GROWTH AND PRODUCTION OF *PHRAGMITES AUSTRALIS* IN LAKE VECHTEN (THE NETHERLANDS)

ELLY P.H. BEST, M. ZIPPIN* AND J.H.A. DASSEN

(Limnological Institute, 'Vijverhof Laboratory', Rijksstraatweg 6, 3631 AC Nieuwersluis, The Netherlands).

INTRODUCTION

Phragmites australis (Cav.) Trin., ex Steudel is a cosmopolitan species. It often constitutes a major component of a littoral vegetation where it grows in almost monospecific stands. From literature it is known that *Phragmites* is one of the most productive aquatic macrophytes of temperate regions (*e.g.* WESTLAKE, 1963; DYKYOVA *et al.*, 1970; MASON and BRYANT, 1975); however, data on its production in the Netherlands are relatively scarce (MOOK and VAN DER TOORN, 1982).

The present study on the production of *Phragmites* in Lake Vechten was done to assess its contribution to the lake's primary production and its nutrient cycles (C, N and P). *Phragmites* predominated the emergent vegetation in this lake for several years. A detailed description of the other emergent, floating-leaved and submerged macrophytes in Lake Vechten is given elsewhere (BEST, 1982). The investigations on production (and also those on decomposition) were part of an integrated study of the whole lake ecosystem, where emphasis was laid on the carbon cycle (BEST *et al.*, 1978).

To study production in this case the multiple harvest method was applied and special attention was paid to the shoot development pattern. The changes in chemical composition of the plants were measured. Distinction was made between aerial and underground organs. All field work was carried out in 1979. The contribution of *Phragmites* to the primary production of the total macrophytic unit of the lake is discussed. The role of *Phragmites* in the nutrient recycling of the lake is assessed mainly in a subsequent paper (BEST *et al.*, 1982).

* present address: State Foundation for Environmental Engineering, Rio de Janeiro, Brazil.

MATERIAL AND METHODS

Mapping.

All macrophytes were mapped regularly. The total areas covered by, respectively, the emergent and floating-leaved plants were outlined in regard to the lake's own coordinates, which were marked by wooden poles along the shoreline. The submerged plants were mapped using SCUBA (BEST, 1981).

Growth and production.

Two different methods for growth analysis were used. (1) Shoot growth. Shoots were tagged at the onset of the growing season (*i.e.* April 1979) and they were subsequently harvested monthly, 3 per harvest. In this way an accurate growth curve is obtained since the effect of differences in age of the plants are avoided. (2) Standing crop. A rectangle of 0.1 m^2 was harvested in duplicate from the centre of the aquatic vegetation, using a scoop. The underground organs were sampled until a depth of 20 cm within the sediment. In this way originally about 10 - 20 % of the underground organs was lost, mainly roots. However, due to high water levels sampling of the root systems was less accurate in the second half of the year.

The plant material was freed from adherent soil and periphyton, and it was divided into shoots, underground organs and litter.

Production calculations.

The relative growth rates of the tagged shoots and those of the aerial and underground organs of the standing crop samples were calculated using the formula:

$$RGR = \frac{1}{t} \ln \frac{W_{t+1}}{W_t}$$

(RGR = relative growth rate; t = time in days; W_{t+1} = organic weight on time $t+1$; W_t = organic weight on time t).

Chemical composition.

The plant material was dried in an oven at 70°C, until constant weight. Subsequently, it was ground into a fine powder with liquid nitrogen in a IKA mill (Janke and Kunkel). Ash was determined at 450°C. C and N were measured using a HCN analyzer (Perkin Elmer, model 240) and P was determined according to a modified molybdate method (GOLTERMAN, 1970).

RESULTS AND DISCUSSION

Mapping.

The littoral region of Lake Vechten, The Netherlands, comprised 16.1 % of the total lake area in 1979 (Fig.1). The occupation by macrophytes was taken as criterion for defining the littoral region. *Phragmites* covered then only a small part of this lake area, *i.e.* 1.6 %, representing 758 m^2. Data on the morphometry and physicochemical characteristics of the lake have been published recently (STEENBERGEN and VERDOUW, 1982; VERDOUW and DEKKERS, 1982).

