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Underground Organs of *Phragmites communis*, Their Growth, Biomass and Net Production

Abstract

The present paper sums up the knowledge obtained from the study of growth periodicity in the underground organs of *Phragmites communis* TRIN. and from the analyses of different *Phragmites* stands in three regions of Czechoslovakia. A period of intense growth of *Phragmites* rhizomes was recorded in summer. Spring (end of April and beginning of May) and autumn (mainly September) seem to be the periods of most active root growth. During July and August, accumulation of reserve material takes place both in new and old rhizomes. In the stands investigated, the biomass of *Phragmites* rhizomes varied from 2 kg/m^2 to 5 kg/m^2, and root dry weight from 0.08 kg/m^2 to 3.6 kg/m^2. The ratio of underground to total aboveground dry weight was highly variable (1.0 to 9.9). The estimated annual net rhizome production of *Phragmites*, in two different stand, was 30 % (Šakvický fishpond) and 60 % (Nesyt fishpond) of the seasonal maximum above-ground biomass.

INTRODUCTION

Phragmites communis TRIN.[1] is an important component of the littoral in many freshwater ecosystems and dominates in various wetland habitats. As a source of nourishment and/or shelter, it forms ecological niches for a great number of other organisms in shallow reservoirs. Information on the growth and production of *Phragmites* is important for understanding its role in these ecosystems. The need to obtain the basic production values for aquatic macrophytes has already been emphasized by WESTLAKE (1965). Most of the emergent plant communities are more productive than phytoplanktonic or submerged macrophyte communities (under the same climatic and trophic conditions and in the same area); their productivity also depends on other habitat conditions such as wave action (WESTLAKE 1963, 1965, DYKYJOVÁ 1971b).

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[1] *Phragmites australis* (CAV.) TRIN. ex STEUDEL proves to be the correct name — cf. CLAYTON (1968).

Vol. 11, No. 2 (113—224)
of the Folia geobotanica et phytotaxonomica was issued
28 July 1976

Folia Geobot. Phytotax., Praha, 11: 225—259, 1976

Studies on the production of reed stands tend to disregard their roots and rhizomes although the underground organs form a considerable part of the total biomass, usually more than 50 % (Westlake 1965, 1968). The present paper deals mainly with the underground organs of *Phragmites* from the point of view of production ecology, in order to find answers to the following questions: (a) What is the growth periodicity of underground organs? (b) How does the content of reserve material in old and new rhizomes change with their age and in the course of the growing season? (c) How much is the biomass of underground organs and what is the ratio of underground to above-ground dry weight in *Phragmites* stands occuring in various habitats? (d) How much is the annual net production of the underground organs?

The work referred to in this paper formed part of the Czechoslovak IBP projects PT/5 and PP-P/3 (see IBP News Nos 13 and 14).

MATERIAL AND METHODS

Assessment of growth periodicity and of seasonal changes in carbohydrate content in the underground organs

During the 1972 growing season, on seven successive dates (10. 3., 6. 5., 22. 5., 27. 6., 31. 7., 28. 8. and 25. 9.) 5 to 6 terminal shoots were sampled from a littoral stand of *Phragmites* in the SE. part of the Nesyt fishpond (48°47′ N, 16°43′ E; altitude 175 m; eutrophic and fertilized fishpond). The bottom was a mineral-rich sandy clay containing in the top layer at 0 to 20 cm in mg per 100 g dry weight: Ca^{2+} 1229.1; Mg^{2+} 217.1; K^{+} 17.5; C 5.6 %, N 0.57 %. The water level, while the fishpond is filled with water, varies between + 10 to + 40 cm during the growing season. In 1971, with the fishpond filled only partly, the underground water table varied between − 10 to − 25 cm. The shoot length, weight, and the dry weight of leaves, stems and inflorescences were estimated. The plant material was oven-dried at 60 °C and weighed. The growth characteristics, i.e. rate of dry matter production (*RDP*) and relative growth rate (*RGR*) were calcuted according to the following formulae: $RDP = (W_2 - W_1) . (t_2 - t_1)^{-1}$, $RGR = (1\mu W_2 - 1\mu W_1) . (t_2 - t_1)^{-1}$ (Květ et al. 1971). These values are related to one terminal shoot.

In addition to the above-ground organs, the upper parts (approximately 40 to 50 cm long) of the 5 to 6 vertical rhizomes bearing the terminal shoots were sampled (i.e., even-aged rhizomes formed during the preceding year 1971) and so were all new rhizomes (both vertical and horizontal) growing from these old vertical rhizomes (see Fig. 1). The roots selected for analysis were sampled close to the terminal shoots, from 3 to 4 monoliths situated below a surface area of 25 cm × 25 cm, to the depth of 25 cm.

In order to determine the total carbohydrate content, fresh rhizomes and roots (4 parallel samples) were hydrolysed for three hours in 2 % HCl over a water bath and analyzed by Nelson's (1944) modification of Somogy's colorimetric method for the determination of reducing sugars.

The volume of both old and new rhizomes was determined in a calibrated glass cylinder (Jeník 1954; 96). The bulk density of rhizomes (dry weight/fresh volume) was then calculated.

The actual growth activity of the underground organs of *Phragmites* was estimated according to the dehydrogenase activity in the roots and rhizomes (Kubíková 1971), using Sator et Bommer's (1971) modification of the method described by Jambor (1960). For details see Fiala (1973b, d). The total carbohydrate content and dehydrogenase activity are related to dry weight estimated at 105 °C.

Assessment of reserve material content in rhizomes of various age

Differences in the content of reserve material in *Phragmites* rhizomes of various age were ascertained in the reed stands at the northern edge of the Nesyt fishpond at the end of the 1971 growing season (30th October). The habitat characteristics are given in the next paragraph.

The 4 to 5 vertical rhizomes of each age category, sampled from the stand to the approximate depth of 50 cm below soil surface, included: young new rhizomes, which had appeared in the course of the year 1971 and bore a terminal bud each; rhizomes in their second growing season, i.e., those bearing a living terminal shoot and giving rise to lateral rhizomes with hibernating buds for the next (third) season; and so on up to rhizomes in their third or fourth growing season. The total carbohydrate content, rhizome volume, and bulk density were estimated using the methods given in the preceding paragraph.

Estimation of the underground biomass in various habitats

Eight *Phragmites* stands were studied in six localities in three regions of Czechoslovakia: southern Bohemia (in the vicinity of Třeboň, 49° N, 14°46′ E; altitude 425 m to 440 m, climate temperate and moderately humid with mild winters — according to Vesecký et al. (1958); southern Moravia (48°47′ to 59′ N, 16°43′ to 57′ E, altitude 175 to 190 m, climate warm and dry with mild winters and prolonged sunshine); southern Slovakia (approximately 70 km SE. of Bratislava, 47°47′ N, 17°44′ E, altitude 110 m, climate warm with mild winters and prolonged sunshine). The stands were situated in the littorals of managed fishponds (Rožmberk — SW. shore, alt. 425 m, 49°03′ N, 14°48′ E; Opatovický fishpond — type V in the central part of the E. shore, alt. 440 m, 48°59′ N, 14°46′ E; Nesyt fishpond — N. shore, alt. 175 m, 48°47′ N, 16°43′ E; Šakvický fishpond — SW. shore, alt. 170 m, 48°53′ N, 16°43′ E), in swamps on flooded arable land

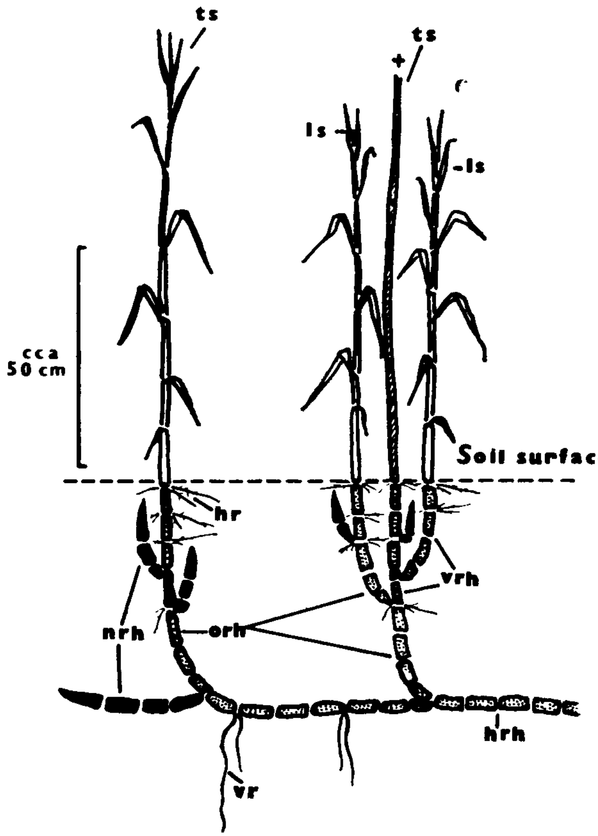


Fig. 1. Schematic representation of underground and aboveground organs in *Phragmites* (ts — terminal shoots, ls — lateral shoots, vrh — vertical rhizomes, hrh — horizontal rhizomes, nrh — new rhizomes, orh — old rhizomes, hr — horizontal roots and their branches, vr — vertical roots and their branches).

Table 1. Meteorological data from southern Bohemia, southern Moravia and southern Slovakia according to Hydrometeorological Institute in Prague

	Mean values per 1 month, year and growing season													
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year	April—Sept.
Temperatures 1901—1950 (°C)														
S. Bohemia														
Třeboň (alt. 433 m)	—2.2	—1.0	3.0	7.5	12.9	15.9	17.7	16.9	13.0	7.8	2.7	—0.7	7.8	14.0
S. Moravia														
Lednice (alt. 164 m)	–1.7	—0.5	4.1	9.3	14.5	17.3	19.2	18.1	14.2	9.0	3.9	0.0	9.0	15.4
Hodonín (alt. 169 m)	–1.5	0.0	4.5	9.8	15.2	18.1	19.8	18.7	15.0	9.6	4.3	0.3	9.5	16.1
S. Slovakia														
Komárno (alt. 112 m)	—1.6	—0.1	4.9	10.1	15.3	18.2	20.3	19.5	15.7	10.1	4.5	0.4	9.8	16.5
Sunshine duration 1926—1950 (hrs)														
S. Bohemia														
Třeboň	54	84	149	168	221	226	239	217	180	115	59	45	1757	1251
S. Moravia														
Podivín (alt. 169 m)	48	82	142	182	240	256	265	245	197	121	55	40	1873	1385
S. Slovakia														
Komárno	62	91	142	181	225	243	264	244	194	143	69	41	1899	1351
Rainfall 1901—1950 (mm)														
S. Bohemia														
Třeboň	30	32	30	48	69	73	94	79	52	47	37	36	627	415
S. Moravia														
Podivín	27	25	26	36	56	60	70	56	48	44	40	28	516	326
Hodonín	31	29	30	40	57	63	87	67	51	50	45	35	585	365
S. Slovakia														
Komárno	32	32	37	44	59	57	59	49	43	50	50	43	555	311

(Kobylí — types M and V — in the former Kobylí Lake — 20 km NW. of the town of Hodonín alt. 180 m, 48°59′ N, 16°57′ E), in the eulittoral of a pond with abundant supply of waste-water from a pig-farm (Opatovický fishpond — type S — central part of the E. shore, alt. 440 m, 48°59′ N, 14°46′ E), and in a periodically flooded part of an oxbow lake at the Danube river (Lake Lion — SW. part, alt. 110 m, 47°47′ N, 17°44′ E).

Table 2. The season with daily temperature averages higher than 10 °C, mean dates of the beginning, the end and their durations in the years 1901—1950 in southern Bohemia, southern Moravia and southern Slovakia according to the Hydrometeorological Institute in Prague.

	Beginning	End	Number of days
S. Bohemia			
Třeboň	29. 4.	2. 10.	157
S. Moravia			
Lednice	19. 4.	10. 10.	175
Hodonín	16. 4.	13. 10.	181
S. Slovakia			
Komárno	14. 4.	16. 10.	186

Table 3. Chemical features of soil of the different *Phragmites communis* stands studied.

