertaken in several lakes of different size. We here describe the results of our investigations from two places: Lake Venematen and Lake Achterweiden.

Lake Venematen has an area of 15 ha. The water depth in the centre is 1.4 m. A thick layer of peat lies upon the sandy subsoil at a depth of 3.2 m below the water level. The western part of the lake ends near the border line of a diluvial boulderclay formation on sandy subsoil. In such places seepage phenomena occur frequently, and this is also the case here. Botanical indicators for seepage phenomena are in this case, e.g., *Hottonia palustris*, *Hippuris vulgaris* and *Wolffia arrhiza* (Segal 1965).

Four zones of Stratiotes can easily be recognized (Fig. 1). From the centre of the lake to the shore the order is:

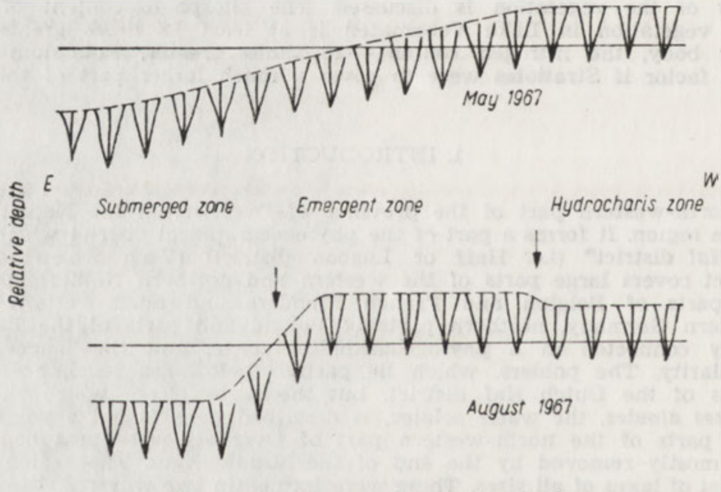

Fig. 1. Zonation of *Stratiotes aloides*

1. A constantly submerged zone in which Stratiotes has limp leaves, each of which is strap shaped and relatively long (up to 0.6 m, sometimes 1.1 m). Between the Stratiotes elodeids and nymphaeids may grow.

2. An emergent zone with few plants of other species. The leaves are mostly shorter than 0.4 m.

3. An emergent zone with an intricate vegetation structure, consisting of stratiotids, hydrocharids, lemnids, ricciellids and ceratophyllids. This zone is here referred to as the Hydrocharis zone.

4. A degradation phase on isolated shallow spots where *Utricularia vulgaris* reaches its maximum abundance and vigour in the zonation, and where Hydrocharis is often abundant too. Stratiotes is either scarce and tiny, or absent.

These zones shift in the direction of the lake centre in the course of the season.

In the Hydrocharis zone floating islands are formed, typically with species such as *Cicuta virosa* and *Carex pseudocyperus*. The plants which form these islands generally establish themselves originally on the rootstocks of helophytes, often *Typha angustifolia*, which have been loosened from the substrate during stormy weather in winter. Stratiotes decreases very quickly when helophytes develop, or if the water becomes very shallow (a few dm). The plants in such places are tiny, and reproduce only vegetatively.

The zonation and succession of hydro- and hygrophytes in such regions is described in more detail elsewhere (e.g. Segal 1966, Segal, Groenhart (1967). In the Netherlands, female as well as male flowers are formed, and fruits are fairly common. Male flowers were found as many times as female flowers in northern Poland too (18 places visited), although mostly female flowers should develop here according to Graebner (1908). But fruits will be rare or absent since mixed populations of male and female plants were not found, and the distance between Stratiotes localities is often relatively great. In contrary to the Netherlands submerged plants of Stratiotes often flower in Poland, but the habit of these plants show the emergent type and the anthers do not form any mature pollen.

Lake Achterweiden has an area of 2 ha, and the water depth is 1.0 m. The sandy subsoil is 2.6 m below the water surface. Stratiotes colonized in 1964, and three years later the lake was covered except for a small area in the centre dominated by *Ceratophyllum demersum*. The Stratiotes zone here was homogeneous: the age, height and distance between the plants was uniform to the eye. The plants were arranged in a hexagonal pattern, like a honeycomb.

2. MATERIALS AND METHODS

Only some of the results of productivity and mineral content will be dealt with in this paper. The measurements were made in a single season. Biomass was measured in Lake Venematen 6 times during the 17 weeks between 5th June and 12th October 1967. For every sample 1 m² was taken. A single similar measurement was made in Lake Achterweiden, but here another method was used too. Every week 3 adult plant were sampled. These were plants which had sprouted from a parent plant during the previous autumn, and had than separated from the parent plant. They could be recognized by the fresh cicatrice at the lower side of the plant. The attached sprouts formed by the adult plants during autumn were sampled as well.

To determine the wet biomass, i.e. plants with adhered water, the plants from both places were put in plastic bags. Two corners of the lower side were cut to let the water drain out and after 15 min the plants were weighed. This wet biomass was constant when repeated. Evaporation through the plastic bags is slow, and losses by evaporation into the air are thus avoided.

The wet volume of the plants was measured by displacement in a large measuring cylinder. The plants, in a cotton bag, were put in a Miele domestic spin drier. Spinning was continued for 7 seconds after the machine had reached its maximal speed (1430 rotations/min). The plants were weighed immediately after centrifuging to give the fresh weight. The fresh volume could be calculated as wet volume (wet weight=fresh weight).

The dry weight was measured after drying at 60°C for 16 hr in an oven with forced air circulation (Heraeus T-UO). Some leaves were used for investigation of the chemical composition of the plant material, following the methods described by Schuffelen et al. (1961).

Water samples were taken at the same time as plant samples. The methods for determination of the chemical factors are given in Segal (1965).

3. RESULTS

BIOMASS, PRODUCTIVITY AND MINERAL CONTENT

Some of the data for Lake Venematen are given in Table I. The maximum difference measured in duplicates of wet weights was 17%.

Table I. Characteristics of *Stratiotes aloides* in three zones of Lake Venematen

Zone	Date (1967)	Dry weight		Specific gravity	Number of adult plants	Total number of plants
		kg/m^2	% of fresh wt.			
Submerged	7.VI	—	—	0.97	12	30
	20.VI	—	—	—	5	6
	18.VII	0.077	—	0.94	5	9
	15.VIII	—	7.0	0.89	—	—
	14.IX	0.175	7.3	0.92	12	56
	12.X	0.113	7.4	0.93	7	29
Emergent	5.VI	0.870	—	0.99	11	38
	20.VI	—	—	0.97	15	39
	18.VII	0.539	—	0.91	19	23
	15.VIII	0.546	6.5	0.86	19	22
	13.IX	0.521	7.9	0.89	12	51
	12.X	0.562	8.0	0.92	11	59
Hydrocharis	20.VI	—	—	0.95	41	97
	18.VII	0.498	—	0.89	30	37
	15.VIII	0.634	7.1	0.89	22	28
	13.IX	0.668	7.8	0.91	16	65
	12.X	0.682	8.0	0.94	20	93

The biomass of the roots of Stratiotes is only a small fraction (about 1%) of the biomass of the whole plant.

The biomass in the submerged zone was much lower than in the other zones. The Stratiotes biomass in the Hydrocharis zone was greater than in the emergent zone. The total biomass of the complete vegetation in the Hydrocharis zone must have been yet larger since this zone contains many other plants of other species. The biomass of these plants, however, is much lower than that of Stratiotes, and probably does not exceed one tenth of the Stratiotes biomass.

The data within one zone cannot be compared without taking into consideration the shifting of the zones. The monthly samples were not taken exactly on the same spots. The Hydrocharis zone extended during the season, but the other zones became smaller. This will be discussed later on.

The biomass in the Hydrocharis zone increases during the vegetation period. The mean net productivity per m^2 per day was 4.9 g (49 kg/ha) between the middle of July and the middle of August, 1.2 g between the middle of August and the middle of September, and 0.5 g between the middle of September and the middle of October. According to the estimation of the coverage the productivity must have been much higher in June and the first half of July, but we had no opportunity to make investigations during that period. The dry weight biomass is about 7—8% of the fresh weight biomass, and increases during the vegetation period.

Plants were considered to be established if they were root-bearing plants upto 2 years old, or well developed young plants from 1967; both are referred to as adult plants in Table I and Fig. 3. Included in the total number of plants are the young sprouts and decaying plants.

From volume and fresh weight, the specific gravity of the plants was found. These figures showed characteristic changes during the vegetation period which were different for the submerged, the emergent and the Hydrocharis zone (Fig. 2). The volume of Stratiotes from 1 m² was 1.5–3 l in the submerged zone, 5–10 l in the emergent zone and, less variable, 9–11 l in the Hydrocharis zone.

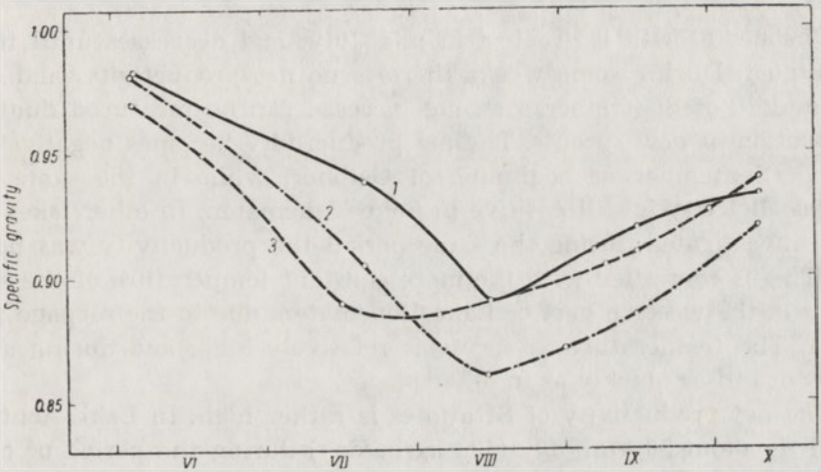

Fig. 2. Specific gravity of *Stratiotes aloides*. 1 — Submerged zone, 2 — emergent zone, 3 — Hydrocharis zone

In Lake Achterweiden the maximum biomass was measured on 21th September, the minimum biomass on 8th June, when we started our investigations. Some data are given in Table II. The increase of 89 g during the period gives the mean minimum productivity of 0.9 g dry wt. per plant per day, or 11.2 g per m² per day (112 kg/ha/day). The increase of dry weight biomass per plant is given in more detail in Table III.

