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Biometry and the Productive Stand Structure of Coenoses of *Sparganium erectum* L.

Biometrie a produkční struktura porostů *Sparganium erectum* L.

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DYKYJOVÁ D. et J. P. ONDOK (1973): Biometry and the productive stand structure of coenoses of *Sparganium erectum* L. — Preslia, Praha, 45 : 19—30.

The present paper deals with the biometrical parameters of aerial organs, the horizontal and vertical productive structures of the stands, the estimation of the photosynthetically active leaf area and some other productive characteristics of *Sparganium erectum* L. growing in littoral habitats of fishponds and channels in southern Bohemia. The work referred to in this paper is a part of the Wetlands project of the Czechoslovak contribution to the International Biological Programme (IBP News No. 13, Czechoslovakia PT 5, p. 28, London 1969).

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Introduction

Among the edificators of reed-bed communities, *Sparganium erectum* L. assumes a rather peculiar position. It expands relatively rapidly in fishponds and invades stands of other species but it does not participate directly in the development of reed-bed coenoses. The plant strikes rhizomes deep in the mud and occupies quickly a new space of the littoral by its offshoots. However, its stands which cover only small separate areas, exhibit a significant affinity to the littoral zones with land formation (HEJNÝ 1960 : 330). *Sparganium erectum* L. most often grows in deeper sapropel, especially in eutrophic to saprobic waters. The solitary vegetative shoots produce leaves spreaded fanlike over the water surface (Pl. I). Plants growing in a dense canopy have leaves with an almost vertical orientation (Pl. II) which is a typical stand physiognomy of monocotyledonous hardy species of the group of ochthohydrophytes (HEJNÝ 1960).

Noteworthy is the morphology and the anatomical structure of the leaves which with the exception of the flowering shoots represent the entire productive above-ground biomass of the stand. The leaf sheaths at the base of the leaf blades are not distinctly differentiated so that the leaves of the sterile shoots with an alternate arrangement show a continuous blade up to 2 meters in length. On the abaxial side there is an abruptly rising keel causing the lower half of the leaf to resemble a 3-sided monofacial leaf with a triangular cross section. The keel diminishes towards the apex and the blade becomes flat in shape. The upper leaf blades of the fertile shoots with branched stems have distinct embracing sheaths at the base resembling flat bifacial leaves. Their dimensions, however, are small and thus their participation in the total leaf biomass is negligible.

The old morphological and anatomical literature tried to solve the problem of monofacial and bifacial leaves from the point of view of the stelar theory considering mainly the distribution and orientation of the vascular bundles.

The fact that this criterion is insufficient was already criticized by L. J. ČELAKOVSKÝ (1903 : 2).

The morphology and the anatomical structure of leaves of the ramose Spargania were studied in this country by L. J. ČELAKOVSKÝ (1896) and L. ČELAKOVSKÝ jr. (1899). The distinguishing anatomical features described by L. J. ČELAKOVSKÝ (1896) enabled us to identify all the plants we measured, such as *S. erectum* subsp. *polyedrum* ASCHERS. et GRAEBN.

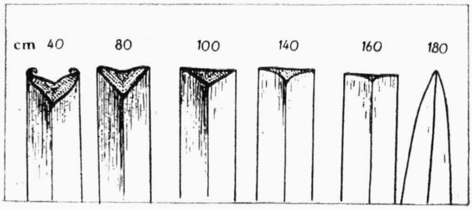

Fig. 1. — Sections of leaf blade of *Sparganium erectum*, total length 180 cm from the base to the apex; arrangement of chlorenchyma in cross section.

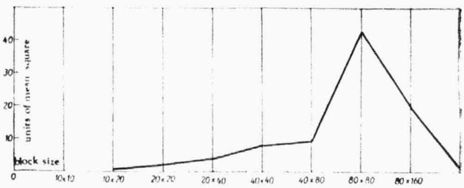

Fig. 2. — Dimension analysis of clusters in the horizontal structure of *Sparganium erectum*. Vertical axis: mean square of density; horizontal axis: block size in cm^2.