		S. Bohemia			S. Moravia				S. Slovakia
	Soil layer (cm)	Rožmberk	Opatovický V	Opatovický S	Kobylí V	Kobylí M	Nesyt	Šakvický	Lion
pH (KCl)	0—20	4.55	5.35	4.45	7.5	7.52	7.25	6.35	7.20
	40—50	5.30	4.40	4.10	7.6	7.6	7.30	6.65	7.35
$CaCO_3$ (%)	0—20	—	0.02	—	7.7	9.4	7.6	0.3	12.0
	40—50	—	0.02	—	7.4	8.4	16.0	0.33	23.0
Ca^{2+} (mg/100 g d.w.)	0—20	32.2	69.4	357.5	1416.1	1297.7	1093.9	200.2	875.2
	40—50	20.0	82.2	55.8	1043.9	1172.6	986.7	143.0	1270.6
Mg^{2+} (mg/100 g d.w.)	0—20	3.0	22.3	77.2	518.6	280.4	151.9	174.9	103.1
	40—50	—	3.0	—	536.7	500.5	158.6	241.2	51.3
P — P_2O_5 (mg/100 g d. w.)	0—20	0.2	0.2	2.2	—	0.1	0.45	0.65	0.2
	40—50	—	0.2	—	—	—	0.2	0.85	0.2
K^+ (mg/100 g d. w.)	0—20	4.25	3.3	19.9	16.6	9.6	8.3	12.45	3.3
	40—50	0.8	5.8	1.7	8.3	6.6	4.9	7.5	3.3
Na^+ (mg/100 g d. w.)	0—20	1.5	2.9	16.3	59.4	67.6	7.4	10.8	10.4
	40—50	0.7	4.5	2.9	96.5	117.2	6.7	9.6	14.1
C (%)	0—20	0.9	1.6	22.8	3.4	3.2	5.9	3.5	2.1
	40—50	0.2	0.3	1.2	2.9	3.0	0.4	0.7	1.5
N (%)	0—20	0.09	0.21	2.80	0.51	0.35	0.93	0.35	0.41
	40—50	0.04	0.13	0.25	0.53	0.84	0.14	0.08	0.28

The principal climatic characteristics of the regions are summarized in Tab. 1. The differences in the beginning and approximate duration of the growing season are shown in Tab. 2. The soil proterties of the habitats are summed up in Tab. 3 and discussed in another part (p. 243) of this paper. The methods of soil chemical analyses are described in the next paragraph. The species composition of the stands is characterized by dominant *Phragmites communis* with relatively few other character species of both the association *Scirpo-Phragmitetum* W. Koch 1926 and the alliance *Phragmition communis* W. Koch 1926, see Tab. 4).

Table 4. Species composition of the eight *Phragmites communis* stands studied (abundance + dominance estimated according to Braun – Blanquet).

	S. Bohemia			S. Moravia			Slovakia S.	
	Rožm-berk	Opato-vický V	Opato-vický S	Kobylí M	Kobylí V	Nesyt	Šak-vický	Lion
Date	10. 8. 1968	11. 8. 1968	14. 10. 1969	24. 10. 1968	24. 10. 1968	3. 7. 1969	2. 7. 1969	1. 7. 1969
Area in sq. m	100	100	100	100	100	100	100	100
Water depth in cm	50	L.*	T.**	T.	T.	30–50	50	10
Cover degree in %	90	95	100	100	90	95	100	90
Phragmites communis Trin.	5	5	5	5	5	5	5	5
Typha latifolia L.	.	.	.	.	1	.	.	.
Persicaria amphibia (L.) S. F. Gray	r	.	.	1	.	.	.	.
Lythrum salicaria ·L.	.	.	+	.	.	r	.	.
Lycopus europaeus L.	.	.	1	.	.	.	.	.
Calystegia sepium (L.) R. Br.	.	.	.	.	.	r	.	.
Galium palustre L.	.	1	.	.	.	.	.	.
Carex riparia Curt.	.	.	.	.	.	.	+	.
Cicuta virosa L.	.	.	+	.	.	.	.	.
Myosotis arvensis (L.) Hill	.	+	.	.	.	.	.	.
Cirsium arvense (L.) Scop.	.	.	r	.	.	.	.	.
Myriophyllum verticillatum L.	.	.	.	.	.	.	.	2–3
Ceratophyllum submersum L.	.	.	.	.	.	.	r	.
Lemna gibba L.	.	.	.	.	.	2	5	.
Lemna minor L.	.	.	.	.	.	1	.	.

*) Limosal ecophase.
**) Terrestrial ecophase.

The biomass of both above- and underground organs of *Phragmites* was sampled in the autumn months of the years 1968 and 1969; at that time, the localities were not flooded (after the fishponds had been cropped), or were artificially drained, or were in a terrestrial ecophase (Hejný 1960) after a period of drought.

A line transect, about 30 m in lenght, was laid down in each stand, parallel with the shore. The shoot density and their biomass were estimated destructively in 10 sampling plots (0.5 m × 1.0 m), selected at random in each transect.

The soil profile was uncovered at the shorter sites (0.5 m wide) of 5 (out of 10) sampling plots chosen for the estimation of shoot biomass. The positions of all rhizomes cut by the vertical plane of each of the 5 profile walls were mapped out by means of a grid of 100 cm^2 squares. The number of rhizomes in the profile wall and the vertical distribution of rhizomes were assessed from these sketches (Schurmann et Goedewangen 1965). The diameters of the cut rhizomes were also measured.

In addition, 5 monoliths were lifted for the determination of underground biomass. They were taken along the profile wall at each sampling plot below an area of 25 cm × 50 cm to the depth of 80 to 100 cm (according to the penetration of rhizomes into the substrate). The rhizomes were picked from the monoliths and, according to their colour and cosistency, the living and dead rhizomes were separated.

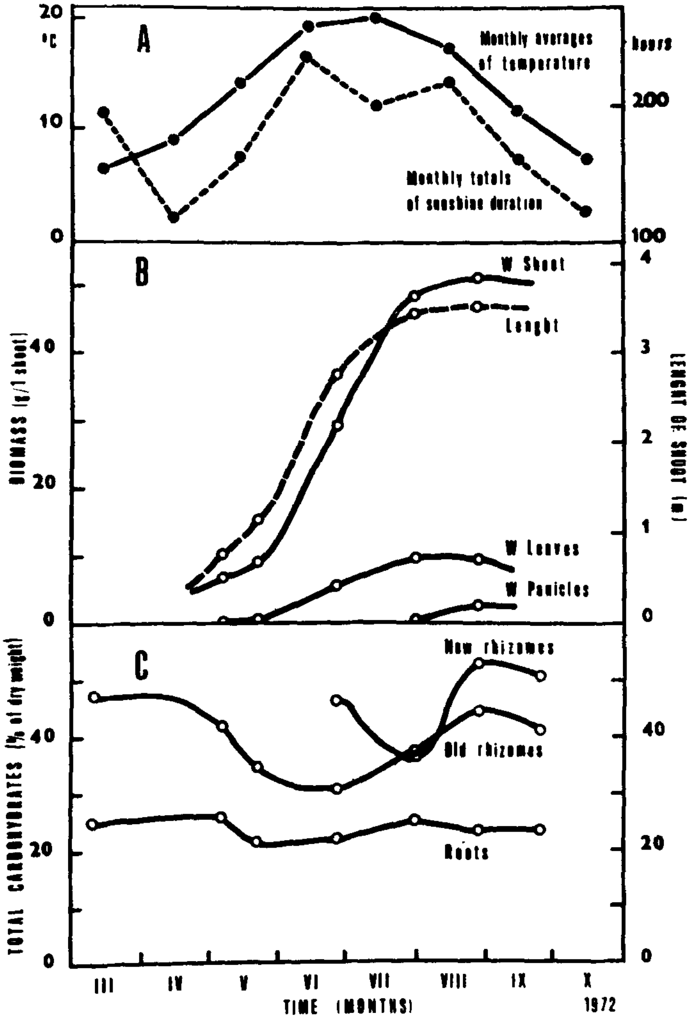


Fig. 2. (A) Course of the monthly averages of air temperatures and monthly totals of sunshine duration at Lednice during the year 1972. — (B) Biomass changes in shoots, leaves and inflorescences of *Phragmites communis* (in g/l shoot) and shoot growth in legth (in m) during the 1972 growing season. — (C) Seasonal course of total carbohydrate contents in the roots and new and old rhizomes of *Phragmites communis* (in % of dry weight).

The root dry weight was estimated only from the upper part of the profile (to the depth of 20 cm below the 25 cm × 50 cm plot). This corresponds approximately to 70 to 80 % of the total root dry weight (FIALA, unpublished). The soil was washed out from the samples which had been put into silon bags (mesh size 1 mm). This was done either immediately in the fishpond water, or at some other suitable place. The loss of the roots during washing represented less than 2 % of their total dry weight (HUSÁK 1971, FIALA 1973d). The plant material was oven-dried at 80° to 90 °C.

Pattern analyses were performed in all eight *Phragmites* stands according to KERSHAW (1964: 104—129). Another transect (25.6 m long and 0.1 m wide) was laid down parallel with the line transect. It consisted of 256 basic units of 10 cm × 10 cm. The number of stems recorded in each of these basic units was used for the calculation of the dependence of mean square (variance of shoot density per block) on block size.

Soil analyses were performed at the laboratory of the Forestry Research Institute, Station Opočno, under the supervision of Mr. J. VACEK. The available nutrient content was assessed in an extract with 1 % citric acid: Ca^{2+} and Mg^{2+} complexometrically, with fluorexone and eriochrome black T, respectively; K^+ and Na^+ by flame photometry, P colorimetrically, using the Photo-Rex method. C were ascertained oxidimetrically, according to SPRINGER and KLEE and N after KJELDAHL, carbonate was with JANKO's limemeter, pH potentiometrically. For all method used see HRAŠKO et al. (1962).

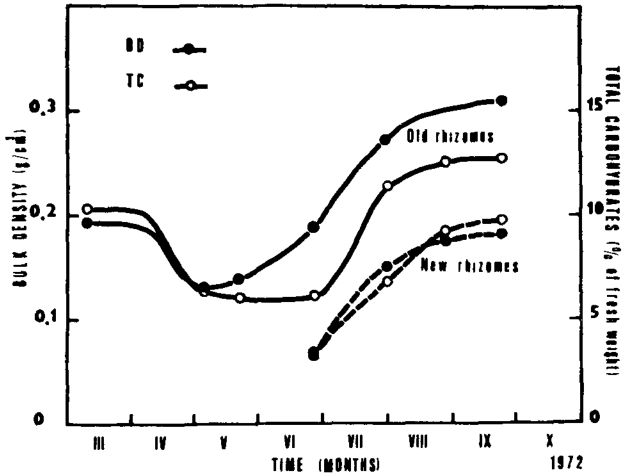


Fig. 3 Changes in bulk density - BD (dry weight/volume of fresh rhizomes) of new and old rhizomes, and in total carbohydrate contents — TC (in % of fresh weight) in new and old rhizomes of *Phragmites communis* during the 1972 growing season.

RESULTS

Growth periodicity and seasonal variation of reserve material in the underground organs

The relationship between the seasonal course of growth in *Phragmites* shoots and the changes in the total carbohydrate content in the roots, old and new rhizomes is shown in Fig. 2. At the end of April and in the first half of May, considerable amounts of reserve material were supplied from the rhizomes to the above-ground organs. This obviously determined the initial rapid shoot growth. In the old rhizomes during the spring, the total carbohydrate content decreased by some 35 % to 40 % of the highest spring value. Both fresh and dry weight of the rhizomes thus became less. The bulk density of the old rhizomes also decreased by about

30 % (Fig. 3). The employment of reserve material for the rapid initial shoot growth results in almost complete formation of the above-ground stand parts during May and June. The highest values of both relative growth rate in the shoots and average daily rate of shoot dry matter production were recorded between May 22 and June 27 (Fig. 4).