Table II. The increase of biomass of *Stratiotes aloides* in Lake Achterweiden

Date (1967)	Fresh weight (kg/plant)	Dry weight (kg/plant)
8.VI 21.IX	0.34 1.49	0.024 0.113
Difference	1.15	0.089

Table III. Mean increase of dry weight biomass per plant in particular periods of growth (Lake Achterweiden)

Period of investigation (1967)	Increase of dry weight per plant (g)	Mean increase of dry weight per plant per day (g)
21. VI—5. VII	23	1.7
5. VII—19. VII	30	2.1
19. VII—2. VIII	4	0.3
2. VIII—16. VIII	6	0.4
16. VIII—23. VIII	7	1.0
23. VIII—7. IX	0	0
7. IX—21. IX	23	1.7
21. X—12. X	−6	−0.3

The net growth is greatest in mid July, and decreases until the end of August. During some weeks there is no net productivity, and during the middle of September a strong increase can be measured due to the production of new sprouts. The net productivity becomes negative at the end of September or beginning of October, while in the same period the productivity is still positive in Lake Venematen. In other lakes which were investigated during the same period the productivity was negative too. This is connected with the more constant temperature of the surface water in the western part of Lake Venematen, due to the seepage phenomena. The temperature in spring is relatively high, and during autumn does not fall as quickly as in other places.

The net productivity of Stratiotes is rather high. In Lake Achterweiden it is about 30 g/m²/day (300 kg/ha/day) during the period of optimal productivity. These figures are 46 g/m²/day (460 kg/ha/day) for the Hydrocharis zone of Lake Venematen. The gross productivity must be considerably higher than twice the net productivity. Apart from respiration, consumption is considerable by a lot of invertebrate species, but dying off of the lower submerged leaves is much more important. Desiccation of the leaf tips and subsequent loss (e.g. in fresh weight) is important too. The lower leaves are replaced by new ones during the vegetation period. The loss of leaves could be deduced from the number of fresh cicatrices or undecayed leaves on the lake bed. These losses are a special feature of Stratiotes; the difference between gross and net productivity is much smaller in most other aquatics (Juday 1940, Westlake 1965, and others).

The chemical composition of plant material out of Lake Venematen gave the following data in percentages of dry weight: nitrogen 3.0, phosphorus 0.4, calcium 1.5, potassium 5.0, and sodium 1.0.

PERIODICITY

Before the growing season the plants are generally attached to the lake bed. The buds are formed during spring. In autumn the parent plants lose their roots, and sink down. The newly formed winter buds form new roots which attach themselves to the sapropel. Only in mild winters do the plants continue to float. During spring many of the young sprouts release from the parent plants and quite a lot of them die. They get yellowish of colour, and float under the large established plants. These established plants have soft submerged leaves; stiff emergent leaves are formed during May or the beginning of June. In the same period the flowers develop. In the beginning of June, 4 types of plants may be distinguished:

1. Old plants without roots or with very short roots (up to a few cm), with mucilaginous pink-brown cicatrices from the last year of about 3 cm, and blackish-green leaves. The centre is healthy, and many of these centres can be found floating in the middle of July.
2. Old plants with roots formed alongside the edges of the cicatrices and between the blackish-green old leaves from last year. The roots are partly inserted at the side.
3. Large adult plants formed from winter buds, which may or may not be attached to the parent plants, and which have as many roots as the parent plants, and of the same size.
4. Small sprouts with a diameter of 5—10 cm. Most of these sprouts soon die.

The data of the number of plants from Table I are given in another way in Fig. 3.

The behaviour of the plants in the submerged zone is quite different from that in the emergent vegetation. Young sprouts are formed during summer instead of autumn in the submerged vegetation, and many of them die during autumn and winter, instead of winter and spring. The submerged plants are not able to stay erect when they are loosened from their roots, as has already been stated by Graebner (1908). In this case they tilt, and this happens also to Stratiotes forms which are constantly submerged. In spring the plants of the emergent zone and the Hydrocharis zone lengthen their roots and become floating. At the end of the summer the plants of the emergent zone rise further above the water level than the plants of the Hydrocharis zone, and the border line between the submerged and the emergent zone becomes marked (Fig. 1). This border line has a particular significance for the whole lake ecosystem. On this line the undercurrent rises to the surface, and debris accumulates. Here the oxygen content and pH show marked changes. Usually the oxygen content related to the content at the water surface falls sharply, the biological oxygen demand (BOD) rise, and so does pH (data of J. Van Raam unpubl.). Feeding of birds is concentrated here. The line is characterized by special planktonic organisms.

The zonation with the different Stratiotes zones is very striking. But this zonation is not of a static character. Changes occur during the

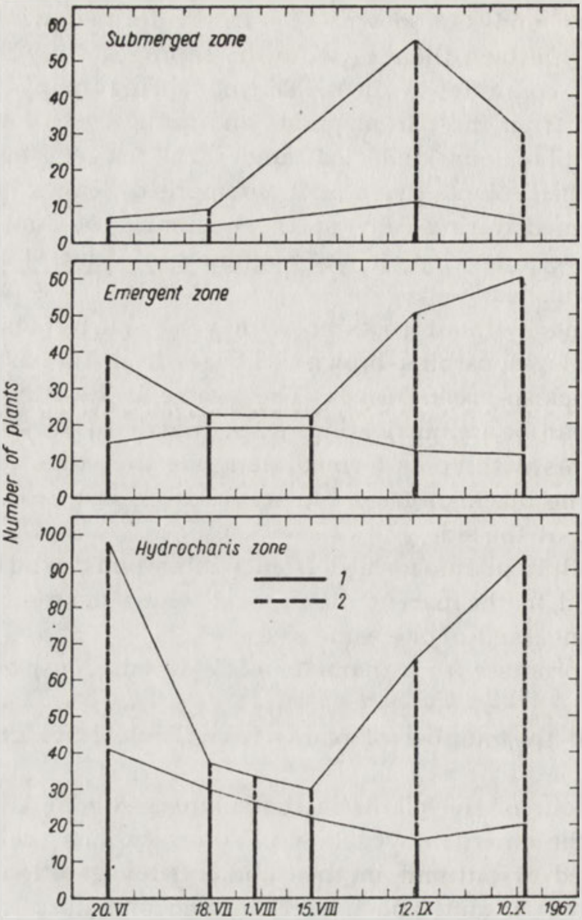

Fig. 3. Periodicity in number of plants of *Stratiotes aloides* in Lake Venematen. 1 — adult plants, 2 — degenerated plants and sprouts

growing season as well as over much longer periods, i.e. succession. During the vegetation season the border lines between the zones shift, the emergent vegetation, especially of the Hydrocharis zone becomes wider and the emergent zone subsequently narrower. The submerged vegetation shifts in the direction of the lake centre.

The emergent vegetation shows its optimal development at about the end of July. Hydrocharis, in the meantime, has shifted from the shores in the direction of the centre of the lake. This species begins to die off somewhat earlier, in the beginning of September.

Differences in time and size of the zonation between years may be considerable due to meteorological differences and other influences. A strong influence may be feeding by coots *(Fulica atra)* and more particularly by mute swans *(Cygnus olor)*. The swans feed on submerged elodeids in the first place, but this has a secondary effect on the Stratiotes zonation, while the wave action becomes stronger, as the sheltering effects of the plants on the waves decreases. The mute swan has bred in many places in the Netherlands during the last 10 or 20 years, previously it was a rare winter visitor.

In spring the cover percentage of Stratiotes is higher in the Hydrocharis zone than in the emergent zone, but after the end of July the contrary is the case. A similar change may be seen in the specific gravity. The plants in the emergent zone stay for a longer time above the water level (Fig. 1). The specific gravity of the plants in the submerged zone does not reach 1. The decrease in specific gravity may be due to the forming of new aerenchymatic foliage tissue. The increase may be explained partly by the formation of starch in the turions and partly by the filling up of the older leaves by water (Fig. 2). The graph showing the emergent zone and that of the Hydrocharis zone cross at about the end of July. Before that time the plants in the Hydrocharis zone rise higher above the water level, but after that time the plants of the emergent zone grow higher. The plants of the Hydrocharis zone start sinking earlier than those of the emergent zone.

The number of the roots increases during the vegetative season until the specific gravity shows its minimum, after that time the plants lose their roots.

4. DISCUSSION

During July the Hydrocharis zone in Lake Venematen covers about 1.5 ha and the emergent zone 0.5 ha. The biomass in these zones is respectively 0.63 and 0.55 kg dry weight per m^2 (6300 and 5500 kg/ha). The total dry weight in these zones is about 12,200 kg. The volume of the lake is about $25 \cdot 10^4$ m^3. We can compare the data of the mineral content in the total plant material with that in the lake water.

The highest measured phosphate content of the water is about 0.05 mg/l (50 mg/m^3). That is 12.5 kg for the whole lake, which means 4 kg of phosphorus. Stratiotes plants have a phosphorus content of 4 g per kg dry weight, that is about 49 kg for only the emergent vegetation in the lake, or about 12 times more than the water content. The phosphorus concentration in the water reached its highest value in August. Therefore it is not very likely that the mineralization could keep step with the primary productivity. The mineralization is far from complete, since Stratiotes forms thick layers of sapropel. We must conclude that an exchange of metabolism products between the water at one side and the mineral and organic lake bed on the other side takes place.