The cross sections of the leaves in the above mentioned paper of L. ČELAKOVSKÝ (1899) give clear evidence that the palisade parenchyma of the adaxial side of the leaf blade occurs in identical cell dimensions and in the same number of cell layers on the two lateral walls of the keel on the abaxial side. The stomata are also evenly distributed on the three sides. Thus all the three sides of the 3-sided blade are equivalent from the point of view of the function of the assimilative surface (Fig. 1). Therefore, during the calculations of the leaf surface, we considered the leaf blades to be analogous to monofacial leaves with three lateral walls.

The determination and calculation of production characteristics by the method of growth analysis considers only one side as the functional area of the bifacial leaf area. This convention is not always appropriate and distorts the final evaluation of the productive structure. See e.g. numerous corrections in the calculations of the assimilative surface not only of the leaf blades but also of the stems, leaf sheaths, green fruits etc. (ŠESTÁK et ČATSKÝ 1966, KVĚT et MARSHALL 1971). It was, therefore, necessary to redraw one's attention to this subject, concerning particularly species with vertically orientated leaves, irradiated from all sides in the thin stands, and in aquatic emergent macrophytes also by the radiation reflected by the water surface.

Several species of littoral emergent macrophytes have either actual or apparent monofacial leaves, such as *Acorus calamus*, *Iris pseudacorus*, *Typha angustifolia*, *T. latifolia*, or the entire assimilative surface is formed by the leafless stem as in *Schoenoplectus lacustris*. In these species it would be misleading to consider only one half of the assimilative area if calculations are made by the growth analysis.

Material and methods

1. The calculation of LAI in *Sparganium erectum*

Measurements of the leaf surface area by means of the electric photoplanimeter constructed to measure only flat leaves were inconvenient. Therefore we used the direct measurement and regression equations. It was necessary to chose such a regression equation which would allow us to make a satisfactory prediction and to obtain starting data without too laborious and time-consuming measurements. (A stand area of 1 sq.m. contains about 500 leaves.) So it is possible to take the length of the leaf and the width of the single sides for the parameters of the regression equation. Of the various types of equations calculated, two are given in Tab. 1 which also compares the effectiveness of the prediction by means of the coefficient of determination. More complex types of these equations can be used only for the biometry of the single shoots. The calculation of the leaf area of 0.5 to 1 sq.m. would require too much work to be done, if the length and the width of all the collected leaves were to be measured. For this reason, we limited our measurements to the prediction by means of the linear regression equation with one single parameter, the leaf length.

Tab. 1. — Two regression equations for calculating leaf area in *Sparganium erectum* using the parameter of leaf length [Y = leaf area (cm^2), x = leaf le ngth (cm)].

	Regression equation	coefficient of determination	range of applicability
1	$Y = 3.594x - 84.607$	0.906	$25 < x < 150$
2	$Y = 0.0124x + 1.442x - 11.164$	0.925	$10 < x < 150$

For the calculation of the regression equations, 100 leaves of a sample taken at random from an area of 1 sq.m. were used. The leaves were cut into sections 40 cm in length and for each of them the surface area was computed as an area of three trapezoids, the height of which was the length of the section and the bases were the widths of the leaf sides. By means of the linear regression, the leaf area was computed for the whole sample from an area of $1m^2$.

2. The biometry of sterile and fertile shoots

At the initial phase of a polycormone development, during the peak of the vegetative phenophase, vigorous sterile shoots prevail. In the invasion phase of the stand a great number of fertile shoots occur; their vertical productive structure differs from that of the non-flowering shoots, as shown by the detailed biometrical measurements. Individual sterile and fertile shoots could be easily separated from the underground rhizomes resting in the bottom. They were sampled near the shore of the Spálený pond in the inundation area of the Nová řeka at a depth of 60 to 70 cm at the end of August, 1965. At that time, the fertile shoots still had green fruits and the leaves also were at full functional development. As the aquatic environment gives rise to considerably homogenous plants, the variability of the dimensions of equally aged organs was small. Thus only 15 sterile and 15 fertile shoots were examined. For aech of them the height, the length of the leaves and of the internodia of fertile shoots was measured and for all organs the fresh and the dry weight was determined from which the percentage dry weight was computed (Tab. 2 and 3).