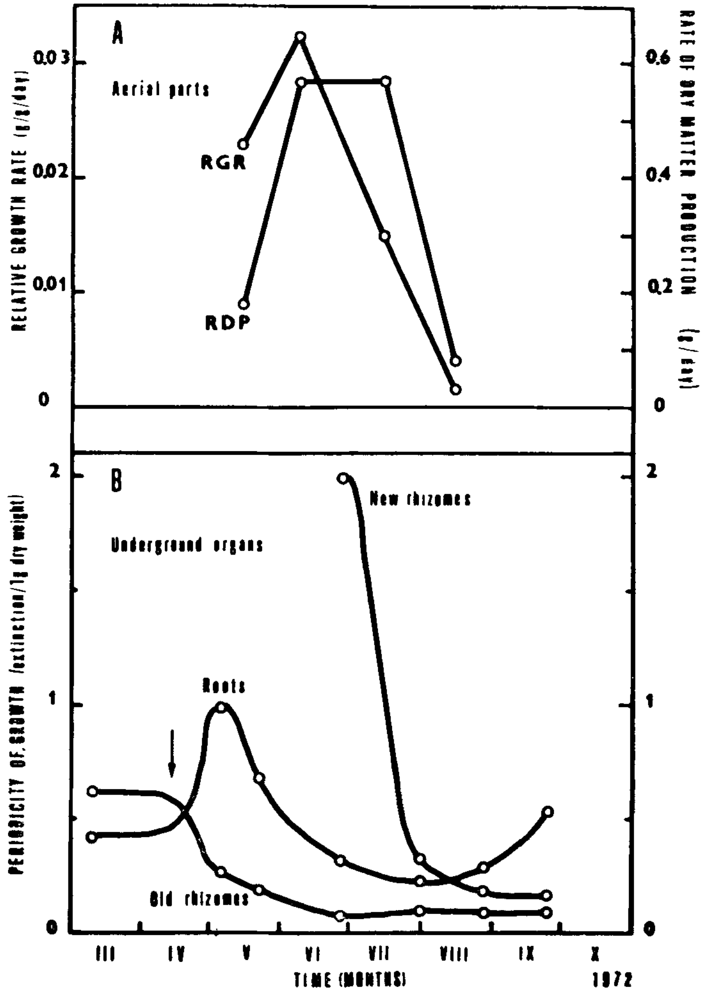


Fig. 4. (A) Course of the average rate of dry matter production (*RDP* in g/day) and relative growth rate (*RGR* in g/g/day) in one aerial shoot of *Phragmites communis* during the 1972 growing season. — (B) Periodicity of the growth of roots and rhizomes of *Phragmites communis* (expressed in relative units of extinction/1 g dry matter). The arrow denotes the approximate beginning of growth of the aerial shoot.

On the other hand, during July and August, reserve material became accumulated not only in the new rhizomes, most of which had obviously been formed during July, but also in older living rhizomes of *Phragmites*. At the end of the growing season, the total carbohydrate content (expressed as percentage of fresh weight) in the old rhizomes surpassed the content recorded at the end of May by a factor of 2 (Fig. 3). Unlike the carbohydrate content, the bulk density began to increase at the end of May; at the end of July it was twice that recorded after the spring exhaustion of reserves, and its autumn values surpassed 0.3 g/cm^3 (Fig. 3). The content of total carbohydrate per unit dry weight found in previous year's *Phragmites* rhizomes in spring exceeded, by 6 to 12 %, the content assessed in the same rhizomes, now about one-year old at the end of the growing season. Most probably more reserve material is taken out of these rhizomes for shoot growth than is returned back to them by the shoots.

The *Phragmites* roots display two periods of marked growth. The first, spring, period comprises the end of April and early May, the other, autumn, period occurs chiefly in September (Fig. 4). In spring, the roots grew mainly from the vertical rhizomes, mostly in the upper humus layer. In autumn, most of the strong vertical roots were formed, growing from plagiotropic rhizomes.

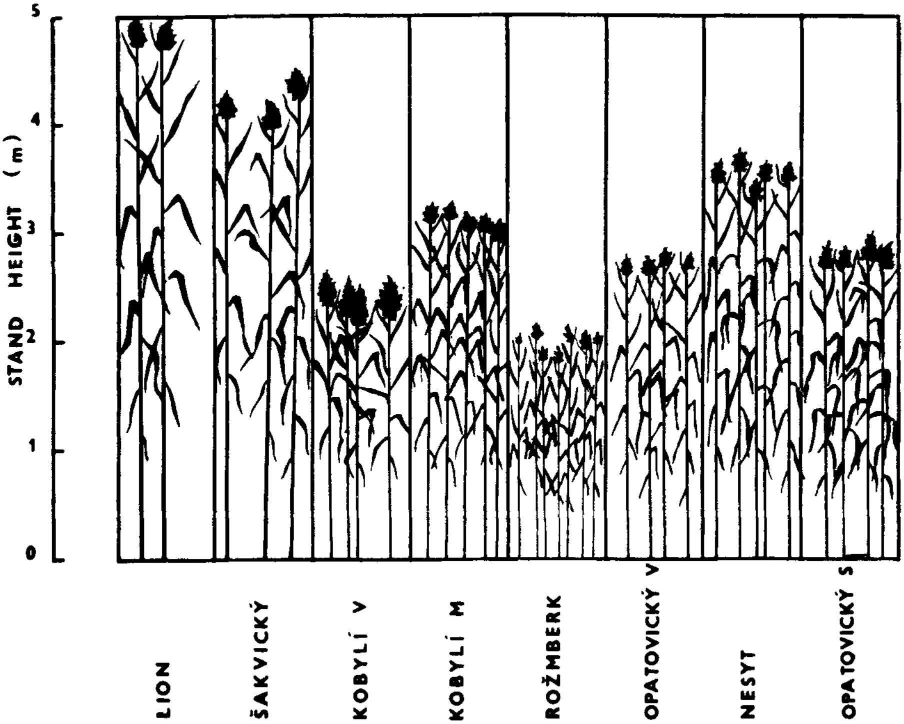


Fig. 5. Schematic representation of above-ground organs in eight stands of *Phragmites communis* studied. Recorded in their maximum biomass.

Underground biomass in various habitats

The eight *Phragmites* stands studied, schematically depicted in Fig. 5, greatly differed in their structure. On the one hand, some of the stands were tall (5 m, in Lion Lake, Šakvický fishpond), while others were relatively low (about 2 m, Rožmberk fishpoud). Another difference concerned stands which grew in much

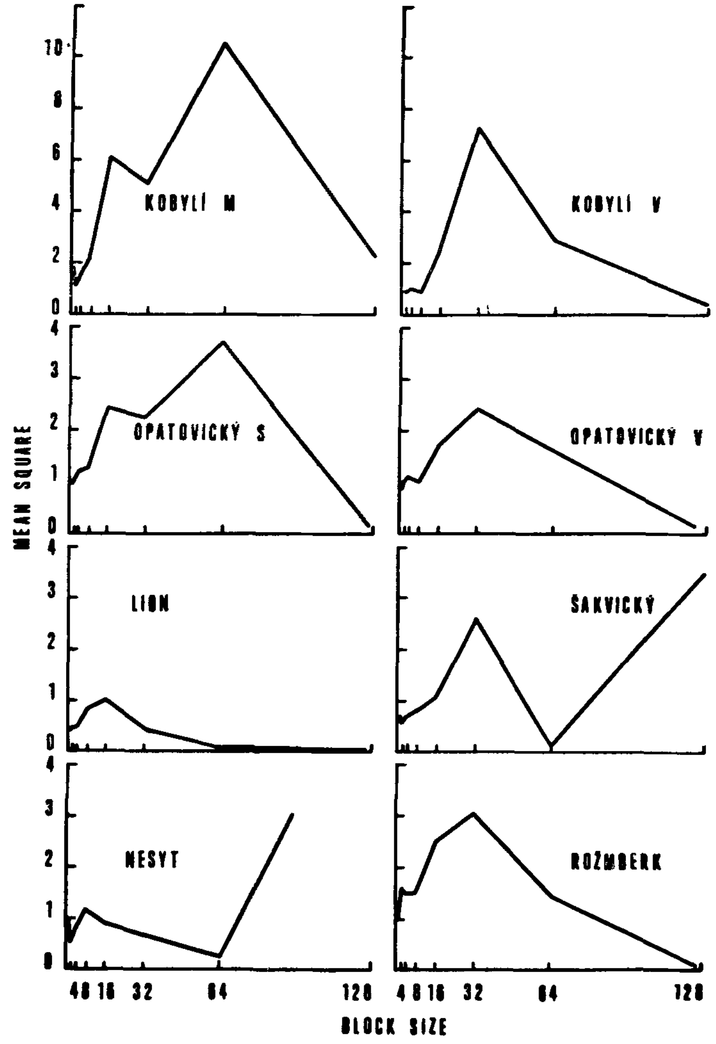


Fig. 6. Comparison of shoot pattern (expressed in values of mean square against block size, for details see text) in eight stands of *Phragmites communis* studied.

Table 5. The mean values of shoot, rhizome and root dry weight and other characteristics in the eight *Phragmites communis* stands studied.

Stand Date	Lion 2. 10. 1969			Šakvický 15. 11. 1968			Kobylí V 24. 10 .1968		
Mean (x), standard error ($s\bar{x}$), variation coefficient (V)	$\bar{x}$	$s\bar{x}$	V(%)	$\bar{x}$	$s\bar{x}$	V(%)	$\bar{x}$	$s\bar{x}$	V(%)
1. Shoot density (no. per 1 m^2)	35.0	3.6	32.9	53.2	4.4	26.3	76.4	5.6	23.2
2. Shoot biomass (g/m^2)	1855	192	32.7	1415	143	21.2	932	65	15.5
3. Rhizome density (no. per 1 m wide profile wall)	24.4	4.2	38.6	33.2	2.5	16.8	42.0	3.4	18.1
4. Rhizome diameter (cm)	2.45	0.12	36.8	2.17	0.07	29.5	1.82	0.05	25.7
5. Living rhizome biomass (g/m^2)	3159	—	—	2181	224	23.0	1949	154	17.7
6. Dead rhizome biomass (g/m^2)	—	—	—	530	175	73.9	144	19	80.0
7. Root biomass (g/m^2, soil layer 0 to 20 cm)	193	27	30.8	469	54	25.8	712	239	74.9
8. Underground biomass, 5 + 7 (g/m^2)	3352	—	—	2650	191	16.1	2661	327	27.5
9. Rhizome biomass: above-ground biomass	1.70	—	—	1.54	—	—	2.06	—	—
10. Root biomass: above-ground biomass	0.10	—	—	0.33	—	—	0.76	—	—
11. Undergr. biomass: above-ground biomass	1.81	—	—	1.87	—	—	2.86	—	—
12. Net production of rhizome, 5:rhizome age (g/m^2/year)	—	—	—	550	—	—	—	—	—

the same habitat but differed in the morphological structure of their shoots (Kobylí Lake, type V — relatively thick stems with broad leaves and conspicuously large inflorescences, Kobylí, type M — thin stems with narrower leaves and small inflorescences). The loosest stand was that at the Lion Lake (35 shoots/m^2, average values), while the dense stand at the Rožmberk fishpond contained up to 135 shoots/m^2. In most instances, the number of shoots per 1 m^2 varied from 70 to 80 (Kobylí Lake, type V, Nesyt fishpond, Opatovický fishpond, type V, Opatovický, type S; - see Tab. 5).