Similar reasoning is applicable to the nitrogen content. In the water we found 0.01 mg NO_2 per l and 0.4 mg NO_3 per l, that makes 23.25 kg nitrogen for the whole lake. The plants consist of 30 g per kg dry weight, or about 366 kg in the emergent vegetation, that is about 16 times more than in the lake water.

For some cations the data are given in Table IV. From these data may be concluded that only potassium could be a limiting factor if a considerable larger part of the lake would be covered by Stratiotes, and if potassium would not be exchanged by the mineral habitat. The chemical composition of plant material out of Lake Venematen shows a striking agreement with the figures of Bernatowicz (1969) especially for phosphorus content, but the difference for calcium is rather great. The contents (%) of dry weight) are compared in Table V. The difference in calcium content may be at least partly explained by the difference in calcium incrustation, which can be considerable especially on the older plants. Stratiotes plants have been used as a source of potassium fertilizer on arable fields, the high potassium content is striking.

Table IV. Data on some cations occurring both in plants and water of Lake Venematen

	Ca^{++}	Na^{+}	K^{+}
Concentration in lake water (mg/l)	40	40	5
Total in lake (kg)	$10 \cdot 10^3$	$10 \cdot 10^3$	1250
Mineral content in plants (g/kg dry weight)	15	10	50
Total in emergent Stratiotes (kg)	198	125	725

Table V. Comparison of mineral compounds in plant material out of Lake Venematen and Lake Warniak (Poland) (after Bernatowicz 1969)

Compound	% of dry weight	
	Lake Venematen	Lake Warniak
Nitrogen	3.0	2.1
Phosphorus	0.4	0.4
Calcium	1.5	0.6
Potassium	5.0	6.4
Sodium	1.0	—

The ratio of dry weight and fresh weight biomass, in our case 7–8%, agree quite well with the figures of Bernatowicz (1969) from which a ratio of 7.2% can be calculated, although his methods differ in some ways. The biomass in the Hydrocharis zone of Lake Venematen per m², however, was about 3 times greater than in Lake Warniak. Biomass in the submerged zone of Lake Venematen was similar to the (emergent)

Stratiotes biomass of Lake Warniak. The second author had the opportunity to visit Lake Warniak in June 1972. He found the Stratiotes vegetation there relatively poorly developed. Some parts were covered with submerged plants. Larger parts were covered by a loose emergent zone.

The figures for net productivity, 30 g/m²/day in Lake Achterweiden and 46 g/m²/day in Lake Venematen during the period of optimal productivity, may be compared with figures given by Forsberg (1959), who gave the following data (g/m²/day) for highest productivity during the vegetation season:

Myriophyllum verticillatum	2.8
Chara fragilis	8.6
Typha latifolia	52.6

Typha latifolia may grow more quickly than Stratiotes does, but in our research region Typha only occasionally covers such large areas as Stratiotes usually does.

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	20	1	207—214	1973

J. M. BERNARD

PRODUCTION ECOLOGY OF WETLAND SEDGES: THE GENUS CAREX

Biology Department, Ithaca College, Ithaca, New York, 14850, U.S.A.

ABSTRACT

Standing crop and primary production in Carex wetlands are discussed in relation to latitudinal and altitudinal gradients, the evidence indicating that these values decrease as latitude and altitude increase. The available data also indicate that Carex wetlands are not as productive as reedswamp or grass fens, sites which usually receive a greater supply of nutrients through silting from the upland. Current studies on *Carex rostrata* and *C. lacustris* have shown the importance of determining seasonal and life history aspects of plant development both above and below ground. Data are presented which indicate that a knowledge of plant activity throughout the year is essential to understanding production processes in these species, and presumably in other perennial wetland species as well.

1. INTRODUCTION

Sedge wetlands are common over most of the world, frequently forming large relatively monotypic stands. There have been few studies of such wetlands, perhaps because the sedges are commonly rough and unpalatable for many animals and therefore considered weeds (Holm et al. 1969).

Whatever the reason, there is a great lack of information on such areas, particularly as relates to primary production and to the role species life history plays in primary production. This lack of basic information is unfortunate since many of these wetlands have been shown to be highly productive. For example, Westlake (1963) in his review noted that the sedge *Scirpus lacustris* was the most productive plant reported from the cool temperate zone.

This paper will discuss sedge wetlands, focusing on the genus, Carex, and paying attention to certain seasonal aspects of life history and primary production. The species discussed here are found in northern temperate regions, usually forming relatively pure stands in shallow water. Although the different species have different environmental requirements, they are all found in minerotrophic sites, that is, sites that receive silt and drainage water from mineral soils.

The first section of this paper discusses standing crop and production in Carex wetlands, summarizing some of the values reported in the literature. The second section discusses some of my recent unpublished data regarding certain seasonal and life history aspects of *Carex rostrata* and *C. lacustris* and the importance of these aspects to primary production.

2. STANDING CROP AND PRIMARY PRODUCTION

Table I illustrates some standing crop values from a number of studies ranging geographically from New Jersey, U.S.A. to Swedish Lap-

Table I. Terminal, aboveground standing crops of green and attached brown material in some Carex wetlands

Author	Species	Location	Standing Crop (g/m^2)
Jervis (1969)	*C. stricta*	New Jersey U.S.A.	955
Bernard (unpubl.)	*C. rostrata*	Minnesota U.S.A.	1071
Pearsall, Gorham (1956)	*C. acutiformis*	England	630
	C. lasiocarpa	England	510
	C. rostrata	England	420
Gorham, Somers (unpubl.)	*C. rostrata*	Alberta Canada	740
	C. spp. (Avg)	Alberta Canada 1428—2044 m	493
Mörnsjö (1970)	*C. elata*	Southern Sweden	440—890
	C. lasiocarpa	—	300—370
	C. riparia	—	530—630
	C. rostrata	—	320—610
	C. vesicaria	—	290—320
Pearsall, Newbould (1957)	*C. spp.*	Swedish Lappland	283

pland. Most of the values represent aboveground harvests taken in the August–September period, the so-called terminal harvest, and do not necessarily denote the maximum seasonal standing crop or the primary productivity of the ecosystem.

Such comparative values are of considerable interest for a number of reasons. First, such values are in general lower than values given for other wetland species such as Typha (Pearsall, Gorham 1956, Penfound 1956, Bray et al. 1959, Jervis 1969, Boyd 1970, Boyd, Hess 1970, Phragmites (Pearsall, Gorham 1956, Björk 1967, Dykyjová, Květ 1970, and Glyceria (Westlake 1966). Pearsall, Gorham (1956) and Gorham (1967) attributed such differences in standing crop to differences in the amount of silting, reedswamp and grass fen sites receiving more nutrient input than Carex fens.

In this regard, Mörnsjö (1969) noted that differences in water depth and the length of time the site was flooded were also important, the Carex in deep water flooded all year had the lowest standing crop values (Table I).

Table I also shows a substantial decrease in standing crop values with increasing latitude. The highest values were reported by Jervis (1969) from New Jersey (40°51′N) and by Bernard (unpublished) from Minnesota (45°30′N), the lowest values were reported by Pearsall, Newbould (1957) from Swedish Lappland (Sub-Arctic). The same trend is noticeable with increasing altitude. Gorham, Somers (private communication) noted a decline in aboveground standing crop from about 800 g/m^2 at 1400 m to about 290 g/m^2 at 2000 m in the mountains near Calgary in Canada. Bliss (1966) recorded a maximum standing crop of just 150 g/m^2 for *Carex bigelowii* in alpine tundra on a north facing slope on Mt. Washington, New Hampshire, U.S.A., at an altitude of 1840 m.

Of greater significance are data on rates and amounts of primary production in Carex wetlands. Table II summarizes some production estimates from two studies of *C. rostrata*. The table clearly shows the greater biomass achieved, the greater yearly production, and the greater rates of production in the more southerly site in Minnesota. Jervis (1969) reported higher values for a *C. stricta* marsh in New Jersey but his data are not strictly comparable since he included both green and attached brown material in his production estimate. Furthermore. other non-sedge species contributed almost half of the production in his marsh.

Table II. Primary production (dry weight of green material) in two Carex wetlands

Type		*C. rostrata* (g/m^2)	
		Minnesota (U.S.A.) (Bernard unpubl.)	Alberta (Canada) (Gorham, Somers private communications)
Standing crop			
maximum		852	640
minimum		114	125
Production			
yearly		738	515
daily	a	11	6
	b	7	4

a — during the period of maximum growth, b — during the period extending from the onset growth until peak standing crop.

Production data for reedswamps (Penfound 1956, Jervis 1969, Boyd 1970) indicate that they are more productive than Carex wetlands, such sites generally producing over 1000 g/m^2/year with rates greater than 15 g/m^2/day common during the period of maximum growth. Such differences in production are probably related to the amount of silting of the site.

3. LIFE HISTORY AND SEASONAL ASPECTS OF PRODUCTION

THE WINTER SEASON

The amount of live material frozen in the ice in winter in wetlands has a profound influence on primary production. Not only do some Carex species retain a considerable amount of live green shoot material aboveground in winter but they also store reserves belowground that can be used for the spring burst of growth.

Data for two species, *C. rostrata* and *C. lacustris* indicate differences in the distribution and amounts of winter standing crop (Table III). *Carex rostrata* was studied in central Minnesota in a marsh frozen to a depth of 40 cm with all shoots and most of the roots frozen in the ice. *C. lacustris* was studied in central New York in a marsh frozen to a depth of approximately 20 cm, with all shoots in the air or snow and much of the underground material in unfrozen soil.