3. The horizontal structure of the stand

In the determination of the average production of the entire stand area, the size of the sampled area should be regulated by the dimensions of the clustres. These clusters are very conspicuous in most of the stands of reed-bed coenoses, being in connection with the morphology of the vegetative polycormone development. It is the clustering which determines the density of the shoot distribution over the given area and thus also the amount of the produced biomass. If the dimensions of the sampled area in the studied species approximate those of the clusters, we obtain in random sampling a high variation of the values of different determinations. Quantitative methods analysing the dimensions of the clusters have been given for instance by Greig-Smith (1964), Kershaw (1964) and Vasilevič (1969). These methods and their application to *Phragmites* stands have been dealt with by Ondok (1970); as for the other species of emergent macrophytes, see Ondok (1971). In *Sparganium* stands we used the method based on a simple criterion, viz. the comparison of the dispersion of the density values of specimens on the level of different sampling areas. A sudden increase of this dispersion in samples with area dimensions of 80 × 80 cm showed that the occurrence of clusters is most frequent in these area dimensions and that the majority of clusters in *Sparganium* stands have just these dimensions (Fig. 2).

Tab. 2. — Length, fresh weight, dry weight and per cent of dry weight of sterile and fertile shoots of *Sparganium erectum*. Spálený pond, 9 September, 1965. Water depth 60—70 cm.

	Sterile shoots				Fertile shoots			
No. of plant	Length cm	Fresh w. g	Dry w. g	% dry w.	Length cm	Fresh w. g	Dry w. g	% dry w.
1	200	410	32.7	7.9	205	380	36.8	9.6
2	200	370	29.9	8.0	200	470	44.1	9.3
3	205	480	39.0	8.1	220	360	34.6	9.6
4	210	500	41.1	8.2	220	350	33.8	9.6
5	220	360	31.5	8.7	200	450	40.4	8.9
6	210	380	29.4	7.7	203	520	52.0	10.0
7	210	370	29.2	7.8	200	350	30.2	8.6
8	190	350	25.1	7.1	203	350	44.4	12.6
9	180	300	30.4	10.1	185	280	32.3	11.5
10	190	340	30.2	8.8	190	420	43.6	10.3
11	183	420	35.3	8.4	185	270	23.7	8.7
12	180	370	28.3	7.6	185	280	26.2	9.3
13	190	280	21.6	7.7	190	350	37.7	10.7
14	180	360	32.5	9.0	170	250	26.3	10.5
15	180	370	24.4	6.0	170	360	33.7	9.3
$\bar{x}$	195	377	30.7	8.1	195	363	38.4	9.9
s_x	3.41	14.96	1.33	0.21	3.35	19.91	2.14	0.28

4. The vertical productive structure

The distribution of the biomass in the individual height strata of the stand is an important criterion of the productivity of the photosynthetic apparatus from the viewpoint of the vertical zonation of the relative air humidity, the carbon dioxide gradient and the vertical gradient of incident radiation density. For the vertical analysis of the biomass distribution individual sterile and fertile shoots were used, as weltas the whole samples of the above-ground biomass sampled in the dense stand from an area of 1 sq.m. The samples were cut into vertical segments of 40 cm height starting from the base to the top. The leaves, the internodes and the fruits from each stratum were then dried and weighed separately. The dynamic analysis of the development of the above ground biomass from the beginning of the season is not discussed in the present paper. The results obtained give only the vertical structure of the above ground biomass, as determined in the stage of the ripening of the fruits. For each estimation the average value from 3 to 5 samplings is given (Tab. 5).

The production of the below ground organs, from the open bottom of a drained fishpond, was assessed. The area sampled was identical with that of the above ground part of the stand. All the results obtained were calculated per square meter of the stand area.

5. The calculation of the stands productivity, ash content, caloric values and the efficiency coefficient of the solar energy conversion

The annual (seasonal) production of the above ground organs may be assessed approximately from the biomass production in the phase of maximum stand development with a correction of about 10 per cent covering the biomass of the organs that either died off during the season before the harvest or would still grow to maturity if the stand were maintained unimpaired. The tables indicate the production of the dry biomass (dried by air-flow at 80° C to a constant weight) with a 10 percentage correction and also the uncorrected production of the dry below ground biomass which of course was not the increment of one season only. The approximate average daily biomass production of the above ground part of the stand was calculated by dividing the production by the number of days from the beginning of the season till the date of the harvest.