The *Phragmites* stands can be divided into two groups according to the horizontal pattern of shoot density, resulting in turn from the character and intensity of tillering. The first group comprises stands with shoots forming small primary clusters (about 10 to 20 cm in diameter), reflecting the morphological properties of the species; the secondary clusters are approximately 160 or 80 cm in diameter (Kobylí Lake, type M, Opatovický fishpond, type S, Lion Lake, Nesyt fishpond). The other group comprises stands with primary clusters of the same size, but the secondary clusters are about 3.2 m in diameter (Kobylí Lake, type V; Opatovický fishpond, type V; Šakvický fishpond; Rožmberk fishpond). The S-type *Phragmites* stands at the Opatovický fishpond and the M-type stand at the Kobylí Lake contained even larger clusters of about 6.4 in diameter. In the relatively young *Phragmites* stands at the Kobylí Lake, the clusters (both 1.6 and 3.2 m in diameter) were obviously more conspicuous as these sources of heterogeneity were more

Kobylí M 22. 10. 1968			Rožmberk 20. 11. 1968			Opatovický V 11. 10. 1969			Nesyt 19. 11. 1969			Opatovický S 14. 10. 1969		
$\bar{x}$	$s\bar{x}$	$V(\%)$	$\bar{x}$	$s\bar{x}$	$V(\%)$	$\bar{x}$	$s\bar{x}$	$V(\%)$	$\bar{x}$	$s\bar{x}$	$V(\%)$	$\bar{x}$	$s\bar{x}$	$V(\%)$
92.6	7.4	25.4	135.2	8.1	18.9	73.4	4.4	18.9	76.4	3.2	13.2	71.8	5.1	22.6
1039	160	34.5	867	70	18.1	1199	94	24.8	1242	89	22.7	779	75	30.4
45.6	4.8	23.5	61.6	8.2	29.7	88.4	14.4	36.3	48.8	8.6	39.4	86.0	16.2	37.7
1.62	0.05	35.2	1.30	0.03	31.2	1.32	0.03	33.2	2.09	0.07	37.9	1.74	0.05	35.3
2495	208	16.7	2249	205	20.4	4789	161	7.5	3753	422	22.5	4496	393	17.5
236	51	43.5	1131	192	37.9	1119	124	19.3	1345	256	38.0	—	—	—
1064	141	29.5	918	129	31.5	84	16	41.1	1374	21	3.5	3605	457	25.3
3569	378	21.2	3166	317	22.4	4873	165	7.6	5128	429	16.7	8101	413	10.2
2.40	—	—	2.59	—	—	3.99	—	—	3.02	—	—	5.49	—	—
1.02	—	—	1.06	—	—	0.07	—	—	1.11	—	—	4.40	—	—
3.42	—	—	3.65	—	—	4.06	—	—	4.13	—	—	9.89	—	—
—	—	—	—	—	—	—	—	—	940	—	—	—	—	—

important in these young stands than in the others, which were older (Fig. 6). Average above-ground biomass varied from 779 g/m^2 (Opatovický fishpond type S) to 1855 g/m^2 (Lion Lake — Tab. 5, all the shoot biomass were assessed in autumn).

The penetration of *Phragmites* rhizomes into the deeper layers of various substrates and the vertical distribution of the rhizomes in the profile wall (i.e., numbers of rhizome sections encountered in a soil profile wall 1 m wide) are shown in Fig. 7. The *Phragmites* rhizomes grew, probably irrespective of the character of the substrate, mostly to the depth of 50 to 70 cm below the bottom surface; in the stands of the Rožmberk fishpond, to the depth of only 40 to 50 cm. They reached to the greatest depth in the V-type stand at the Opatovický fishpond (maximum depth 70 to 80 cm) and in the stands of the Lion Lake (90 to 100 cm). Most rhizomes were usually recorded in the 10 to 30 cm layer in most stands. The number of rhizomes in this layer usually varied between 20 to 30 (the width of the wall being 1 m). In a deeper layer (30 to 50 cm), the greatest number of rhizomes was found only in the V-type *Phragmites* stand at the Opatovický fishpond and at the Lion Lake. In the latter case, 8 rhizomes were present in this layer on the average, while 38 rhizomes were present in the V-type *Phragmites* at the Opatovický fishpond, which is the absolutely highest average value recorded.

The average total number of rhizomes present in the 1 m wide profile wall varied from 24.4 (Lion Lake) to 88.4 (Opatovický fishpond type V — see Tab. 5 and Fig. 8). A negative correlation apparently exists between the number of rhizomes in the profile wall and their diameter (Fig. 9). The average rhizome diameters were smallest — 1.30 and 1.32, respectively, in the stands at the Rožmberk fishpond and of the V-type at the Opatovický fishpond, with the greatest numbers of rhizomes found in the profile wall; the average rhizome diameter was the largest of all, 2.45 cm (Fig. 8), in the stand at the Lion Lake, with a small number of rhizomes.

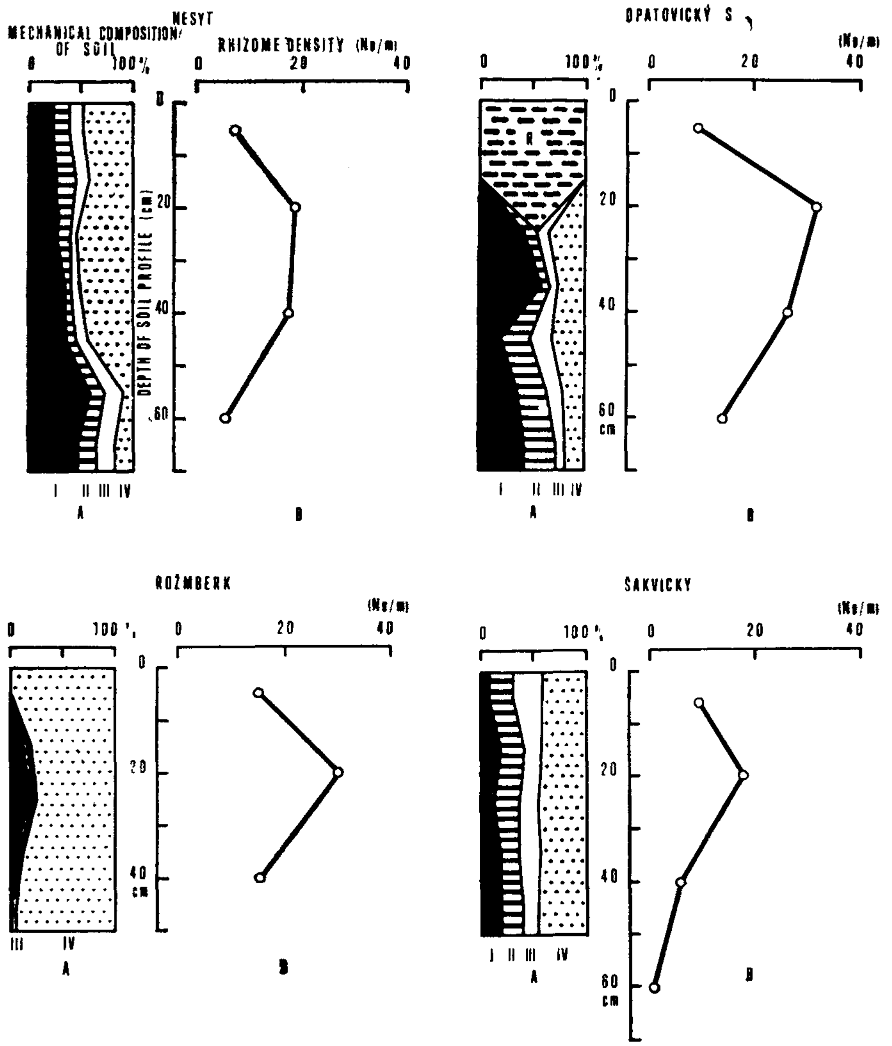
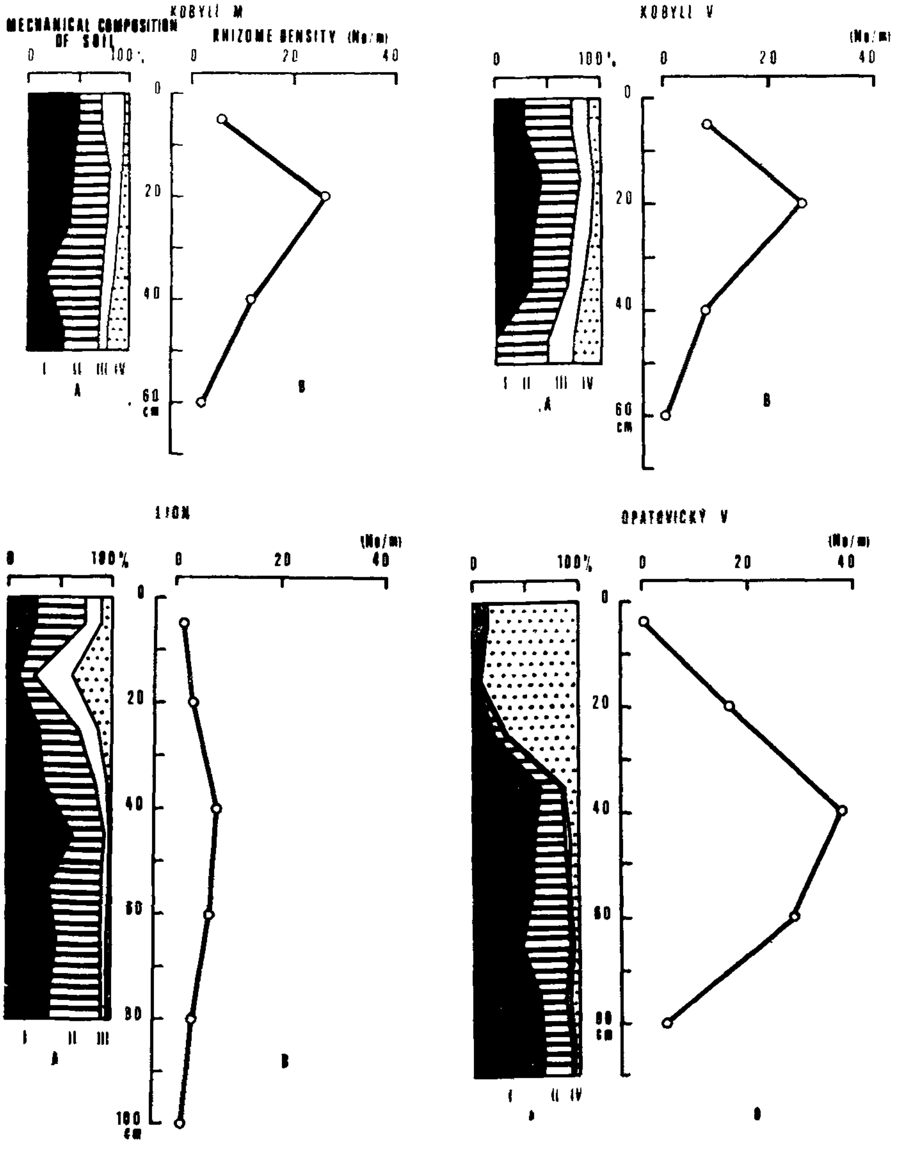


Fig. 7. Distribution of the rhizomes of *Phragmites communis* into the substrate in 8 stands. — (A) Mechanical composition of soil in various layers of the soil profile (according to Kopecký; in % of various categories according to grain size: I upto 0.01 mm, II 0.01—0.05 mm, III 0.05 to

The biomass of the *Phragmites* rhizomes and roots is given in Fig. 8. Rhizome biomass varied widely in the *Phragmites* stands from about 2 kg/m^2 (Kobylí Lake type V) to almost 5 kg/m^2 (Opatovický fishpond type V). A close relation exists



0.1 mm, IV 0.1—2.0 mm, R — organic particles). — (B) Vertical distribution of average rhizome density in a profile wall 1 m in width.