Table III. Winter standing crops for *Carex rostrata* from central Minnesota and *C. lacustris* from central New York. Young shoots are those < 30 cm in length

Type	*C. rostrata*	*C. lacustris*
Young shoots		
Number/m^2	91	259
Weight (g/m^2)	13	180
Old shoots		
Number/m^2	85	none
Weight (green) (g/m^2)	101	living
Total weight green (g/m^2)	114	180
Attached brown (g/m^2)	443	517
Underground (g/m^2)	325	387
Total living material (g/m^2)	439	568
Green as % of total living material	24	31

Both species had young (< 30 cm in length) shoots but *C. lacustris* had considerably more of them and they weighed 180 g/m^2, a significant amount of material. The old shoots of both species were all brown and appeared dead but *C. rostrata* had a large central core of green material, *C. lacustris* did not. Although the distribution varied, a considerable amount of green material was present aboveground in both species.

Both species had about the same amount of material underground but most (ca. 90%) of the *C. rostrata* material was roots while ca. 90% of *C. lacustris* material was rhizomes, few roots being present.

The significance of the amounts of winter standing crop in these two species can be appreciated when one notes that the total below and aboveground live material equals or exceeds many of the values for aboveground standing crop given in Table I.

It is important to measure this winter biomass for two reasons. The first is that this material does not belong to the present year's production and if winter standing crop was not determined there would result a considerable over estimation of production. In the case of *C. rostrata* production would have been 114 g/m^2/year greater aboveground if sampling did not take this winter condition into consideration.

The second reason is that the amount of underground reserve material has been shown to be intimately associated with growth and production through the year (Mooney, Billings 1960, Fonda, Bliss 1966). They showed for *Carex elynoides* and *C. bigelowii* respectively, that a considerable portion of spring growth aboveground was from reserve translocation, not photosynthesis, and in fact, Oshima (1961) estimated that all new spring growth may be budgeted by stored material in Sasa communities in Japan.

A final comment about winter condition. There may be some growth and some emergence of new shoots even in winter. Gorham, Somers (private communication) noted a possible increase in standing crop of *Carex rostrata* and an increase in the number of shoots of *C. aquatilis* in winter, changes which they believed were probably owing to translocation of food reserves present belowground. In this regard, Mutoh et al. (1968) noted a decrease in belowground standing crop in the grass Miscanthus throughout the winter, the greater decrease coming in the November-December period, the time of bud formation.

Some of my data indicate that *Carex lacustris* may grow during the winter in the central New York area. If so, then the 180 g/m^2 figure in Table III represents a possible over-estimate of winter standing crop since sampling was done toward the end of the season. If sampling was done earlier, the amount of green material as a percent of the total living material would be more similar to the *C. rostrata* value than shown in Table III, even though the two species differ greatly in the distribution of this living material.

In any event, the winter is a time of special significance to production study and many more data are necessary for understanding this season with its complex growth pattern.

SHOOT EMERGENCE AND SHOOT MORTALITY

The emergence and growth of new shoots increase and mortality decreases production estimates so these two events are important to production studies. Recent work by Gorham, Somers (private communication) and Bernard (unpublished) has indicated that new shoots of *C. rostrata* have two major times of emergence, spring and fall, although some new shoots may appear at any time during the summer and perhaps during the winter in favourable sites.

The spring emergence begins after the ice has melted and these new shoots, together with the young shoots frozen in the ice, fuel the spring burst of growth. During the summer, only a few scattered shoots emerge but beginning in early July in Minnesota and mid-July in Canada, a long sustained emergence begins, one that was not completed by early November in either site. It is of interest to note that the early shoots emerging in July were from the axils of flowering shoots as they were dying. Most of the later shoots arose from rhizomes as in Phragmites (Haslam 1969).

Mathews, Westlake (1969) noted the necessity of determining mortality in perennial species in order to determine net production accurately. There was some mortality of *C. rostrata* in Minnesota throughout the growing season but two major times were most evident. The first was early spring when a number of shoots died after the ice thawed. Levitt (1969) suggests that even mild frost may kill a formerly cold-hardened species once it begins growth.

The second major period of mortality is in the late August—early September period when all flowering shoots die. Together, in the year studied, these losses accounted for approximately 65 shoots/m^2 out of a total maximum density of 238 shoots/m^2.

AUTUMN CONDITION

My studies have indicated that the autumn is a very important time in the cyclical nature of plant growth and data collected in autumn and into winter are essential to understanding production.

The first reason for studying autumn condition is that many new shoots emerge, shoots that will fuel the next year's spring and early summer growth. Second, the flowering shoots and the leaves of mature plants are dying and presumably translocating their materials to new rhizomes which begin growth in late summer and thus a considerable amount of production is evident, much of it underground. My studies indicate that approximately 1 g/m^2/day is added underground in *Carex rostrata* beginning in early July and continuing until at least November 1. Thus, even though aboveground production based on mature shoots is negative, the growth of young shoots, roots and rhizomes may offset this apparent loss.

4. SUMMARY

Terminal aboveground standing crop values from a number of Carex wetlands indicate that they are not as productive as reedswamps or grass fens. Such differences are probably the result of differences in the amount of silting, reedswamps and grass fens receiving more nutrient input than Carex fens.

Available evidence suggests there is a substantial decrease in standing crop along latitudinal and altitudinal gradients. Depending on the species, most temperate zone Carex sites average a terminal aboveground standing crop of 300—1000 g/m^2. Those at high latitudes and high elevations average less than 300 g/m^2.

Seasonal and life history studies of *Carex rostrata*, coupled with winter studies of *C. lacustris*, have shown the importance of such factors to primary production. Winter studies of these species has revealed that both have a con-

siderable amount of live green shoot material present, the former about 114 g/m², the latter about 180 g/m². Both species have over 300 g/m² belowground, some of which is probably budgeted for early spring growth of aboveground shoots. Finally, there is some evidence that growth of shoots and even emergence of new shoots may take place in these species in the winter.

Carex rostrata shoots may emerge at any time during the year but most emergence takes place during two periods, spring and fall. Similarly, some shoot mortality was evident in spring when the ice melted and in early fall when all flowering shoots died. The losses during these two periods accounted for some 65 shoots/m² out of a seasonal maximum of 238/m².

During the autumn, *Carex rostrata* had many new shoots emerge, many old flowering shoots die, and produced many new roots and rhizomes. This season is one of great significance for studies in primary production.

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S. G. SMITH

ECOLOGY OF THE *SCIRPUS LACUSTRIS* COMPLEX IN NORTH AMERICA

Department of Biology, University of Wisconsin, Whitewater, Wisconsin 53190, U. S. A.

ABSTRACT

The ecological characteristics of three Scirpus species, occurring in wide range of North America, is given. The species form natural hybrids, especially in man-disturbed habitats. *S. acutus* is associated with the widest range of habitats and it is the most abundant species of the *S. lacustris* group. All three species are attacked by stem-boring insects which cause considerable ecological effects.

Scirpus lacustris complex ranges over most of North America except the high Arctic-boreal and high mountain regions. Its ecology is poorly known in North America compared with Europe. The present review is based on published data and the author's own observations. Most data are available from north-central United States.

The three North America species: *S. acutus, S. validus* and *S. heterochaetus*, are readily distinguishable from each other within a particular geographical region; *S. acutus* and *S. validus*, however, are only weakly distinguishable from each other and from Eurasian *S. lacustris* and *S. tabernaemontani* when the total geographical ranges of the species are considered. Morphologically distinct geographical races exist in both *S. acutus* and *S. validus*.

The species form natural hybrids, especially in man-disturbed habitats but also in some apparently undisturbed shallow water marshes in the prairie region of e.g. North Dakota and Iowa. *Scirpus acutus* also hybridizes with *S. californicus* in California.

Scirpus acutus is associated with the widest range of habitats from wet soil to water up to 2 m deep; often extreme hardness (calcium) of the water, marly soils, and moderately salty or alkaline conditions (pH to 9.0, sulphate to 1300 ppm, and electrical conductivities to 10,000 mmhos per cm^2 at 25°C). It is the most abundant species of the *S.*

lacustris group in hard-water regions, including the important waterfowl nesting region of the glacial "potholes" (shallow depressions) of the prairies of North Dakota and adjacent Canada. It is especially characteristic of the littoral zones of natural lakes with mineral substrates.

Scirpus validus, in contrast with *S. acutus,* is associated with shallower water (less than about 0.7 m) and lower concentrations of dissolved solids (electrical conductivities below about 2000). At least in hard-water regions, this species is apparently restricted to either naturally unstable habitats such as streambanks, estuaries where streams enter lakes, and pools formed by storms along sandy shores of large lakes, or to man-disturbed habitats such as roadside ditches, heavily grazed pond margins, and places that are dry in some seasons and reflooded in other seasons. Near the south shore of the Straits of Mackinac in northern Michigan, the extreme disturbance of the habitats of the *S. validus* stands is reflected by the presence of weeds in the terrestrial ecophase; for example, a sum of 23 species of introduced Eurasian plants were associated with 5 stands of *S. validus* whereas only native plants were associated with the seven adjacent stands of *S. acutus.*

Scirpus heterochaetus is poorly understood and has a relatively limited geographical distribution. It is associated with a narrow range of habitats: usually moderately deep water (to 2 m) that is permanent and relatively low in dissolved solids (conductivity less than about 700 mmhos and sulphate less than about 280 ppm).

All three species are attacked by stem-boring insects that may have pronounced ecological effects. For example, in the Straits of Mackinac region the Lepidoptera Leucania (fam. Noctuidae) and Crambis or related genera (fam. Pyralidae) prevent flowering and kill by mid-August up to half of the culms emergent stands of both *S. validus* and *S. acutus.*

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K. A. DOBROWOLSKI

ROLE OF BIRDS IN POLISH WETLAND ECOSYSTEMS

Department of Vertebrate Zoology, University of Warsaw, Krakowskie Przedmieście 26/28, Warszawa, Poland

ABSTRACT

Various utilization of lakes, ponds and marshes by water-fowl was discussed. The plant-feeding birds, i. e. coots and muteswans, were analysed in detail for 4 lakes in the Mazurian Lakeland. The quantities of consumed plants and produced faeces by these species were estimated. It was found that water-fowl consume about 2% of lake macrophyte production.