The coefficient of the utilization of incident radiation which is the criterion of the photosynthetic efficiency of the stand may be calculated from the production of the net organic (ash-free) matter of a stand converted to the caloric value. *Sparganium erectum* is a species with a considerable absorptive capacity for the mineral constituents of the substrate: its ash content equals approximately 15 per cent of the absolute dry weight (Vavruška 1966). This high ash content was proved by the analyses of the main nutrients carried out for the samples of the stand in one biotope (Tab. 4). The caloric value of the net organic matter of the stand was computed from the data in the literature (Westlake 1965, Straškraba 1968) by the coefficient of 1 g of organic matter equalling 3.5 kcal. The total values of the incident global radiation per season were recorded by means of the Kipp et Zonnen solarimeter and converted in the photosynthetically active radiation PhAR by the coefficient 0.45. The efficiency of the solar energy conversion in the energy of the organic matter is given by the equation

$$\eta = \frac{\text{energy bound in organic matter (kcal m}^{-2}\text{ . }\Delta t^{-1}\text{ . 100\%)}}{\text{energy of PhAR incident on the stand (kcal m}^{-2}\text{ . }\Delta t^{-1}\text{)}}$$

where Δt = the number of days from the start of the growing season till the date of harvest.

Results and discussion

The results of the biometrical measurements of the shoots are indicated in Tab. 2 and 3 and Fig. 3 and 4; the production parameters are given in Tab. 5 and Fig. 5.

The functional area of the assimilatory surface of the leaves taken from an area of 1 m^2, computed by means of the linear regression equation, amounted to 14.5 m^2; thus the leaf area index (LAI) is 14.5. This high value in leaves nearly 2 m long corresponds to the values measured for *Typha* species (Dykyjová et Květ 1970, Dykyjová 1971a, b).

The biometrical parameters of the shoots sampled from depths between 60 and 70 cm also show a considerable productive capacity of this species. The length of the sterile shoots surpassed sometimes 2 m; the longest leaves of the fertile plants were a little shorter. At the time of sampling (August, September) the first, second and third oldest leaves at the base of the shoot died off still in the water, so that no dry weight was recorded for these leaves. The sterile shoots had 6 to 9 fully developed leaves and 1 to 3 leaves which were dying off. Fertile shoots had 9 to 12 leaves, of which 1 to 2 died off at the base and the leaves at the top of the fertile stems were considerably shorter attaining the character of little spathes. Tab. 2 gives in comparison the values of length, dry weight and fresh weight of the whole sterile and fertile shoots and the percentage content of the dry matter. In Tab. 3 the length and dry weight of the gradually inserting leaves of sterile shoot and internodes as well as the fruits of fertile shoot are given. In both types of the shoots the leaves and internodia are characterized by the initially increasing and then decreasing gradient of their length and dry weight. Fig. 3 shows graphically these relations as well as the difference between the vertical distribution of the biomass in sterile and fertile shoots. The last internode of the fertile shoots is typically prolonged, resemding that of the grasses or the *Typha* species.

The total weight of fresh sterile shoots and their total dry weight were higner as compared with the fertile shoots, which however show a higner per cent of dry matter during the ripening of fruits (Tab. 2).

Tab. 3. — The biometrical characteristics of sterile and fertile shoots of *Sparganium erectum*. from the oldest to the youngest organ. Spálený

sterile shoots				
No. of plant	6.		9.	
	leaf length cm	leaf dry w. g	leaf length cm	leaf dry w. g
No. of organ				
1	dead	dead	148	2.35
2	142	2.70	149	3.00
3	143	3.10	156	3.20
4	175	4.25	169	3.40
5	182	4.90	174	3.40
6	175	4.70	193	4.20
7	173	4.50	203	4.70
8	163	3.30	192	4.10
9	123	1.50	183	3.00
10	—	—	—	—
11	—	—	—	—
total dry weight of shoot	28.95		31.35	

The structural diagrams of the vertical distribution of the dry biomass from individual shoots of solitary plants, growing in deep water (Fig. 4), correspond to the vertical biomass distribution of the whole dense stand from an area of 1 m² in a close stand. This sample was taken in the limosal ecophase with the underground water level at soil surface, so that the whole above-ground part of the stand developed on dry land. The weight of individual shoots of solitary plants, growing in deeper water, is higher as compared with the shoots growing in the close stand. The vertical distribution of organic matter in different height strata of the stand show characteristic differences in sterile and fertile shoots. The sterile shoots accumulate most of the biomass in their lower part due to the large and voluminous clasping leaf bases (sheaths), which change quickly into fan-like orientated open