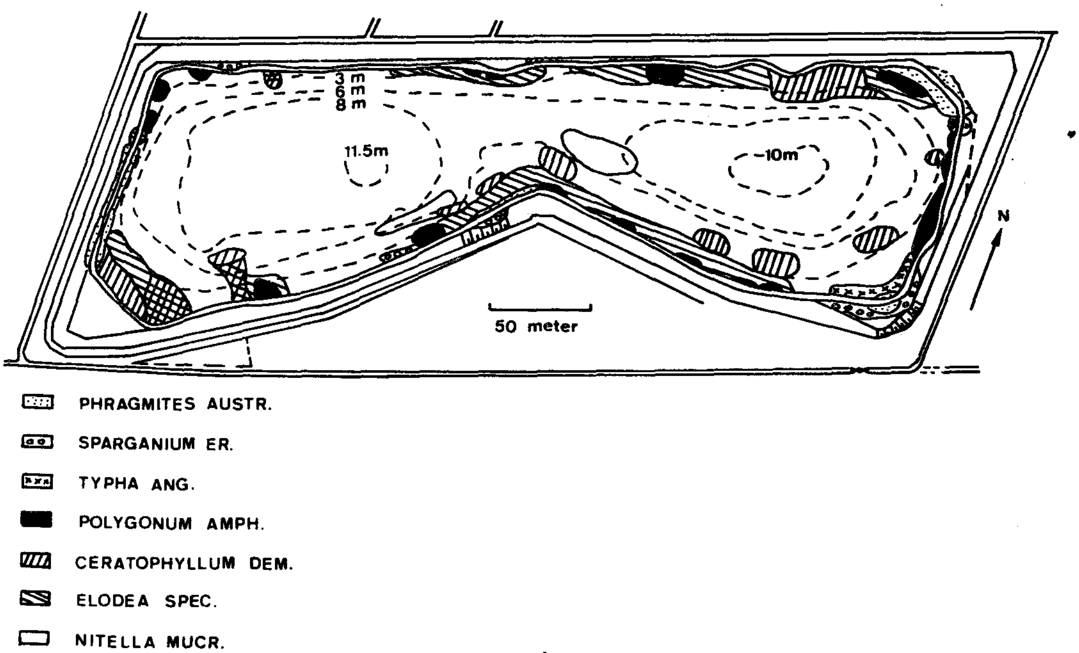

Fig.1. Distribution of the predominant macrophytic species in Lake Vechten, The Netherlands, during 1979. The emergent plants are represented by *Phragmites australis, Sparganium erectum, Typha angustifolia*, the floating-leaved plants by *Polygonum amphibium*, and the submerged ones by *Ceratophyllum demersum, Elodea* sp. and *Nitella mucronata.*

In the area occupied by *Phragmites* two zones were distinguished on basis of plant morphology and biomass characteristics, *viz.* a terrestrial zone, which was only occasionally flooded by lake water, and an aquatic zone. The former showed less dense plant growth than the latter (DYKYOVA, 1971; MOCKNACKA-LAWACZ, 1974). The terrestrial and aquatic zones covered 58.2 and 41.8 %, respectively, of the area occupied by reed.

Biomass and growth.

In Fig.2 the seasonal changes in biomass of *Phragmites* are depicted. The shoot weight increased greatly during summer and reached its maximum at the end of August, being 1247 g ash-free dr.wt.m^{-2}. In the same period the highest root biomass was measured, being 286 g ash-free dr.wt.m^{-2}. The relatively high value found at the beginning of the season was probably due to selective sampling. The shoot:root ratio was almost always > 1.0 (only the first, probably faulty, value was < 1) indicating permanently higher shoot than root biomass (Table I). At the end of the season still fairly high values were measured which were not affected in quantitative respect by sloughed plant parts. According to DYKYOVA *et al.* (1971) a shoot:root ratio > 1 is normal for 1 - 2 years old reed plants; lower values occur in old plants only.