It is rather difficult to differentiate between the water-fowl and birds dependent on aquatic or swammy areas. Mobility of this group of animals, the easiness in changing places and general ecological tolerance cause that some typical terrestrial species strongly depend on the aquatic habitats if there are such in their neighbourhood. Various aquatic and swampy areas have different environmental conditions, and different groups of birds inhabit these places. An example is the differentiation of water-fowl of lakes, ponds and swamps as given by Dunajewski (1943) (Fig. 1). The lake shore and a belt of emergent macrophytes is the main nesting area whereas the other lake zones are the regions of food resources. The swamps are not so well differentiated from the point of view of birds. The majority of the swamp area is a nesting and feeding ground at the same time. The ponds are similar to lakes, but a large part of them can be used by birds similarly as swamps. These habitats are thus the intermediary ones. In all three habitats three trophic groups of birds can be distinguished: mainly the predatory group (divided into birds feeding on fish and birds not feeding on fish), a group feeding on animals and plants, and a group of birds eating mainly plants (Fig. 2).

The aquatic, swampy and near shore habitats are suitable for numerous bird species, and the adaptative radiation of this group of animals results in numerous forms closely adapted to such habitats. It seems that various groups of birds that had inhabited these habitats at different times have also different positions in the food webs of these eco-

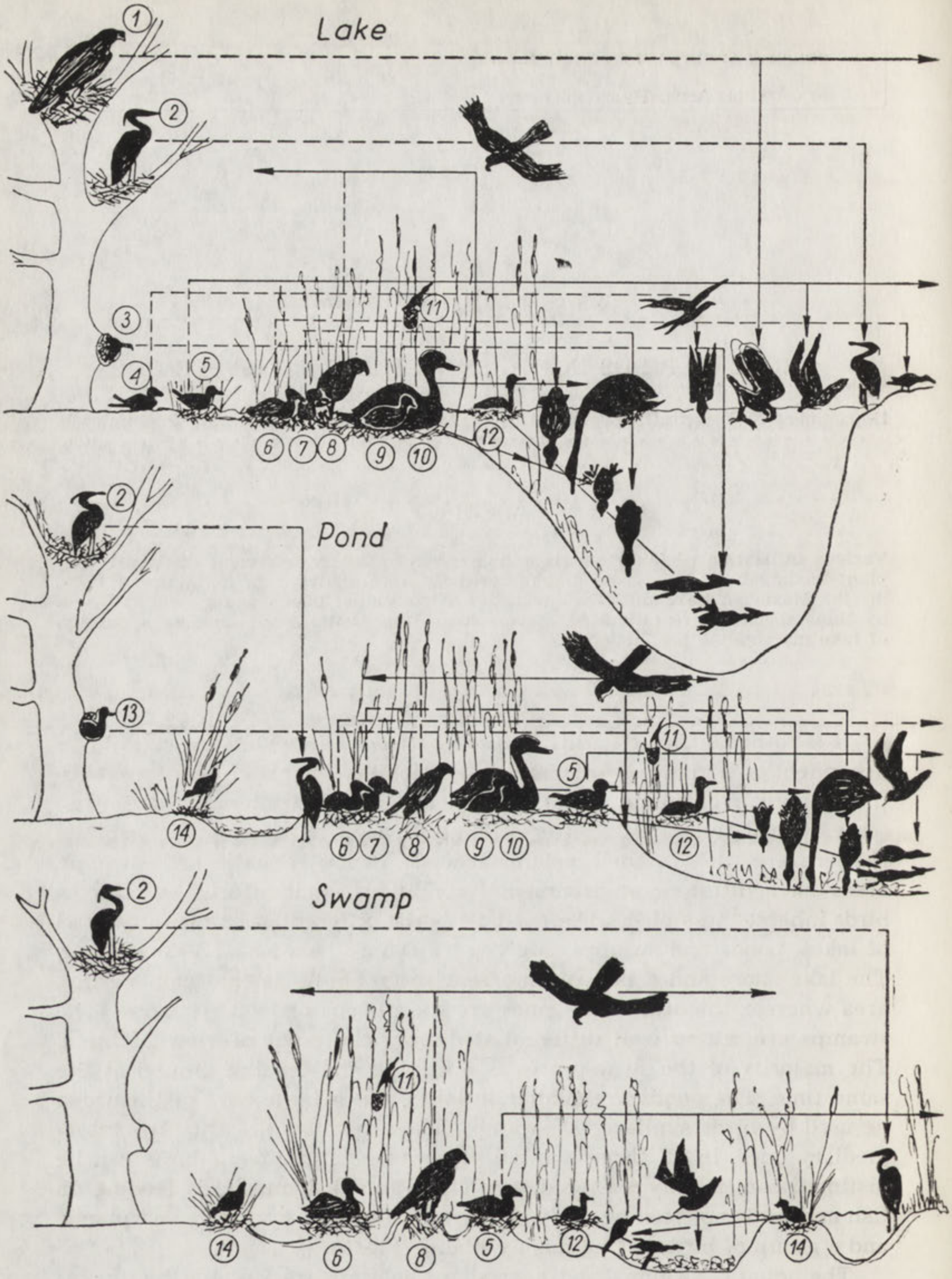

Fig. 1. Differentiation of water-fowl of lakes, ponds, and swamps (after Dunajewski 1943 — completed). — — — — nesting places, ———— feeding places. 1 — osprey *(Pandion haliaetus)* or white tail eagle *(Haliaetus albicilla)*, 2 — herons *(Aerdea sp.)*, 3 — merganser *(Mergus sp.)*, 4 — terns *(Sterna sp.)*, 5 — black-headed gull *(Larus ridibundus)*, 6 — surface-feeding ducks (Anas), 7 — diving duck (Nyroca), — marsh harrier *(Circus aeruginosus)*, 9 — coot *(Fulica atra)*, 10 — mute swan *(Cygnus olor)*, 11 — small Passeriformes, 12 — grebes (Podiceps), 13 — goldeneye *(Bucephala clangula)*, 14 — moorhen *(Gallinula chloropus)*

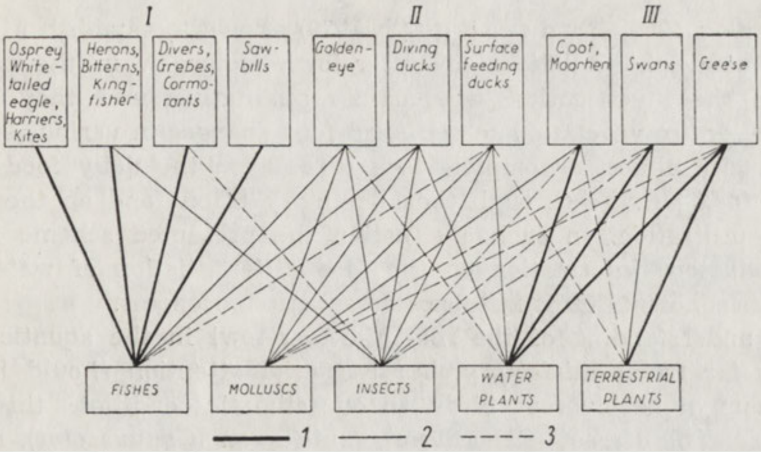

Fig. 2. Three trophic groups of water-fowl: I — fish-eating birds, II — omnivorous birds, III — plant-eating birds. 1 — food taken more than 70%, 2 — food taken 20–70%, 3 — food taken less than 20%

systems. The birds form typical ecological equivalents in the zoogeographic sense and also in the case of micro differentiations of habitats. The examples of these equivalents are the coot (*Fulica atra*) occurring mainly on shallow lakes, large ponds and on slow flowing rivers, and the moorhen (*Gallinula chloropus*) found in similar zones on small ponds and swamps. The second example is a similar biocenotic function in various types of water bodies which can be fulfilled by various species of grebes (Podiceps).

Both these phenomenons, i. e. the zonation of water-fowl occurrence and ecological equivalents are important to understand the role of water-fowl in trophic webs of aquatic and swampy ecosystems. The knowledge of population numbers, kinds of food and of individual and populational energetics is also necessary. However, the majority of ornithologists working on water-fowl studied the significance of birds in parasite cycles and the effect of birds on fish cultures. The latter is closely related with the problem of quality and quantity of taken food with special consideration to the birds eating fish. Recently the research on the influence of birds faeces on freshwater reservoirs has been carried out in the German People's Republic, which was connected with tests of mass cultures of ducks on lakes. The investigations and calculations showed that 80,000 ducks per lake is the same as a drainage of not treated municipal sewage of a town with a population of 10—12,000 (Kalbe 1969). This shows that we should take into consideration not only what is taken out by birds from the ecosystem, but also their influence on eutrophication of waters.

Relatively rich literature on birds diet (Dementev 1940, Dunajewski 1943, Hilprecht 1956, Kistyakovski 1957, Bopp 1959, Van Tyne, Berger 1959, Uspenski 1965, Bezzel 1969, Schröder 1969, Hudec, Rooth 1970) allows to establish a general pattern of trophic relations of water-fowl. However, in the majority of cases the investigations are mainly qualitative, and they do not cover the entire vegetation season (bird food changes in various seasons), there is also almost a complete lack of data on the daily food ration, time of food passage through the alimentary tracts, and on the degree of food utilization. In such a situation the presented scheme is only an introductory information on the food differentiation of water-fowl, and on directions of birds influence on aquatic biocenoses.