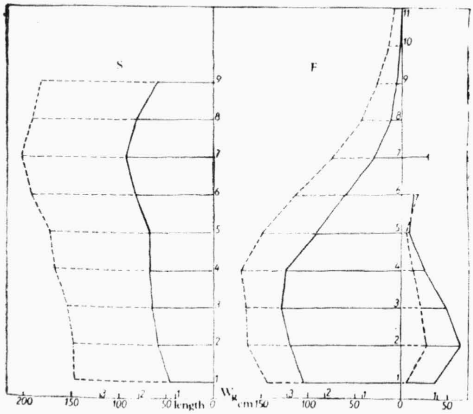

Fig. 3. — Biometrical characteristics of leaf laminae, internodia and fruits of the sterile (S) and the fertile (F) shoot of *Sparganium erectum*. Horizontal axis: the length of leaves (- - - -, left), and of the internodia (- - - -, right), and the dry weight in g of the same organs (——). Vertical axis: Number of successive leaves and internodes from the base to the top.

The growth gradients of the length and dry weight of leaves and internodes in successive order pond, 7 September, 1965. Water depth 50 – 60 cm.

fertile shoots							
3.				6.			
leaf length cm	leaf dry w. g	internod. length cm	internod. dry w. g	leaf length cm	leaf dry w. g	internod. length cm	internod. dry w. g
142	2.60	6	0.90	dead	dead		
163	2.95	26	1.60	159	3.55	35	2.80
165	3.20	21	1.20	171	3.10	26	1.70
170	3.05	12	0.60	164	1.65	19	0.95
148	2.25	5.5	0.20	110	0.85	30	1.10
115	1.50	17	0.30	72	0.40		
74	0.75	fruits dry w.		42	0.20	fruits dry w.	2.00
43	0.30	fruits dry w.	0.70	26	0.10		
27	0.15			14.5	0.03		
15	0.05			8	—		
9	—			—	—		
22.30				19.40			

blades (Pl. I : B). In accordance with the dimensions of individual leaves of sterile shoots, also the dry weight of the successive height strata of sterile shoots, also the dry weight of the successive height strata decreases proportionally from the base to the tope. On the other hand, the fertile shoots with successively ripening fruits on the branched stem show a sudden increase of the dry weight at the height of the stratum where the fruits are mostly concentrated (see the structural diagram, Fig. 5). This process is evident in both the vertical structure of each shoot and in the whole sample of

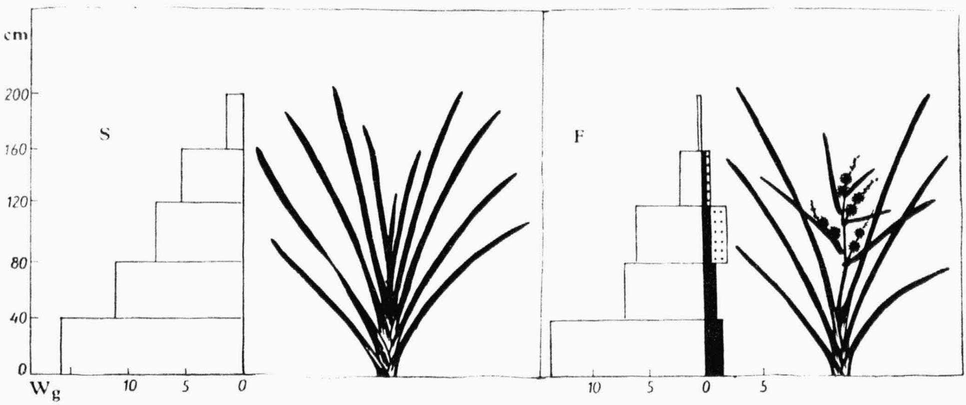

Fig. 4. — The vertical productive structure of a single sterile (S) and fertile (F) shoot of *Sparganium erectum*. Horizontal axis: (left) the dry weight of the photosynthetic organs (white area); (right) the dry weight of non-photosynthetic organs, internodes and fruits (black and dotted area). Vertical axis: the height of individual vertical strata in cm.