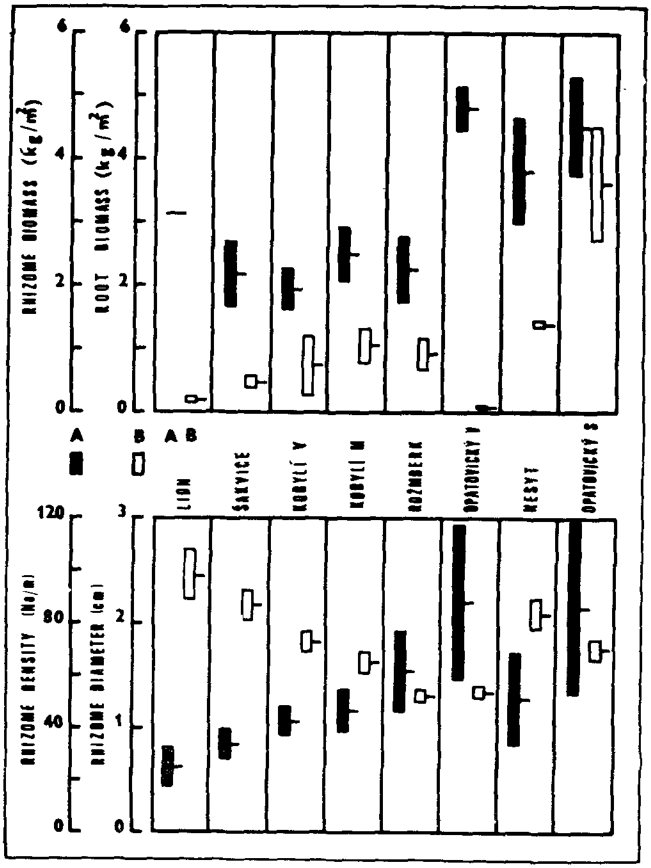


Fig. 8. Root and rhizome biomass (in kg/m²), total rhizome density in the profile wall 1 m in width, and the rhizome diameters (in cm) in 8 stands of *Phragmites communis* studied. The vertical bars indicate ± two standard errors.

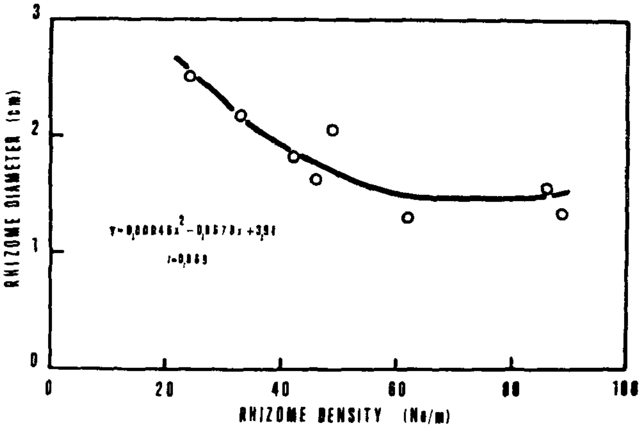


Fig. 9. Correlation between the total number of rhizomes in the profile wall 1 m width (rhizome density) and rhizome diameter of *Phragmites communis*.

between the number of rhizomes in the profile wall (in the 30 to 70 cm layer) and the total biomass of *Phragmites* rhizomes (Fig. 10). The increasing number of rhizomes in this layer (up to 50 to 60 rhizomes) is accompanied by an increase in rhizome biomass. Beyond this number of rhizomes, their biomass does not increase any more.

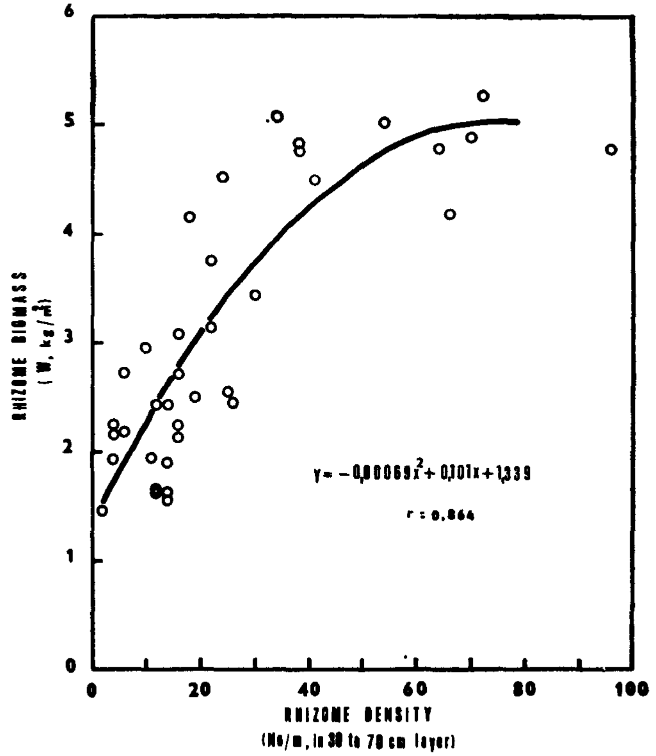


Fig. 10. Correlation between number of rhizomes (rhizome density in the 30 to 50 cm layer of the profile wall 1 m in width) and rhizome biomass of *Phragmites communis* (in kg/m²).

The dry weight of dead *Phragmites* rhizomes varied about 1 kg/m² in most cases (Tab. 5). The smallest number of dead rhizomes was found in *Phragmites* stands at the Kobylí Lake: only 143.5 g/m² in the V-type and 236.2 g/m² in the M-type on the average. This was probably due to the young age of these stands.

The dry weight of the *Phragmites* roots (in the 0 to 20 cm layer) varied within a much wider range than the rhizome biomass (Fig. 8). The lowest average values were recorded in the V-type stand at the Opatovický fishpond and at the Lion Lake (84.4 g/m² and 192.7 g/m², respectively). In four stands, the root biomass was about 1 kg/m²; only in the S-type stand of the Opatovický fishpond did it reach the extreme value of 3.6 kg/m².

The total biomass of the underground organs (rhizomes and roots) was about 8 kg/m² in the S-type *Phragmites* stand at the Opatovický fishpond; in the V-type and in the Nesyt fishpond it varied about 5 kg/m², and in the remaining stands about 3 kg/m² (Tab. 5).

The values of the rhizomes/shoot dry weight ratio were highly variable — approximately from 1.5 to 5.5 (Fig. 11, Tab. 5, all ratios were calculated from the autumn shoot biomass). In eutrophic habitats, in the limosal to terrestrial ecophases (HEJNÝ 1957, 1960) in late summer, this ratio was the smallest of all (Šakvický fishpond — 1.54, Lion Lake — 1.70). In habitats with a relatively well-balanced hydrological regime during the growing season, this ratio surpassed 3.0 (Nesyt fishpond — 3.02, Opatovický fishpond, type V — 3.99, Opatovický, type S — 5.49).

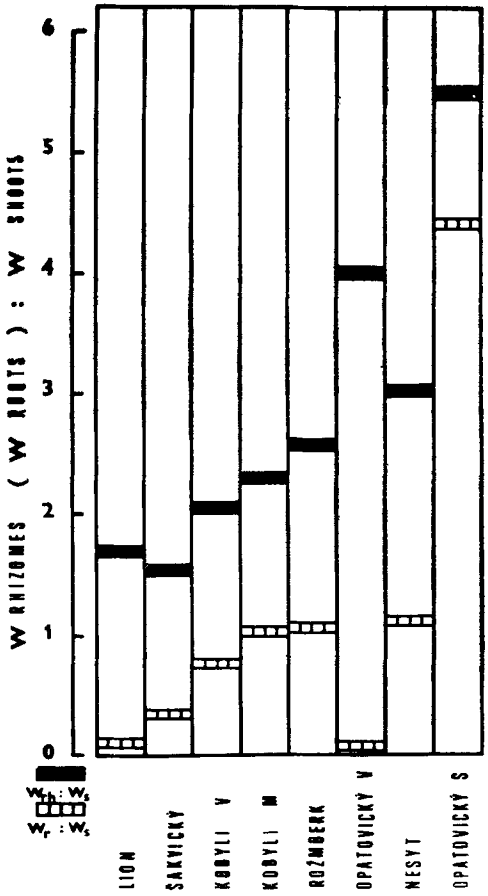


Fig. 11. Ratio between rhizome dry weight (*Wrh*) or root dry weight (*Wr*) and shoot dry weight (*Ws*) in 8 stands of *Phragmites communis*.

The ratio between root dry weight (in the 0 to 20 cm layer) and above-ground dry weight of *Phragmites* varied from very low values of approximately 0.1 (Lion Lake, Opatovický fishpond, type V) up to 4.4 (Opatovický fishpond, type S), (Fig. 11, Tab. 5).

The ratio of total underground dry weight to above-ground biomass of *Phragmites* reached values of 1.9 and 1.8 at the Šakvický fishpond and Lion Lake, respectively. At the Opatovický fishpond, S-type, the dry weight of underground organs was obviously ten times as high as the biomass of above-ground parts (Tab. 5). In the other stands, the ratio varied between 2.86 (Kobylí Lake, type V) and 4.13 (Nesyt fishpond).

The habitat, above all the nutrient supply and the water regime and temperature, appears to influence the growth and production of underground organs of *Phragmites* in a highly complex way. It is perhaps the total nitrogen content in the soil (0 to 20 cm layer) that is correlated with the underground biomass of *Phragmites* most closely of all factors examined. This relationship was obviously positive with respect to both the rhizome biomass (regression coefficient $r = 0.787$) and to the dry weight of *Phragmites* roots ($r = 0.884$). The *Phragmites* stands of the Opatovický fishpond, V-type, with a large rhizome biomass and small nitrogen content in the soil, were the only exception; in this case, however, the fishpond water is polluted with waste-water from a nearby pig-farm. A positive correlation was also established between total carbon content in the soil and root dry weight ($r = 0.889$).

DISCUSSION

Seasonal changes in the growth of underground organs

The following stages can be considered as basic components of the seasonal growth cycle of *Phragmites* underground organs: growth of new roots and rhizomes, the accumulation of reserve material in rhizomes and roots and exploitation of these reserves, dying-off of old undeground organs and their subsequent decomposition.

As far as the seasonal changes of rhizome growth are concerned, Troughton (1957) summarizes the observations of several authors as follows: "There seem to be few common features between the accounts of the seasonal cycle of rhizome growth." (l.c.: 34). Nevertheless, the intense growth of *Phragmites* rhizomes in summer (a period with the most favourable climatic factors, above all radiation input and temperature), when the leaf area index reaches its largest values and the above-ground biomass is almost maximum (Květ et al. 1969, Dykyjová et al. 1970, Květ et Svoboda 1970, Husák 1971, Van der Valk et Bliss 1971, Květ 1971) is paralelled by the highest rate of rhizome growth in other plants as well (Iwaki et al. 1969, Kimura 1970a, Fiala 1970a, 1971a, 1971b, Bernard 1974).

The intense growth of *Phragmites* roots recorded in spring and autumn corresponds to the data describing root growth of terrestrial plants (e.g., Stuckey 1941, Kotańska 1967, 1970, 1973, Pilát 1969, Kimura 1970a, Nilsson 1970, Troughton 1970, Speidel et Weiss 1971, 1972, Druzina et al. 1973, Titljanova et Šatochina 1974). Among helophytes, the lowest summer values and the highest spring or autumn values of underground biomass were recorded in *Glyceria maxima* (Hartm.) Holmb. by Westlake (1966), in *Equisetum fluviatile* (L.) em. Ehrh. by Niemi et Kansanen (1973), and in *Carex rostrata* Stokes and *C. lacustris* by Bernard (1974) and Bernard et MacDonald (1974). Summer is the period of intense decomposition of dead roots (cf. Titljanova et Šatochina 1974); and this results in a decrease in the total weight of underground organs. Hoffmann (1972) reports that the most intense root development occurs in many tree species in May to September and remarks: ,,Die widersprechenden Ergebnisse über die sommerliche Ruheperiode sind wahrscheinlich durch methodische Fehler und durch die Ausserachtlassung von Witterungseinflüssen bedingt". ("The contradictory results concerning the summer period of rest are probably due to faulty methods and to insufficient respect paid to the influence of weather." l.c.: 314). In *Phragmites* root growth is probably restricted by intense growth of new rhizomes and by accumulation of reserve material in both new and old rhizomes.

during July and August. A similar dependence was found in *Typha angustifolia* L. and *T. latifolia* L. (FIALA 1971b, 1973d).

The age of the *Phragmites* rhizomes and roots and, above all, their dying-off and decomposition receive less attention here than they deserve; they are discussed only in part in the following paragraph (p. 248). This represents the greatest gap in the present study.