Our understanding of the role of water-fowl in the aquatic biocenoses is far from satisfactory, but a special attention should be paid to a group of herbivorous birds. In our climatic conditions this group mainly consists of coot (*Fulica atra*), mute swan (*Cygnus olor*), mallard duck (*Anas platyrhynchos*), pochard (*Aythia ferina*) and some other rare surface-feeding and diving ducks (Anatinae and Nyrocinae), moorhen (*Gallinula chloropus*), geese (*Anser sp.*), here mainly grey lag goose — *Anser anser*). The plant food is for all these species the predominating kind of food, or at least as important as the animal food. These relations are valid for freshwater habitats. Not all these birds feed only on aquatic macrophytes, some of them consume also terrestrial plants. However, it should be pointed out that the majority of these birds eat not the seeds but the green parts of plants, and some birds are also feeding on detritus (Dzięciołowski, Frankiewicz 1970).

The most common among the plants consumed by water-fowl are the Characeae, *Potamogeton sp.*, *Ceratophyllum sp.*, *Lemna sp.*, *Typha sp.*, *Elodea canadensis* and *Phragmites communis*. Among the animals eaten by these birds the molluscs are the most frequent ones (snails and mussels) and also the larvae of insects (mainly Chironomidae).

The rough estimates of the quantities of food taken per day by birds are as follows: coot and moorhen — about 100 g, various ducks — 120–150 g, geese and swans — 1000 g or slightly above. If we multiply these values by the number of days spent by these birds on our waters, we obtain the quantity of food taken by an individual during the vegetation season. This amounts to 26.5 kg for coot and moorhen, out of which 85% is plant material (up to 22.5 kg per bird), for ducks 31.8–39.8 kg, out of which about 50% is plant material (15.5–19.5 kg per bird) and for gees and swans above 265 kg with about 90% of plant material (238.5 kg per bird).

These data make possible the further calculations when the numbers of birds are known. Our quantitative materials are still under elaboration and I shall present the introductory data only for coots and swans on some lakes. Coots sonsume during the vegetation season 29 t fresh weight of macrophytes on Lake Łuknajno, 0.72 t on Lake Warniak, 41 t on Lake Śniardwy and 1.2 t on Mikołajskie Lake.

These data can be calculated per hectare of the area overgrown by macrophytes. Then the plant consumption is 55 kg fresh weight from a hectare for Lake Łuknajno, 21 kg for Lake Warniak, 14 kg for Mikołajskie Lake and 11 kg from a hectare for Lake Śniardwy. These values include both the submerged and emergent macrophytes, as common reed is a permanent component of the coots diet. A similar calculation for swans shows that these birds consume on Lake Łuknajno (characteristic for its numerous population of swans) 50 t of macrophytes per year, i.e. about 95 kg per hectare of the overgrown area. Thus only the two discussed species (coot and swan) consume on Lake Łuknajno 150 kg fresh weight per ha of the overgrown area per year. At the same time the production of faeces by coots is 3.75 t in Lake Łuknajno, 5.5 t in Lake Śniardwy, 156 kg in Mikołajskie Lake and 100 kg in Lake Warniak. The swans produce 1.7 t of faeces in Lake Łuknajno during the vegetation season.

As the final number of ducks is not calculated yet, the utilization of plants by water-fowl cannot be fully estimated.

Although the presented figures of macrophyte consumption by water-fowl can be quite impresive, the percentage of biomass consumed is in our conditions relatively low. In all of the discussed lakes, water-fowl consume during their stay there about 2% of yearly macrophyte production. However, it should be pointed out that these birds in situations where they are much more numerous, can consume up to 90% of plant production (17—18 t out of 20 t of macrophytes — Uspenski 1967).

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H. SUKOPP

CONSERVATION OF WETLANDS IN CENTRAL EUROPE

Institut für Angewandte Botanik, TU Berlin, Rothenburgstrasse 12, Berlin (West)

ABSTRACT

Examples of wetland plant communities in Central Europe which are retreating, endangered, or changing floristically are shown. Literature is cited concerning measures for preserving and regenerating wetlands in West Germany. A system of means for conserving reed-belts in Berlin comprises a special "law for shelter of reed-swamps", installation of reed-fences, planting of new stands, regulating the size of swan and muskrat populations, proclamation of orders concerning motor boat traffic and bathing-sites, and more complex means of lake restoration.

1. URGENCY OF CONSERVATION OF WETLANDS

In Central Europe many wetlands[1] of ecological and scientific importance are increasingly being endangered and destroyed by reclamation, drainage, eutrophication of mesotrophic and oligotrophic wetlands, pollution, use of wetlands as refuse dumps and by various recreational activities.

The retreat of wetland plant communities in Central Europe since 1850 is summarized for different vegetation types in Table I.

Table I. Retreat of wetland plant communities in Central Europe (according to Sukopp 1972)

Type	1850—1950	1950—1970	Future
Reed swamps (Phragmition, Magnocaricion)	— —	—	?
Oligotrophic waters (Schlatts)	—	— —	—
Vegetation of flowing waters	—	— —	?
Spring fens	— —	— —	—
Transition and valley bogs without trees	— — —	—	—

— little retreat, — — fair retreat, — — — strong retreat, ? unknown.

Special works concerning the retreat and floristic changes of wetland vegetation in Central Europe are those of Hild (1960), Stauffer (1960), Knapp,

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[1] A "wetland" is an area dominated by emergent hydrophytes, helophytes, pleusto-helophytes and eu-ochthophytes.

Stoffers (1962), Tüxen, Jahns (1962), Krausch (1964), Bittmann (1965), Lang (1967, 1968), Richter (1967), Carbiener (1969), Sukopp (1971), Weber-Oldecop (1971).

The changes in wetland vegetation are shown in more detail in Table II, which contains extinct, endangered, impoverished or floristically altered plant communities of eastern Saarland (ca. 2100 km^2). Only the number of localities of *Typhetum angustifolio-latifoliae* has increased.

When comparing different ecosystems, so far as the absolute and relative numbers of extinct species are concerned, one will find that wetlands belong to the most endangered ecosystems (Table III).

2. CONSERVATION OF WETLANDS IN CENTRAL EUROPE

There are three annotated lists containing data about wetlands already being conserved on the basis of their scientific value: Institut für Landesforschung und Naturschutz (1964), Ant, Engelke (1970), Luther, Rzóska (1971). There is a need to complete these lists by including other sites that also deserve conservation.

The need for the IBP Synthesis Volume on wetlands to contain a chapter on "Conservation" will also depend on the results already gained by IUCN, Project Aqua, Project Mar, Project Telma and others.

Special remarks upon measures for preserving and regenerating wetlands are made by Kloss (1966), Tüxen (1967), Sukopp, Kunick (1969), Bayerische Landesstelle für Naturschutz (1970), Braun (1970), Succow (1970), Kadner (1971), Kaule (1971), Schlüter (1971).

3. CONSERVATION OF REED-BEDS IN BERLIN

This year only some short remarks about conservation and regeneration of reed-beds in Berlin can be made. The Berlin Havel lakes have been taken as an example for waters intensely used for different kinds of recreation (Sukopp 1971). In order to estimate the effects of these recreational activities on reed swamp vegetation we mapped the littoral vegetation in 1962 and 1967 and are going to do so in 1972. Results can be given in 1973.

Conservation and regeneration of reed-beds have proved to be difficult under strong recreational pressure. Although nearly half of the shore-line in Berlin is protected in the form of nature reserves or landscape reserves, this has not meant any real protection against damage by recreational activities. Stands in spawn shelters are better protected. Since the importance and value of sound open waters including shore vegetation have been recognized by the administration we have begun to manage a system by the following means. The legal frame work is a special "law for shelter of reed-swamps" of November 1969, which forbids any treading and boating in reed-swamps. Boats are only allowed to anchor

Table II. Extinct and alterations of wetland plant communities of eastern Saarland (according to Sauer unpubl.)

Plant comunity (acc. to Oberdorfer 1970)	Frequency ($n=16$) (Grid units of 10′ long. x 6′ lat. ca. 2100 km^2)	Endangered	Retreat (density decrease)	Impoverished (retreat of characteristic species	Other floristic changes
Nanocyperian	3	— — —	>50%		
Bidentetalia tripartiti	12	—	no change	— —	*
Chenopodietum glauco-rubri	1	— — —	>50%	— — —	
Juncetum bulbosi	1	— — —	?		
Ranunculetum hederacei	0				
Philonotido-Montietum	1	— —	?		
Carici remotae-Cerdaminetum flexuosae	5	—	no change		
Typhetum angustifolio-latifoliae	8	—	increase	— —	
Phragmitetum communis	11	—	no change	— —	
Acoretum calami	3	— —	<50%		
Scirpetum lacustris	1	— — —	>50%		
Glycerietum maximae	4	— —	<50%		
Caricetum pseudocyperi	0				
Rorippo-Oenanthetum aquaticae	2	— —	>50%		
Butometum	1	— — —	>50%		
Scirpetum maritimi	1	— — —	>50%		
Scirpetum tabernaemontani	0				
Eleocharido-Sagittarion	1	— — —	>50%	— — —	
Sparganio-Glycerietum	4	— — —	>50%	— — —	
Caricion rostratae	5	— — —	<50%	— — —	
Juncetea maritimi	0				
Juncetum acutiflori	8	— — —	>50%		
Juncus subnodulosus-Ges.	1	—	>50%		N
Eriophorion gracilis	0				
Caricetum fuscae	3	— — —	>50%	— — —	
Eriophorion latifoliae	(2)	— — —	>50%	— — —	

— not or scarcely, — — fairly, — — — strongly. N — protected in conservation areas. * moderate spreading of neophytes.

Table III. Extinction of species (Pteridophyta et Spermatophyta) in wetlands in Berlin (acc. to Sukopp 1966)

Vegetation type or habitat	No. of species	Extinction		Change of habitat size
		No.	%	
Water vegetation	56	15	12	no change
Shore vegetation	102	2	2	fair
Vegetation of pools (mainly Nanocyperion)	18	8	7	strong
Bogs	61	10	8	strong
Wet meadows	91	12	10	strong

at least 2 m distance from reed-swamp border. Further, the existing spawn shelters have been enlarged and new ones built up.