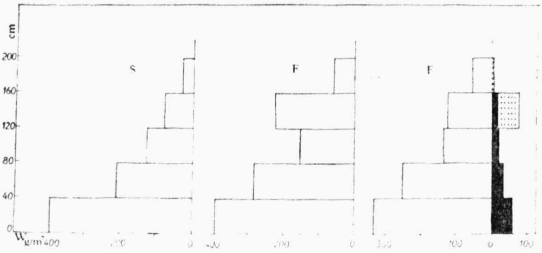

Fig. 5. — The vertical productive structure of a dense stand of *Sparganium erectum* from the sampling plot of 1 m² with the sterile shoots (left, S), and sterile and fertile shoots (F, middle). (Right): the same sample of dry biomass differentiated in the photosynthetic organs (white area) and non-photosynthetic organs (black and dotted area). The structure is analogous to that of a single shoot in Fig. 4.

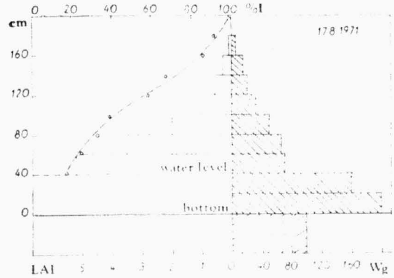

Fig. 6. — Vertical structure of a *Sparganium* stand. Ordinate height of individual layers; upper abscissa — percentage of diffuse solar radiation at different stand levels measured in the spectral range of PhAR; 100 % = radiation above the stand; lower abscissa — cummulative LAI left and dry weight of plant biomass right.

Tab. 4. — Mineral nutrients in dry biomass of a flowering stand of *S. erectum*. Zliv pond, 5 August, 1970. Water depth 75 cm, mud (sapropel).

	N	P	K	Na	Ca	Mg
mg/100 g dry biomass	1680	484	3500	397	1230	294
g per 1423 g of dry biomass at 1 m² of stand area	23.9	6.9	49.8	5.6	17.5	4.2

Tab. 5. — Production characteristics of stand of *S.*

fishpond and sampling date	biotope and stage of the stand		w. depth cm	Number of shoots/m²	height of the stand cm	W shoots g/m²
Velké Stavidlo 1 October, 1966 1 October, 1966 1 October, 1966	fishpond littoral	initial invasion invasion	15 25 25	36 84 80	200 220 220	942 1348 1400
Opatovický 23 July, 1969 23 July, 1969	swamp saprobic	invasion invasion	0 0	109 90	215 215	1610 1330
Zliv 5 August, 1970	fishpond littoral, sapropel	invasion	75	—	220	1423

the stand with fertile or only sterile shoots. The fruit bearing stems of *Sparganium* did not occupy any great space (they are also shorter than the leaf blades), so that they did not shade the leaves which can accumulate the assimilates for the development of new rhizomes and for the storage of reserve substances until late autumn.'

In 1971 a more detailed analysis of vertical structure was made on a locality of Opatovický pond. The vertical distribution of total biomass and of cummulative LAI was determined. Simultaneously the penetration of radiation in the stand was measured by means of a phytoactiometer. The percentage of diffuse radiation at individual horizontal levels indicates that the incoming solar radiation is reduced in the stand owing to mutual shadowing of aerial plant organs (Fig. 6).

The seasonal biomass production of *Sparganium erectum* is relatively slow in contrast to other species of reed-bed coenoses. The largest biomass increment occurs in this species as late as in the period of the maximum irradiation density in June and July (HEJNÝ 1960 : 354). At that time, the fertile shoots were still flowering. During August throuth September, the below ground rhizomes spread out and the reserve substances accumulated in the root-stock. This seasonal rhythm was also evident in the different amount of the below ground biomass in the samples collected in the summer and autumn months, i.e. between July and October (Tab. 5). The initial phases of the stands with prevailing sterile shoots (Tab. 5, biotope Velké Stavidlo pond, No. I) also displayed a lower production of the below ground organs as compared with the older invasion phase of the stand (No. II and III).

The production characteristics of *Sparganium erectum* are apparent from three samples taken from the close stand. The first two samplings were made during the peak of the season (July 23, 1969 and July 5, 1970), the third sampling was made after the end of the season in the stage of fruit ripening (October 1, 1966). At that time, the leaves and achenes were still quite green, but the increments of below the ground organs were already plentiful.