As in many other plants, the accumulation of reserve material occurs in *Phragmites* rhizomes mainly at the end of the growing season (WOODS et al. 1959, MOONEY et BILLINGS 1960, WEINMANN 1961, SMITH et GROTELUESCHEN 1966, IWAKI et MIDORIKAWA 1968, IWAKI et al. 1969, KIMURA 1970a, SPEIDEL et WEISS 1971, 1972, STEWART et BANNISTER 1973). A course of changes in the carbohydrate content in *Phragmites* rhizomes similar to that described here was recorded by KROTKEVIČ (1966): the highest content of starch was observed in *Phragmites* rhizomes in January (12.5 %), the minimum values were recorded at the beginning of July (1.51 %), while in the autumn months (September, October) an increase was observed. The maximum content of reducing sugars was recorded in September (20.61 %). The content of total carbohydrate, recorded in the rhizomes and shoot bases of *Typha angustifolia* and *T. latifolia* (one-year-old polycormones) in autumn, was two to three times that recorded in the summer months (FIALA 1973b, d). The total carbohydrate content varied in the *Typha angustifolia* and *T. latifolia* rhizomes between 20 to 30 % of dry weight in autumn. The duration of the period during which the reserve material accumulates in the underground organs seems to be determined by climatic factors. ROMAN et al. (1969) report that in the Danube delta the accumulation (in this case of phosphorus), in rhizomes of *Phragmites* takes place in September and often also October and November. In Central Europe, the photosynthetic activity of *Phragmites* suffers a conspicuous decrease at the end of September (BURIAN 1969, 1971); the accumulation of reserve material in underground organs comes to an end as well. In the *Typha* species, accumulation of reserve material apparently takes place later (mostly in September and October) than it does in *Phragmites* (FIALA 1973b, d). The difference between the highest autumn bulk density of *Typha* rhizomes and that ascertained in these rhizomes in the subsequent spring, after reserve material had been used for the growth of above-ground shoots, corresponded to about 40 % loss in *Typha latifolia* and 60 % in *Typha angustifolia*. These differences are relatively higner than those reported in young *Phragmites* rhizomes. The increase in the bulk density of "old" *Phragmites* rhizomes, occuring during late May and June (with the content of hydrolyzable carbohydrates remaining unchanged) shows that the formation of mechanical tissues probably precedes the accumulation of reserve material in one-year-old rhizomes.

The growth of *Phragmites* roots both in early spring and in autumn, and obviously also the formation of hibernating buds, probably draw on the reserve material accumulated in rhizomes (Figs. 2 and 4). The autumnal loss of the reserve material deposited in the underground organs and shoot bases of other plants is explained in this way by WEINMANN (1948), TROUGHTON (1951), MUTOH et al. (1968) and KIMURA (1970a).

Intense root growth in early spring (prior to the most rapid growth of the above-ground organs) has already been reported by STUCKEY (1941), TROUGHTON (1957), HOFFMANN (1972), and others.

The rapid initial growth of *Phragmites* in spring, making use of the relatively large amounts of reserve material accumulated in the underground organs in autumn, is reflected in the relatively high *RGR*, *RDP* and other growth characteristics at the beginning of the growing season (KVĚT et al. 1969, KVĚT et SVOBODA 1970, DYKYJOVÁ et al. 1970, KVĚT 1971, VAN DER VALK et BLISS 1971, HUSÁK 1971). This rapid growth of the above-ground parts leads to an almost complete formation of the vertical structure of the aerial stand parts as early as June (HÜRLIMANN 1951, NEUHÄUSL 1965, RUDESCU et al. 1965, HASLAM 1969b, c, KVĚT et al. 1969, ŠECHOV 1969, KVĚT et SVOBODA 1970, GEISSLHOFER et BURIAN 1970). This is one of the important features enabling *Phragmites* to compete successfully with other plants (BUTTERY et al. 1965, FIALA et KVĚT 1971, FIALA 1974).

Underground biomass in various habitats

A considerable variation in the morphological structure, characteristic of *Phragmites communis* is due — in addition to genotypical differences — to its very wide ecological amplitude (MATYUK 1960, CONERT 1961, BJÖRK 1967, RUDESCU 1969, GEISSLHOFER et BURIAN 1970, DYKYJOVÁ 1969, 1970, 1971a, VAN DER TOORN 1971, 1972, HASLAM 1973, HRADECKÁ 1973a, b, PAZOURKOVÁ 1973, SVOBODA, HRADECKÁ et KVĚT unpublished). The differences in the morphological characteristics of *Phragmites* are reflected in the biomass both above — and underground and most probably also in the different distribution of dry matter in various organs. While the above-ground dry weight of *Phragmites* usually varies only within the limits of 0.8 kg/m^2 to 2.5 kg/m^2 (GORHAM et PEARSALL 1956, STRAŠKRABA 1963, TOTH et al. 1963, BERNATOWICZ et RADZIEJ 1964, DEMIDOVSKAYA et al. 1964, KENIG 1964, ISAMBAJEV 1964a, BERNATOWICZ et PIECZYŃSKA 1965, RUDESCU et al. 1965, KOWALCZEWSKI et WASILEWSKI 1966, KROTKEVIČ 1966, BERNATOWICZ et al. 1968, BERNATOWICZ 1969, KVĚT et al. 1969, RUDESCU 1969, DYKYJOVÁ et al. 1970, DYKYJOVÁ et KVĚT 1970, KVĚT et SVOBODA 1970, DYKYJOVÁ 1971a, b, BELAVSKAJA 1971, BURIAN 1971, HUSÁK 1971, KAUL 1971, KVĚT 1971, VAN DER VALK et BLISS 1971, DYKYJOVÁ 1973, KVĚT 1973a, KVĚT et ONDOK 1973, ONDOK 1973, WALLENTINUS et al. 1973), the underground biomass (formed in the course of several years) apparently reflects differences between habitat characteristics much more distinctly (KRASOVSKIJ 1962, ISAMBAJEV 1964b, RUDESCU et al. 1965, FIALA et al. 1968, DYKYJOVÁ et KVĚT 1970, FIALA 1970a, SCHIERUP 1970, DYKYJOVÁ 1971a, FIALA et KVĚT 1971, HUSÁK 1971, FIALA 1973b, c). For instance, relatively low underground biomass values of *Phragmites* (1.98 to 2.94 kg/m^2) have been reported from the area of the Syr-Darja (ISAMBAJEV 1964b) while from Denmark SCHIERUP (1970) reports values of 7.47 to 12.23 kg/m^2, of which roots formed 5.42 to 9.59 kg/m^2.

KRASOVSKIJ (1962) suggested that with taller shoots, a deeper layer will be occupied by plagiotrophic rhizomes and the rhizome biomass will be greater. This assumption, however, does not apply everywhere. For example, in the littoral stand in the Opatovický fishpond, V-type, with large rhizome biomass, the shoots were only about 2.7 m high while the rhizomes reached to the depth of 80 cm. At the Šakvický fishpond, on the other hand, the shoots were up to about 4.5 m high and the rhizomes, whose biomass was relatively small, were found in the 70 cm layer. Neither do observations of MATJUK (1960), ISAMBAJEV (1964b), BJÖRK (1967), van der TOORN (1972) and KVĚT et HUSÁK (unpublished) support the existence of the above-mentioned relationship between shoot height, depth of rhizome penetration and rhizome biomass.

The habitat characteristics (above all the temperature regime which is often determined by the hydrological regime in littoral stands) apparently influence the rate of storage of reserve materials in the underground organs (McNAUGHTON 1966, DAVIDSON 1969c, ROBSON 1973). In the youngest vertical rhizomes (bearing terminal buds) at the Šakvický fishpond (in limosal to terrestrial ecophase in late summer) the total carbohydrate content was relatively less than at the Nesyt fishpond, N. shore, (39.1 % of dry weight as compared with 53.8 %). *Phragmites* apparently grows in relatively more favourable trophic and temperature conditions at the Nesyt fishpond, where the hydrological regime is more balanced. At the end of the growing season, the lower temperatures of water and soil at Nesyt probably favour a more rapid accumulation of reserve material and reduce the respiratory losses (McNAUGHTONN 1966, KIMURA 1970b).

The content of reserve material in the underground organs probably affects the intensity of tillering (AUDA et al. 1966, FIALA 1973c, ROBSON 1973). Water defficiency in the soil reduces the final number of shoots in a stand (NIKOLAEVSKIJ et al 1966, BROWN et BLASSER 1970). In a given habitat, the following factors determine the horizontal stand structure: character of rhizome branching, rhizome length (which usually corresponds with their average annual increment), and the intensity of tillering (PHILLIPS 1954, KERSHAW 1959, FIALA 1971a). The horizontal structure of *Phragmites* stands is apparently related to their biomass both above and underground (ONDOK 1970, 1971, FIALA 1970a, 1973b, c). In *Phragmites* stands with extensive rhizome systems and a relatively low intensity of tillering, in which the shoots form only inconspicuous, small primary clusters (about 0.1 to 0.2 m in diameter) and large secondary clusters (about 3 m in diameter), the rhizome biomass is relatively less than in stands characterized by conspicuous smaller secondary clusters (about 1.6 in diameter and smaller; see Figs. 6, 8 and 12).

The character of the rhizome system is apparently reflected in the number of rhizomes encountered in the profile wall and in their vertical distribution. The *Phragmites* stands from the

Šakvický and Nesyt fishponds can again serve as example. At the Šakvický fishpond, lateral shoots grew only from several nodes of the oldest vertical rhizome (at the maximum soil depth of about 20 to 30 cm), while at the Nesyt fishpond, they grew from a greater depth, often as much as 40 to 50 cm (see Fig. 12). These data may perhaps explain the close correlation between the number of rhizomes in the soil profile wall (in the 30 to 70 cm layer) and the rhizome biomass of *Phragmites* (Fiala 1973b, c).

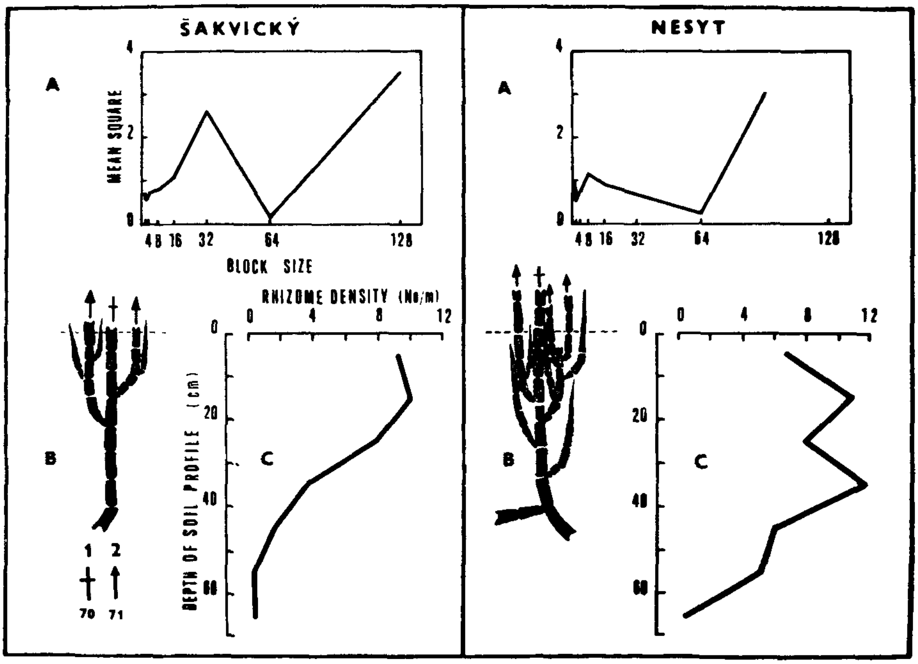


Fig. 12. Comparison of shoot pattern and its intensity (A, for details see text) with the character of tillering (B, 1 — dead terminal aerial shoot from the previous year, 2 — living lateral shoot growing during the current year and recorded at the end of the growing season) and with the vertical variation in rhizome density (the number of rhizomes in different layers of the profile wall 1 m in width, C) in the *Phragmites communis* stand at the Šakvický and Nesyt fihsponds.