Well preserved stands have been enclosed by reed-fences (Fig. 1). The reed-fences are to be established at places, either where still existing reed-beds have to be protected or where sheets of water along bank-areas are to be delimited in order to the planting of new reed-banks.

These fences are made of tubular stakes, 5 m apart, which are generally rammed into the ground about 2 m in front of the water edge of

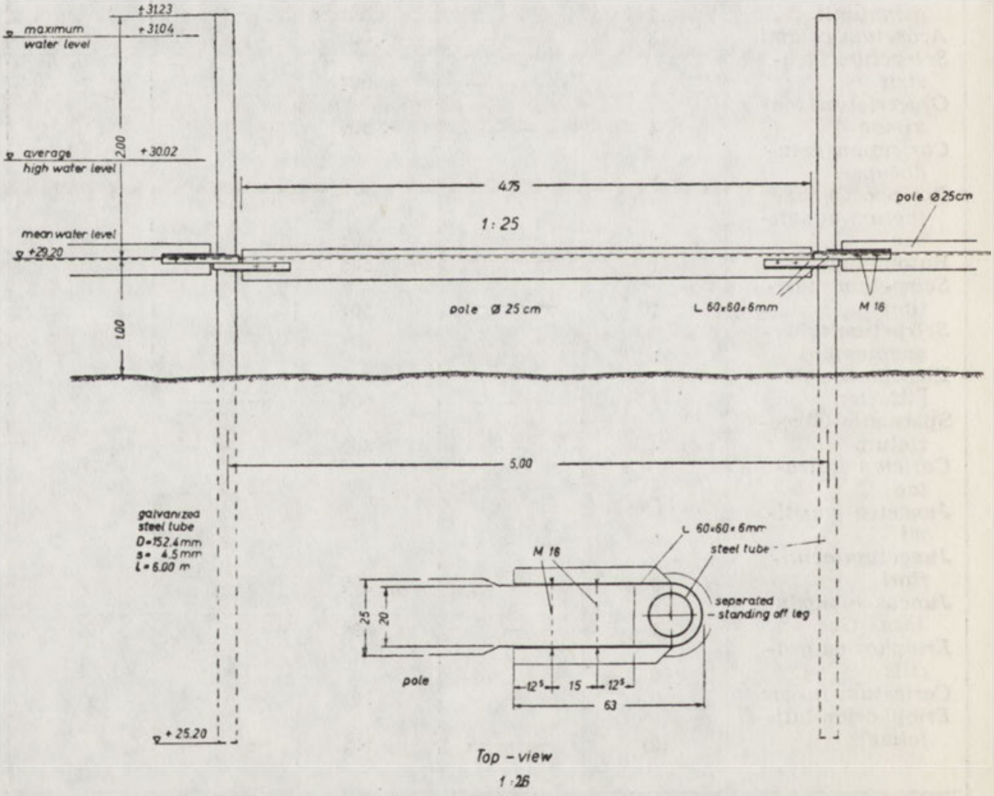

Fig. 1. Reed-fence (Röhrichtsperre) for Unterhavel (Der Senator für Bau-und Wohnungswesen Berlin VII)

the reed-belt. There are round poles, floating in the water between the stakes (diameter 25 cm) connected to them by clamps. These clamps are fitted with enough free play for the poles to be able to rise or fall without impediment according to every change in the water level.

The fences can only give mechanical protection. First of all they prevent boats and drift material from entering the reed-beds. Besides that they break the tops of approaching waves in such a way that the energy of the waves is reduced to some extent. These fences cannot give protection against influences originating from the water quality or from the fauna.

For an expenditure of an average sum of 100 DM per running meter, altogether 830 m of the described kind of fence have been installed in 1970 and 1971.

New stands of reed have been planted, but only *Scirpus lacustris*, Typha and *Carex gracilis* succeeded, whereas Phragmites plantations failed at most places almost completely.

In order to diminish the effects of overpopulation by mute swans *(Cygnus olor* Gm.) (on 1–2 March, 1969, 718 individuals living in Western Berlin Havel lakes) 140 swans have been given away during 1970–1972 to other cities in West Germany, Switzerland, Spain, etc. Muskrats populations are also controlled.

In some places motor boat traffic is prohibited or the speed is limited. Some bathing-sites have been marked by buoys. For purpose of conserving the natural health of environment and preventing its deterioration the greatest Havel lake, the Tegel Lake (4 km²), shall be restored in the years 1972–1987 at first by eliminating phosphate from incoming water, then pumping off the upper part of lake sediments.

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F. KLÖTZLI and S. ZÜST

CONSERVATION OF REED-BEDS IN SWITZERLAND

Institute of Geobotany, Swiss Federal Institute of Technology, Zürichbergstrasse 38,
8044 Zürich, Switzerland

ABSTRACT

By fencing reed-beds in "reed-death" areas and other heavily influenced lake shores can be protected sufficiently. In highly eutrophicated lakes, exclosures do not fully protect from the spreading of reed-death (speed: 1–3 m/year), but at least the critical action of algae-mats is prevented. The algae-mats especially weaken stands showing little sclerenchymatic tissues. Best management of stands in eutrophicated areas is regular mowing and harvesting. Exposed stands in the shore line, to the contrary, should not be mown. Cut stands are most dense, slightly less productive, but locally less eutrophicated.

1. INTRODUCTION

Well-growing undisturbed reed-beds are becoming an absolute rarity in Switzerland. So far 80 km of reed-belts distributed on 370 km of lake shore have been investigated of which only about 35 km (9.5%) show the normal zonation of an open thick-stemmed outer zone with few dispersed minor shoots and a dense thick to medium stemmed inner zone (littoral to limosal ecophase, according to Hejný). Most belts lack the outer zone and the inner zone is split up into groups. In many cases the actual reed-belt is reduced completely or growing with a suboptimal habitus (Haslam 1970 a) as one would normally find in gravely areas or exposed to heavy winds (Hurlimann 1951, Markgraf 1959). More elevated "pseudo reed-belts", overgrowing other plant communities (e.g. sedge belt), are as a rule not retreating (compare the Spartina-die-back, in depressions only, Goodman et al. 1959).

The probable causes for this retreat are still being investigated (see Klötzli 1971). The same time it was urgent to find a means to conserve these last well-growing reed-belts, to restore them or "to build them up" again. Control of management practises and fencing were thought to be the best access to get an idea of the optimal way to conserve these reed-belts.

Measuring productivity and density showed to be a suitable analysis to assess the efficiency of protective measures (see preliminary report of Züst in press).

2. METHODS AND MATERIAL

Fencing

Homogeneous reed-belts were partly fenced by constructing solid iron exclosures to exclude any mechanical damage (algae-mats, boats etc.). Some were also covered with wire net (exclusion of birds). Details of construction will be submitted in concluding paper. Other areas were protected by plastic nets.

Management

The special area (500 m of lake shore) was split up into 4 groups of "divisions" repeating every harvesting practise 3 times giving 12 divisions:

A — mowing+removal of litter,
B — mowing, no removal,
C — mowing, chopping litter (not dealt with in this paper),
D — no mowing.
Reed was cut in December or January.

Productivity and density

These stand qualities were measured on 5 hazardly chosen but permanent plots of 1 m^2 in each the homogeneous divisions (2500 m^2) (proceedings compare Project Phragmites 1969), during the period of autumn 1967 (density), autumn 1970 (productivity) respectively, till now (spring 1972, project till 1977). The values for productivity and density were taken as a medium of these 5 plots of each division.

An aliquot part, at least 200 stems ($\approx 10\%$) were not only measured (length to the bud, stem diameter at base) but weighed separately. These values gave the base for the construction of allometric curves (weight as a function of height for material of the same diameter). The productivity of the non-harvested divisions, where all the stems had been measured, could thus be determined. All other productivity measurements will be evaluated later as well as details on allometric curves.

Density was determined twice: once at the beginning, once at the end of the growing season (May and October normally). The figures show the medium values.

3. RESULTS

Retreat of reed stand

The special area lies in a zone with intensive reed retreat (Fig. 1). Since about 1945 reed has vanished from a belt of about 150 m large. In 1966 the plots were installed and retreat was observed in detail. On most shore parts the actual reed zone is now destroyed, retreat having averaged around 1–3 m or more in the last years.

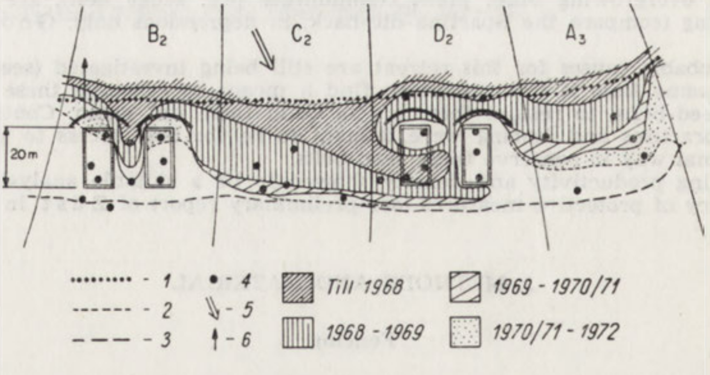

Fig. 1. Retreat of reed-belt in partly fenced special area. B$_2$, C$_2$, D$_2$, A$_3$ — management divisions, 1 — medium water line (shore line of 5.V.1966), 2 — limit of reed-belt, 3 — probable retreat line at the end of 1972, 4 — control plots, 5 — chief wind direction, 6 — distance to former limit of reed-belt on the side of the water

Influence of the exclosures

Undoubtedly fencing had a beneficial influence on the development of reed in protecting it from the noxious mechanical factors, one of the chief causes for retreating reed-belts. As can be seen from Fig. 2 (detailed tables in concluding paper) productivity and mostly density is higher in the exclosures than outside in the rest of the divisions.

On an average, density is rather diminishing generally in all the divisions, even in some parts of the exclosures, a secondary effect still investigated and commonly called " reed-death".