***erectum* in different ecotopes of South Bohemia ponds.**

W belowgr. g/m²	W total g/m²	LAI	C g/m²/day	PhAR kcal/m²/day	η PhAR shoots %	days of growing season
520	1462	—				153
1230	2578	—				153
1370	2770	—				153
310	1920	14.5	19.4	2122	3.4	83
—		—	16.0	2122	3.0	83
—	—	—	14.8	1780	3.1	96

(1) July 23, 1969 — Samples from an area of 3×1 m^2 of a pure stand in the limose ecophase within the accumulation zone of the densely overgrown bay of the Opatovický pond. The soil was characterized by a high layer of autochthonous sediments enriched by waste water flowing through a drain from the nearby stables of a farm. The underground water reached to the surface of the soil. In one sample the biomass of belowground organs was also estimated. The shoots displayed a slightly variable height and were predominantly sterile due to the strongly auxotrophized environment. The maximum height of the shoots was 215 cm; their dry weight, however, did not attain the values of the solitary shoots from the littoral zone of the Spálený pond. It is *most probable that there was a strong competition for light in a dense stand (90 shoots growing over an area of 1 m²).*

(2) July 5, 1970 — Samples were taken from a pure stand flowering abundantly in a dense canopy near the shore of a small fishpond between Hluboká and Zliv. The heigh of the water column was 75 cm; the sapropelic layer was very deep. In this stand, the horizontal structure of clustering was assessed simultaneously. The total production of dry matter was 1,112 g m^2, the height of the shoots being 210 cm. The samples of the dry biomass were analyzed for the content of the main ash components. From Tab. 4 it is apparent that the substantial amount of mineral nutrients was absorbed from the substrate by the above-ground biomass.

(3) October 1, 1966 — Samples were taken from a pure stand at the end of the season in the littoral region of the drained fishpond Velké Stavidlo near Třeboň, at the sandy bottom with a thin sapropelic layer. Sampling area was 3×1 m^2. In the season, the height of the water column measured approximately 25 cm. One sample was collected from the initial phase of the stand containing sterile shoots, the two following samples were taken from the dense stand with a larger number of shoots including fertile ones (Tab. 5). The belowground biomass from the invasion phase of the stand was higher than in the summer sampling.

The total production of the above-ground biomass and the height of the stand in all sampling sites did not differ very much, though the biotopes were dissimilar. The first and the third sampling site are near the laboratory, where the incident radiation was measured. Tab. 5 gives the coefficients of energy conversion (PhAR) as a mean value of the whole growing season. Although these values are lower than those of very productive species of macrophytes, such as *Phragmites* and *Typha* (DYKYJOVÁ 1971), yet they are fairly significant.

Conclusion

Sparganium erectum does not form extensive and continuous stands as the other species of reed-bed coenoses do. Its production characteristics, however, are considerably high. The spatial geometry of the individual leaves and of the foliage ensures a high assimilative area without shading other organs at various height of the stand. Thus the large leaf area index with the vertical leaf orientation is one of the factors that effects the considerable production of the species. The total dry biomass including the below ground organs surpassed in some cases 2,500 g/m^2. This classes the species with the most productive components of natural communities of the temperate zone. The relatively scarce stands may receive incident radiation falling down to the lower strata of the stand even below the water surface and, additionally, also the part of the radiation reflected from the water surface. The verticaly orientated leaves with the assimilative tissue and the stomata spaced evenly over the entire surface of three-sided leaf blades may receive incident radiation from different directions. In eutrophic water bodies, new shoots may pronptly occupy an aerial space and an area of the pond bottom, so that neither water nor carbon dioxide, radiation density or mineral nutrients may limit their photosynthetic efficiency. In rapidly overgrowing sites, however, this species is not successful in the competition with other emergent macrophytes, in particular with high reed-bed plants. A detailed measurement of the photosynthetic process at saturation densities is required to find whether one of the causes of the small competitive force is the need for a high radiation density.

Summary

1. The functional surface area of the photosynthetic apparatus of *Sparganium erectum* L. is given by the morphological and anatomical structure of the leaf blades. The three-dimensional leaves and the distribution of the assimilative tissues — palisade parenchyma and stomata — are analogous to the anatomical structure of monofacial leaves. Thus the assimilative surface area and the LAI were calculated as the total of all three surface areas of the leaf blades. The LAI is therefore high and corresponds to the values measured in *Typha angustifolia* L. and *T. latifolia* L.