The considerable variation in the ratios of rhizome: shoot biomass and root: shoot biomass apparently reflects great differences between habitats. All the values of the total underground to above-ground biomass ratio (*R*/*S* ratio) would most probably be smaller if shoot biomass were assessed in summer. Nevertheless, they display relative differences between the eight stands studied (Fig. 11, Tab. 5). The great differences in the *R*/*S* ratio in *Phragmites* prove that the underground biomass of *Phragmites* cannot be estimated from the above-ground biomass by applying a fixed *R*/*S* ratio (see Szczepański 1969). Many literature data suggest that an increased concentration of mineral elements in soil or water brings about a decrease in the *R*/*S* ratio (e.g., Brouwer 1966, Troughton 1967, 1970, Davidson 1969b, Schuurman 1971). In *Typha latifolia*, this effect was demonstrated by Boyd (1971). Hürlimann (1951) drew attention to the increase in the relative weight of *Phragmites* underground organs due to nitrogen deficiency. On the other hand, Boyd et Hess (1970) and van der Toorn (1972) found a positive correlation between the growth and production of *Typha latifolia* and *Phragmites*, and the phosphorus content in the soil. Krotkevič (1966) recorded an increase only in above-ground production in *Phragmites* on sites fertilized with both nitrogen and phosphorus. DAVIDSON (1969b) draws attention to the fact that the relationship between the moisture, nitrogen and phosphorus contents in the soil and the *R/S* ratio is rather complicated. This is also supported by the present suggestion of a positive correlation between the nitrogen content in the soil and the biomass of *Phragmites* rhizomes and roots, which differs from the information supplied by other authors (see above).

Root biomass and the organic matter content in the soil are apparently closely correlated (DAHLMAN et KUCERA 1965); this is also supported by the present results concerning *Phragmites*.

With increasing temperature, the biomass of underground organs and the *R/S* ratio decrease (BROUWER 1966, MCNAUGHTON 1966, DAVIDSON 1969a, SIMS et SINGH 1971, TURNER 1972). From various habitat factors exerting complex influence on the growth and production of underground organs in *Phragmites*, the temperature regime of the site (also determined by hydrological regime) was perhaps most closely related to the *R/S* ratio (see Fig. 13).

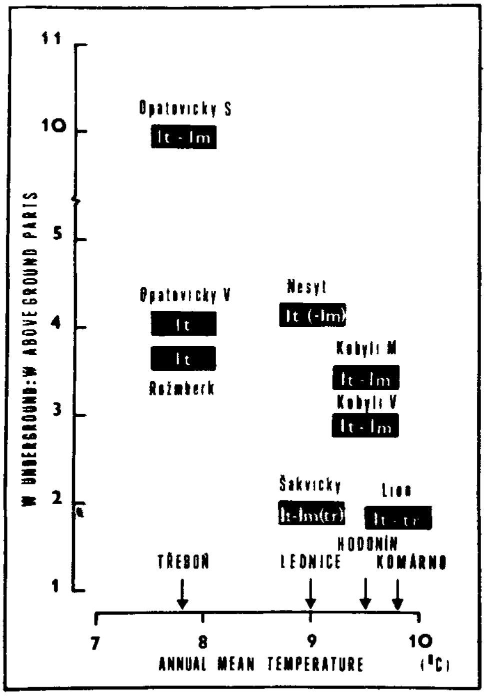


Fig. 13. Relationship between the annual mean air temperature (in °C from the period 1901 to 1950 according to the Institute of Hydrometeorology in Prague), hydrological regime of the stand during the growing season (lt — littoral ecophase, lm — limosal ecophase, tr — terrestrial ecophase) and the ratio of underground to above-ground dry weight in 8 stands of *Phragmites communis* studied.

WESTKAKE (1968), summarizing several authors' observations including his own, suggests that the share of underground organs in the total *Phragmites* biomass represents 36 % to 60 % (to 90 %) in late summer. It is the widest range of all helophytes. A similar range was found only in *Schoenoplectus lacustris* (L.) PALLA (46 % to 90 %); the highest values found in *Typha* sp. were about 60 % (WESTLAKE 1968). The underground biomass in the *Phragmites* stands dealt with in this paper varied between 65 % to 90 % of total biomass. These figures thus belong to the higher figures within the range mentioned above.

Estimation of net production of underground organs

The net production (= annual increment of biomass) in *Phragmites* rhizomes and roots cannot be calculated from the difference between their minimum (e.g., spring value after exploitation of reserve material) and maximum biomass recorded later on (see WEAVER et ZINK 1946, DAHLMAN et KUCERA 1965, KOTAŃSKA 1967, 1973, IWAKI et MIDORIKAWA 1968). The calculation is complicated, above all by considerable variation of the field estimates (FIALA et al. 1968), by slow spreading of the polycormones when cultivated (ORECHOVSKIJ 1969) and by the relatively long survival time of the *Phragmites* rhizomes. According to literature data (HÜRLIMANN 1951, WESTLAKE 1965, 1968, HASLAM 1970a), *Phragmites* rhizomes live for (2) 3 to 6 years. The observations described in this paper have revealed that *Phragmites* rhizomes live mostly for 4 years in the stands of the Šakvický and Nesyt fishponds. A critical period for the growth of underground organs, and especially for the formation of new rhizomes and lateral shoots, appears to be the fourth growing season of the thickest vertical rhizome, which bears the terminal aerial shoot (see Fig. 14 for the *Phragmites* stand at the Nesyt fishpond). A conspicuous decrease in bulk density and in carbohydrate content in these rhizomes recorded at the end of the fourth growing season is an indicator of considerable exploitation of reserve material in the spring of that season and of its poor accumulation in the autumn. At the end of the vertical rhizome's third growing season, numerous hibernating buds (lateral shoots for the next year, see Fig. 15) grow from the terminal and old lateral shoots. The lateral shoots from the

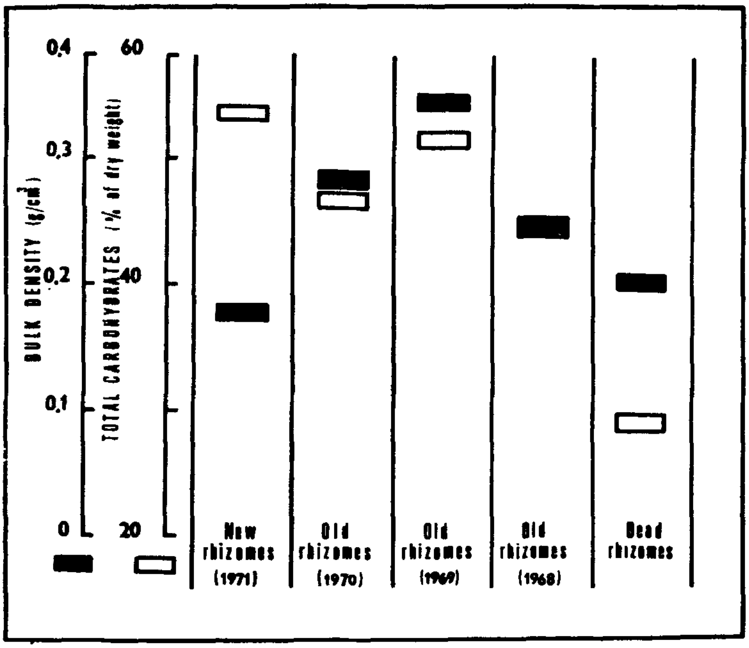


Fig. 14. Bulk density and total carbohydrate content in *Phragmites communis* rhizomes of various age. Recorded at the N. shore of the Nesyt fishpond in October 1971.

fourth (or even fifth) growing season are much thinner and shorter' than both the terminal shoot and the lateral shoots from preceding years (see also Kaikko 1934, Krasovskij 1962, Orechovskij 1969, Haslam 1969a, 1970). The irradiance of these shorter shoots is rather poor, and they often die off; hence the density of *Phragmites* stands usually decreases during the second half of the growing season (Květ et al. 1969, Květ 1971). At the end of the fourth growing season only few lateral buds are formed for the fifth growing season and *Phragmites* rhizomes probably die off at the Nesyt fishpond during the fifth growing season.

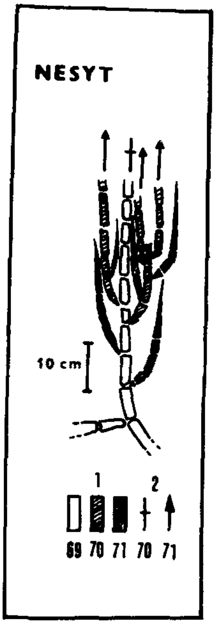


Fig. 15. Character of tillering in the stand of *Phragmites communis* at the N. shore of the Nesyt fishpond. Recorded in October 1971 — 1. Living rhizomes: two-year old rhizomes formed in the year 1969 (69), one-year old rhizomes formed in the year 1970 (70), newly formed rhizomes with hibernating buds (71); — 2. above-ground shoots: dead terminal shoot (70), lateral living shoots growing during the year 1971 (71).

A similar dependence on carbohydrate content was reported for *Convallaria majalis* L. rhizomes of different age by Ljubarskij (1967); the carbohydrate content in the rhizomes regularly decreased, on the average, from 50.9 % in the youngest rhizomes to 15.2 % in oldest living rhizomes, about 10 years old.

The annual net production of rhizome biomass can be approximated if the total biomass of living rhizomes is divided by their age. Schierup (1970) solved this problem in a similar manner. The average annual net production of rhizome biomass would thus be 940 g/m^2 from the *Phragmites* stand at the Nesyt fishpond, and 550 g/m^2 at the Šakvický fishpond. These values represent about 60 % (Nesyt fishpond) and 30 % (Šakvický fishpond) of the maximum above-ground biomass values presented by Květ (1973a) and Dykyjová et Květ (1970).

Estimation of the annual net production of root biomass is still less accurate and more complicated than that of rhizome biomass, for it is very difficult to separate roots into living and dead. The decomposition rate of dead roots apparently differs considerably from stand to stand; this fact was probably one of the reasons explaining the great differences in root dry weight found in the *Phragmites* stands studied. WESTLAKE (1965) suggests that the roots of most helophytes probably live for a period shorter than one year. SCHIERUP (1970) claims a turnover time of five years for *Phragmites* roots. The length of this period will perhaps again differ from site to site, and it would be wrong to use a certain figure as valid for all *Phragmites* stands. For instance, according to data in literature (REMEZOV et al. 1963, DAHLMAN et KUCERA 1965, RAJCHEL 1965, KOTAŃSKA 1967, 1970, 1973, DAHLMAN 1968, PRÉCSÉNYI 1969, NILSSON 1970, KAZMIERCZAKOWA 1971, MIROŠNIČENKO et al. 1972, SPEIDEL et WEISS 1972, DŽALILOVA 1973) the turnover time is two to four years for root biomass in meadow plant communities and the herb layers of forest stands, but TITLJANOVA (1971) and TITLJANOVA et ŠATOCHINA (1974) claim this to be only one year.

Relatively high values of the annual underground production of *Phragmites* are given by SCHIERUP (1970): about 380 g of rhizomes/m^2 (about 40 % of maximum above-ground biomass) and 1200 g of roots/m^2 (about 130 % of maximum above-ground biomass). The annual net production of all *Phragmites* underground organs would thus be about 1500 g/m^2 (with the above-ground biomass of 930 g/m^2). MOOK et VAN DER TOORN (1974) report that the yearly increase in rhizome biomass of *Phragmites* was 182 g/m^2 and 313 g/m^2 (approximately 10 % and 20 % of the yearly increase in shoot biomass) in a wet experimental reed field, and 245 g/m^2 and 509 g/m^2 (20 % and 40 % of yearly increase in shoot biomass) in a dry experimental reed field. These values were obtained from relatively young (4 year-old) stands. BERNARD J. et BERNARD F. (1973), who base their conclusions only on observations of the growth of new rhizomes of *Typha glauca*, estimated the annual production of the underground organs to be 247 g/m^2; this represents approximately 25 % of above-ground production. In two-year old polycormones of *Typha latifolia* and *T. angustifolia* the annual increments in underground biomass represent 40 % and 90 %, respectively, of the above-ground biomass recorded at the end of the growing season (FIALA 1973b, d). DYKYJOVÁ et al. (1971) have reported that the annual net production of underground organs of helophytes in experimental cultivation was equal to 0.5 to 1.2 times their above-ground production.