The ratio productivity/density is greater in exclosures, i. e. sturdy, vital stems grow in less dense stands. No difference between covered and uncovered exclosures can be detected.

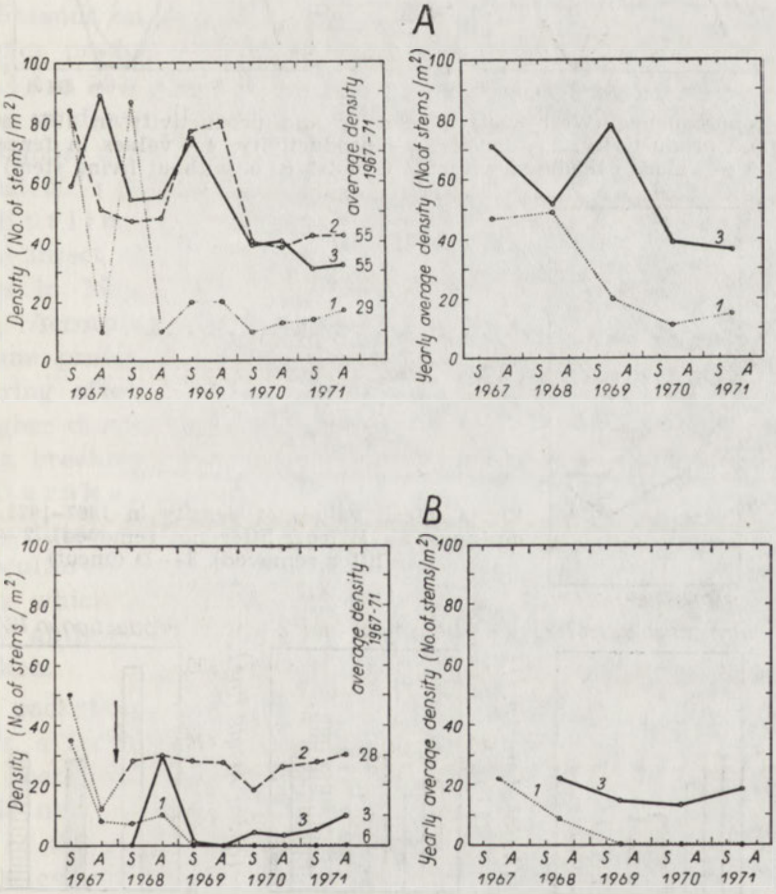

Fig. 2. Comparison of density in fenced and unfenced areas in A — B_2 division fenced in winter 1966/1967 (cut, no litter removed), B — D_2 division fenced in winter 1967/1968 (uncut). 1 — open area, 2 — fenced, open (not covered), 3 — fenced, closed (covered), or average for fenced areas (right). S — spring, A — autumn

Influence of management

Harvesting (cutting and removing litter) usually means improvement of density, but lower productivity, whereas uncut stands show a rather low density combined with higher productivity (and higher N-turnover). Simple cutting, no removing, give values which show even a greater difference than those which are not cut (Fig. 3, 4, 5).

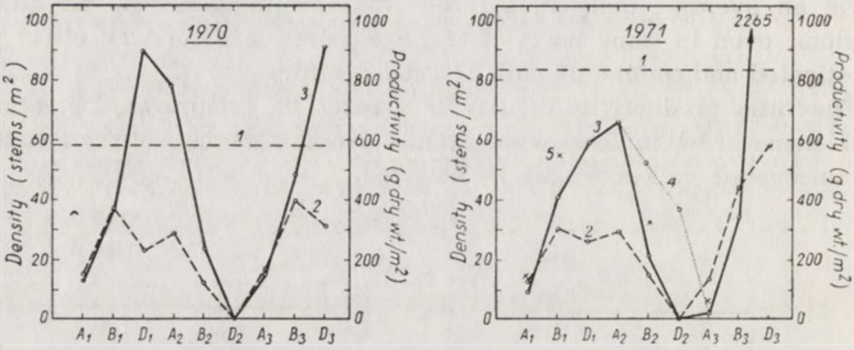

Fig. 3. Toposequence (West–East) of density and productivity in 1970 and 1971. 1 — average productivity, 2 — density, 3 — productivity, 4 — values in fenced areas, 5 — values calculated without "0-plots" (i. e. without living stem)

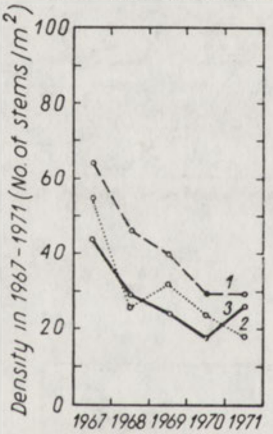

Fig. 4. Mean values of density in 1967–1971 for the divisions 1 — B (cut, litter not removed), 2 — A (cut, litter removed), 3 — D (uncut)

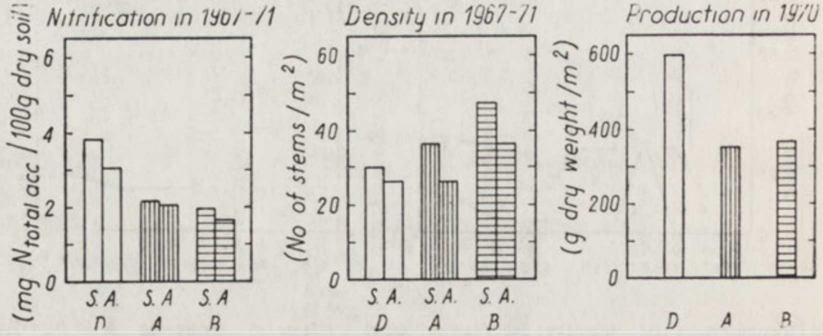

Fig. 5. Influence of management on nitrification, density, and productivity. S — spring, A — autumn

4. DISCUSSION AND CONCLUSION

The questions: whether to harvest or not, and whether fencing is of any value, can be answered as follows:

Best management practise for normally growing and little affected stands is cutting and removing litter, well-growing stands being little affected by wind and waves (compare e. g. Hürlimann 1951, Kurimo 1970, there references). In special cases, e. g. heavy exposition to algae-mats (depending on P content of lake water; for provenience of P compare Thomas 1963, Pleisch 1970), to sewage of factories (compare e. g. Perttula 1952), to boat traffic (detailes see e. g. Sukopp 1968, 1971), a narrow belt should not be mown, the old stems protecting the old shoots (compare Hürlimann 1951).

To the contrary of Hübl's (1966) statements of Lake Neusiedlersee, uncut stands on our lakes have not only higher stems, but mostly also a higher productivity. Frost damage in cut areas can be quite high (Haslam 1970 b), no litter protecting the shoots, initiating the formation of denser but weaker populations. Especially in uncut, suboptimal stands, drier periods give rise to heavier insect calamities, killing at least 50% (1972: up to 95%) of the primary spring shoots (compare also Hürlimann 1951). This occurs particularly often on drier sites where insect stages can hibernate better (Haslam 1970 b, "reed bug" effects in May/June, *Arenostola phragmitis,* on the lower 30 cm of stem). According to Mook (1967, 1971) *Lipara lucens* lays its eggs in June preferably on stems of 3.5—5.0 mm diameter, a stem class occurring often in affected suboptimal stands, but survives on stems of higher diameter, which are also preferred by Giraudiella thus influencing breaking resistance (algae-mats!) and stem-length of the stands (see Durska 1970, Szczepański 1970).

By these statements it is obvious that reed is in any case (as a monoculture), even under natural conditions, exposed to various calamities which have a far greater significance when stands are under heavy anthropogenic influence. Then the necessary measures should be taken.

If packets of lake detritus and waste are regularly pushed into the stands, a fence should be put up. In order to keep the shore-line free from permanently installed fences, a temporarly restricted fence of plastic nets can be hung between solid posts in the most dangerous time of the year, i.e. when the young shoots are growing up from 50 to 100 cm during May and June and the formation of algae-mats is accelerated by warmer periods.

The influence of birds has turned out to be negligible as can be judged from the uncovered but fenced stands. (An exception is of course a plantation of reed which attracts any water fowl or then too high densities of white swan).

An open question remains the die-back of reed in exclosures. This phenomenon, "reed-death" acts like an epidemic, tearing up chiefly weakened reed-belts and giving rise to conical gaps which can start from places with natural gap formation (see first observations by Hürlimann 1951, Klötzli 1971) or harvest gap formation (see Weisser 1970, litter heaps, too low cutting). Further work has to be done on this matter. So far it appears that reed-death is connected with primarily weakened reed-beds, as can occur by heavy trodding or boating and other activities of man (compare Sukopp 1968, 1971) or then by the general eutrophication, and disturbance of nutrient balance of our lakes, provoking weaker, less sclerenchymatic stems and more algae. According to Nikolajevskij (1971), about 6% of the diameter of the stem are normally occupied by sclerenchymatic bundles of conducts. In our case this is much less (compare microphotos in Klötzli 1971). Experiments are running to assess the influence of N-regime on the development of sclerenchymatic tissues.

Under more or less natural conditions (e. g. little eutrophication) reed-beds seem to develop in a circular way: aging stands become less dense, are more apt to form gaps which are then colonized by nitrophilus plants (e. g. meadows with *Ranunculus sceleratus, Epilobium hirsutum, Veronica anagallis-aquatica, Polygonum lapathifolium, Catabrosa aquatica*) as long as new stolons of reed have not conquered the gap again. In our eutrophicated lakes these gaps open by the action of algae- and detritus-mats and the stands are then weakened so as to succumbe to that obscure epidemic "reed-death".

Fencing can thus inhibit die-back of reed populations. If it can prevent reed-death in exposed areas is still not clear, as the disease can spread into exclosures. Considering the effects of eutrophic lake water, a general improvement can only derive by the oligotrophication of our lakes regarding P and N by the action of purification plant.

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