2. The horizontal structure of aerial organs shows the pattern of the density distribution. The higher clumping occurs in the quadrate size of 80 × 80 cm. Therefore the representative samples in the production analysis of a stand must be taken from plots surpassing this area.

3. The biometrical values show the characteristic growth gradients in the ontogenetic development of individual organs. The fresh and the dry weight are higher in sterile solitary shoots than in the shoots of a closed stand. The percentage dry weight of the fertile shoots is higher. The high ash content, up to 15 per cent of dry biomass, makes it possible to suggest an intensive circulation of water and dissolved nutrients.

4. The vertical productive stand structure differs in sterile and fertile shoots. The results of measurement in the representative individual shoots taken from initial stage of stand development and from sampling areas of close stands are analogous and correspond to the growth gradients in the ontogeny of assimilative organs.

5. The seasonal biomass (standing crop) production is not so high as in the other species of emergent macrophytes. The conversion efficiency of incident radiant energy is not very high, either; with regard to the relatively short vegetative period of this species, the productivity per day (C, g/m^2/day) and the energy conversion efficiency coefficient per day (η, % kcal/m^2/day) may be fairly significant.

6. The small colonies — polycormones — of *Sparganium erectum* occupy mostly the free aerial space of the littoral. They do not survive in competition for light with other species of emergent macrophytes, especially the reedswamp communities. Only the photosynthesis measurement at the saturating radiation densities make it possible to prove that the high irradiation need and the competition for light can be one of the reasons of the low competitive power of this species.

Souhrn

1. Funkční plocha povrchu asimilačního aparátu *Sparganium erectum* L. je určena morfologicko-anatomickou stavbou listových čepelí. Rozložením asimilačních pletiv a průduchů na celém obvodu trojboké listové čepele jsou listy tohoto druhu analogické listům monofaciálním. Asimilační povrch a pokryvnost listoví (LAI) byly počítány ze součtu povrchů všech tří stran listové čepele. Index pokryvnosti listoví je proto velmi vysoký a odpovídá hodnotám naměřeným u orobinců, *T. latifolia* L. a *T. angustifolia* L.

2. Horizontální struktura porostu jeví ostře vyhraněné shlukování prýtů (pattern) v rozmezí plochy 80 × 80 cm. Odběry reprezentativních vzorků pro analýzu produkce musí proto zabírat větší plochu.

3. Biometrické hodnoty délky, plochy a sušiny jednotlivých orgánů vykazují charakteristické růstové gradienty během ontogeneze. Čerstvá váha i sušina sterilních prýtů solitérních rostlin je mnohem vyšší než u prýtů v hustém zápoji. Fertilní prýty vykazují vyšší procentický obsah sušiny. Na celkové váze sušiny se podílí až 15 % popelovin. Jejich vysoký obsah nasvědčuje intenzívní sorpci iontů a cirkulaci vody i rozpuštěných minerálních složek substrátu.

4. Vertikální produkční struktura porostu je odchylná u prýtů sterilních a fertilních. Výsledky měření na reprezentativních jedincích z iniciálních stadií porostu a na odběrových plochách sevřeného porostu jsou analogické a odpovídají růstovým gradientům v ontogenezi asimilačních orgánů.

5. Sezónní produkce biomasy (standing crop) ve srovnání s jinými druhy emersních makrofytů je poměrně nízká, někdy však dosahuje hodnot přes 2500 g/m^2 (včetně hmoty podzemních orgánů). Také koeficienty využití energie dopadajícího záření nejsou tak vysoké jako u jiných emersních makrofytů. Vzhledem k poměrně krátké vegetační době tohoto druhu jsou však produkční charakteristiky zejména denní produktivita (C, g/m^2/den) a denní koeficienty využití záření (η, % kcal/m^2/den) dosti významné.

6. Polykormóny *Sparganium erectum* obsazují většinou jen volný prostor litorálu vodní nádrže a v konkurenci s jinými druhy emersních makrofytů, zejména rákosin, neobstojí. Podrobná měření průběhu fotosyntézy za sytících intenzit ozáření by mohla ukázat, zda jednou z příčin malé konkurenční schopnosti tohoto druhu jsou značné nároky na světlo.

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See also plates I. – II. in the appendix.