Production data on *Glyceria aquatica* WAHLB. (WESTLAKE 1966, JAKRLOVÁ 1971) make it possible to estimate its annual underground net production as corresponding with 40 % to 70 % of maximum above-ground biomass. For emergent aquatic macrophytes, VAN DER VALK et BLISS (1971) estimate, on the basis of literature data, the annual net underground production to be 20 % to 40 % of above-ground net production. BERNARD (1974) reports that the annual net underground production of *Carex rostrata* STOKES reaches 25 % of their above-ground production. For *Carex lacustris*, BERNARD et MCDONALD (1974) estimate this to be only 20 %. For several species of the genus *Miscanthus*, which is structurally similar to *Phragmites*, IWAKI et MIDORIKAWA (1968) report the annual increment of underground organs to be 40 % of maximum above-ground biomass. The present values of net production of *Phragmites* rhizomes fall within the limits reported by other authors for helophytes. As opposed to helophytes, in some grassland communities the annual increments of underground biomass are higher: up to 2 to 4 times the above-ground production (NILSSON 1970, KOTAŃSKA 1967, 1973, TITLJANOVA et ŠATOCHINA 1974).

Acknowledgements

The author is grateful to S. HEJNÝ, DrSc., Corresponding Member of the Czechoslovak Academy of Sciences, and to Dr. J. KVĚT, CSc., for valuable suggestions and advice given to him in tackling difficult problems discussed in the present paper.

SUMMARY

Eight stands of *Phragmites communis* were investigated in the littoral zones of fishponds, in marshes, on flooded arable land and in swampy backwaters in six localities in three regions of Czechoslovakia (southern Bohemia, southern Moravia and southern Slovakia). The seasonal changes in the growth of underground organs and seasonal variation in the content of reserve material in these organs were studied in one *Phragmites* stand. The results of the observations are summarized as follows:

1. Intense rhizome growth was recorded in summer (end of June to July) during a period characterized by favourable climatic factors; at that time the leaf area index reaches its highest values and the above-ground biomass is almost at its maximum (Figs. 2 and 4). *Phragmites* roots have evidently two distinct periods of growth. The first occurs in spring (end of April to beginning of May), and the other in autumn, above all in September (Fig. 4).

2. Accumulation of reserve material in the underground organs (especially in rhizomes) is considerable in *Phragmites*. Reserve material was accumulated even in older living rhizomes (Figs. 2, 3). In these rhizomes, the bulk density and total carbohydrate content (in % of fresh weight) recorded at the end of the growing season were twice those recorded after the spring exploitation of reserves (Fig. 3). The total carbohydrate content (in % of dry weight) found in the previous year's *Phragmites* rhizomes in spring was probably 6 % to 12 % higher than that recorded at the end of the growing season, when the rhizomes were about one year old.

3. A conspicuous decrease in bulk density and a decrease in total carbohydrate content were recorded in vertical rhizomes, bearing terminal aerial shoots, at the end of their fourth growing season (*Phragmites* stand at the Nesyt fishpond — Fig. 14). This probably indicates a considerable exploitation of reserve material in the spring of the fourth growing season and its relatively poor subsequent accumulation during that autumn. This situation is apparently critical for further growth of the rhizome and for the formation of new lateral rhizomes and aerial shoots. At the end of the fourth growing season, only few lateral buds are formed, and the rhizomes die off, probably during the fifth growing season.

4. The underground biomass of *Phragmites* (formed in the course of several years) apparently reflects the habitat much better than does the biomass of above-ground organs (Fig. 8). The rhizome biomass of the stands investigated varied within broad limits from about 2 kg/m^2 (Kobylí Lake, type V) to 5 kg/m^2 (Opatovický fishpond, type V). Root dry weight (from the 0 to 20 cm layer) varied from low values (84.4 g/m^2 — Opatovický fishpond, type V; 192.7 g/m^2 — Lion Lake) to a very high value of 3 605.2 g/m^2 (Opatovický fishpond, S type).

5. The special character of the rhizome system in *Phragmites*, determined above all by the character of rhizome branching and the intensity of tillering, is reflected both in the horizontal structure of these stands and in the vertical arrangement of the rhizomes and their biomass (Fig. 12). A close correlation was established between the number of rhizomes in the wall of a soil profile (in the 30 to 70 cm layer) and total rhizome biomass (Fig. 10).

6. The values of the ratio of rhizomes to above-ground dry weight were highly variable (from 1.5 to 5.5 — Fig. 11, Tab. 5). This ratio was lowest in eutrophic stands in the limosal to terrestrial ecophase in late spring (1.54 — Šakvický fishpond; 1.70 — Lion Lake). In stands with a relatively well-balanced hydrological regime during the growing season, the ratio surpassed 3.0 (3.02 — Nesyt fishpond; 3.99 — Opatovický fishpond V type; 5.49 — Opatovický fishpond, S type).

The ratio of root dry weight (from 0 to 20 cm layer) to total above-ground biomass of *Phragmites* was about 1.0 in the stands at the Rožmberk and Nesyt fishponds and at the Kobylí Lake types V and M (Fig. 11, Tab. 5). In the other stands, the ratio varied from very low values of about 0.1 (Opatovický fishpond V type, Lion Lake) to 4.4 (Opatovický fishpond S type).

7. Out of the various habitat factors which exert a considerable and complex influence on the growth and production of underground organs, the temperature regime (also determined by the hydrological regime is probably most closely related to the R/S ratio (Fig. 13).

8. The annual net production of *Phragmites* underground organs will probably be different in different habitats. The estimation of the annual net production of the rhizomes (calculated as the dry weight of living rhizomes divided by their age) was approximately 60 % of the maximum above-ground biomass at the Nesyt fishpond and only about 30 % at the Šakvický fishpond.

ZUSAMMENFASSUNG

Acht Bestände von *Phragmites communis* wurden untersucht. Sie befinden sich in der Litoralzone der bewirtschafteten Teiche, an Sümpfen, auf überflutetem Ackerboden und im sumpfigen Stauwasser an 6 Lokalitäten in 3 Regionen der Tschechoslowakei (Südböhmen, Südmähren und Südslowakei). In einem der Schilfbestände wurden die änderungen im Wuchs der unterirdischen Organe im Laufe einer Vegetationsperiode und die Saisonvariabilität des Inhaltes ihrer Vorratsstoffe studiert. Die Forschungsergebnisse sind nachfolgend zusammengefasst:

1. Intensiver Wuchs der Rhizome wurde im Sommer (Ende Juni, Juli) vermerkt, im Zeitraum mit günstigen Klimafaktoren, wo der Blattflächenindex (*LAI*) am grössten ist und auch die oberirdische Biomasse fast ihr Maximum erreicht. (Abb. 2, 4). Für die Wurzeln von *Phragmites* sind offensichtlich zwei deutliche Wuchsperioden bezeichnend. Die erste im Frühjahr (Ende April bis Anfang Mai), die zweite im Herbst (besonders im September, Abb. 4).

2. Die Speicherung von Reservestoffen in den unterirdischen Organen (vor allem in den Rhizomen) ist bei *Phragmites* ziemlich gross. Die Vorratsstoffe speicherten sich auch in älteren lebendigen Rhizomen (Abb. 2, 3). Die Werte der Volumendichte („bulk density“ Trockengewicht/Volumen der frischen Rhizome) und auch des Gesamtgehalts an Kohlenhydraten (in % Frischgewicht) erreichten auch in den 2—3 Jahre alten Rhizomen am Ende der Vegetationsperiode bis das Zweifache der Werte, die nach dem Abschöpfen der Reserven im Frühjahr vermerkt wurden (Abb. 3). Die Menge der sämtlichen Kohlenhydrate (in % Trockengewicht), die im Frühjahr den alten *Phragmites*-Rhizomen entnommen wurde, war wahrscheinlich um 6—12 % höher als die in die alten Rhizome (ungefähr 1 Jahr alt) zurückgeführte Menge am Ende der Vegetationsperiode.

3. Gegen Ende der vierten Vegetationsperiode vermerkte man einen auffallenden Rückgang der Volumendichtewerte und ebenfalls eine Verminderung des Gesamtgehaltes an Kohlenhydraten in den vertikalen Rhizomen, die die terminalen oberirdischen *Phragmites*-Triebe tragen (Schilfbestand am Teich Nesyt, Abb. 14). Dies dürfte von ziemlich hoher Abschöpfung der Vorratsstoffe im Frühjahr dieser Vegetationsperiode und von ihrer verhältnismässig geringer Speicherung im Herbst zeugen. Eine solche Vegetationsperiode ist offensichtlich für weiteren Wuchs der unterirdischen Organe kritisch, besonders für die Ausbildung neuer Rhizome und Seitentriebe. Ende der vierten Vegetationsperiode wachsen die Seitenknospen für die.fünfte Vegetationsperiode nur selten aus und die Rhizome sterben höchstwahrscheinlich während dieser fünften Periode ab.

4. Die Biomasse der unterirdischen Organe von *Phragmites* (die im Laufe einiger Jahre entstanden ist), widerspiegelt die Unterschiede der Standortsbedingungen viel deutlicher als die oberirdische Biomasse (Abb. 8). Die Rhizomemasse schwankte in den untersuchten Beständen im weiten Bereich zwischen 2 kg/m^2 (Kobylí V) bis 5 kg/m^2 (Opatovický V). Das Trockengewicht der Wurzeln (aus der Schicht von 0—20 cm) bewegte sich von niedrigeren Werten (84,4 g/m^2 — Opatovický V, 192,7 g/m^2 — See Lion) bis 3605,2 g/m^2 (Opatovický S).

5. Der unterschiedliche Charakter der *Phragmites*rhizome-Systeme, der vor allem durch die Art der Rhizomeverzweigung und Bestockungsintensität gegeben ist, widerspiegelt sich sowohl in der horizontalen Struktur dieser Bestände als auch in der vertikalen Anordnung der Rhizome und ihrer Biomasse (Abb. 12). Es wurde eine enge Korrelation zwischen der Anzahl der Rhizome in der Wand der Bodenprofile (in der Schicht 30—70 cm) und der sämtlichen Rhizomebiomasse festgestellt (Abb. 10).

6. Das Verhältnis der Trockengewichtswerte der Rhizome zum Trockengewicht der oberirdischen Teile war sehr veränderlich (von 1,5 bis 5,5; Abb. 11, Tab. 5). An eutrophen Standorten (im Spätsommer in der limosen bis terrestrischen Ökophase) war dieses Verhältnis am geringsten (1,54 — Šakvický Teich, 1,70 — See Lion). In Ökotopen wo die hydrologischen Bedingungen während der Vegetationsperiode verhältnismässig ausgeglichen sind, wurden die Verhältniswerte 3,0 überstiegen (3,02 — Nesyt, 3,99 — Opatovický V, 5,49 — Opatovický S). Das Verhältnis des Trockengewichts der Wurzeln (aus der Schicht 0—20 cm) zum Trockengewicht sämtlicher oberirdischen Teile von *Phragmites* bewegte sich in Beständen am Rožmberk, Nesyt, Kobylí V und Kobylí M um 1,0 (Abb. 11, Tab. 5). In den übrigen Beständen bewegte sich dieses Verhältnis von sehr niedrigen Werten um 0,1 (Opatovický V, Lion) bis zu 4,4 (Opatovický S).

7. Von den einzelnen Faktoren, die ziemlich komplex auf den Wuchs und Produktion der unterirdischen Organe wirken, stand wahrscheinlich das Temperaturregime des Standortes (auch durch hydrologische Verhältnisse bestimmt) im relativ engsten Zusammenhang mit den Werten des Verhältnisses *R*/*S* (Abb. 13).

8. Der Jahreszuwachs der unterirdichen Biomasse von *Phragmites* wird höchstwahrscheinlich an verschiedenen Standorten verschieden sein. Die Netto-Produktion der Rhizome pro Jahr (ermittelt als das Trockengewicht der lebendigen Rhizome dividiert durch ihr Alter) wird ungefähr auf 60 % der maximalen Biomasse der oberirdischen Teile im Schilfbestand am Nesyt und nur auf ungefähr 30 % im Bestand am Šakvický Teich abgeschätzt.

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Received 17 July 1975