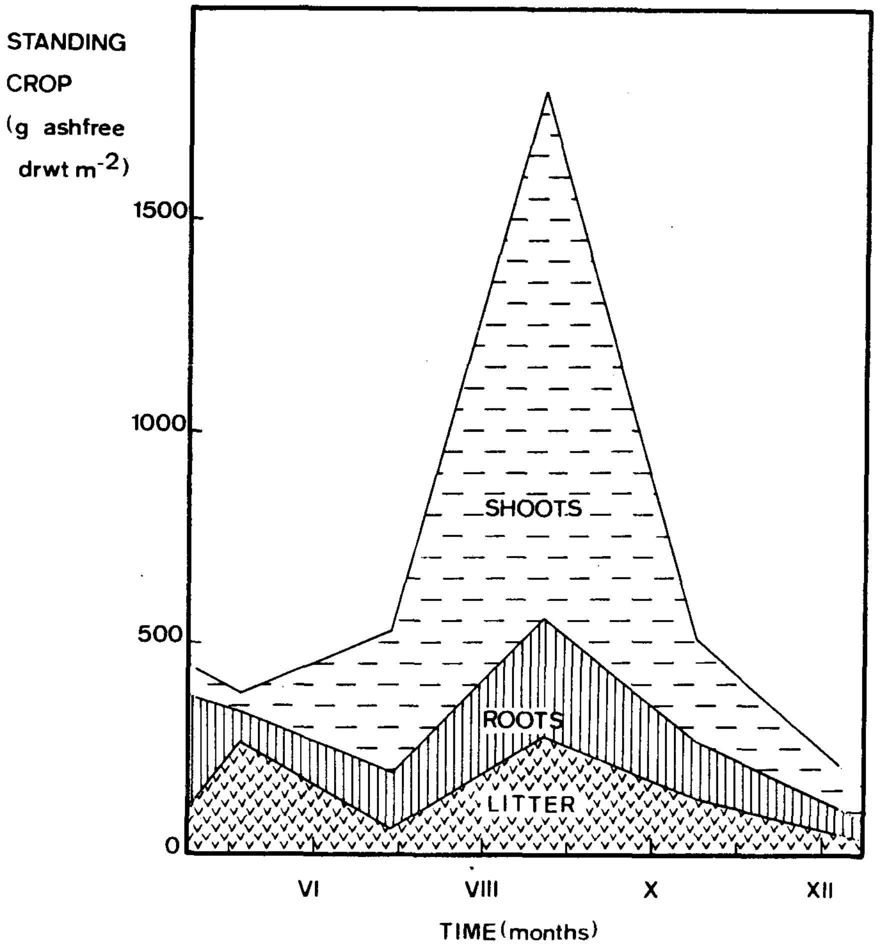

Fig.2. The seasonal changes in biomass of *Phragmites australis* in 1979. The plant material was divided into shoots, rootstocks + roots, and litter.

sampling date	plant organ	shoot:root ratio	C:N ratio	C:P ratio (x10^{-3})	ash (%dr.wt.)
April	shoots	0.15	24.31	0.51	7.0±0.2
	roots		42.22	0.84	17.1±3.1
	litter		38.60	0.80	8.7±3.8
May	shoots	1.0	27.27	0.71	5.1±0.1
	roots		34.46	0.61	40.0±2.7
	litter		55.29	0.99	19.5±2.8
June	shoots	2.5	21.00	0.41	6.6±0.1
	roots		23.18	0.61	8.3±2.3
	litter		38.60	0.86	4.8±0.2
August	shoots	5.0	34.45	0.44	13.4±0.4
	roots		42.11	0.79	9.0±4.0
	litter		63.83	1.09	4.2±3.2
October	shoots	1.7	57.43	0.52	6.2±0.8
	roots		66.67	0.52	13.5±2.6
	litter		58.00	0.58	10.3±3.0
December	shoots	1.4	55.14	0.52	5.2±0.9
	roots		42.33	0.59	7.4±0.9
	litter		65.33	0.71	5.2±2.6

Table I. Seasonal changes in ratio's and ash in standing crop samples of *Phragmites.*

The RGR's were calculated from the biomass values presented in Fig.2 and Table II, respectively. By comparing the RGR's of the aerial and underground organs (Table III) it became clear that the relative growth as well as decay rates were much higher in shoots than in root systems. The maximum shoot RGR in spring coincided with a very low root RGR; the latter value might even be temporarily negative due to use of the reserves, which was not found here.

sampling date	biomass (g ash-free dr.wt.shoot $^{-1}$)	ash (%dr.wt.)	C (% ash-free dr.wt.)	N (% ash-free dr.wt.)	P (% ash-free dr.wt.)
April	0.812	7.52	45.63	2.35	0.36
May	2.256	7.76	50.94	2.88	0.34
June	3.162	6.62	46.47	2.76	0.34
July	4.712	7.55	45.68	1.36	0.22
August	4.098	5.75	46.45	1.48	0.23
September	----	7.26	44.13	0.79	0.20
October	----	4.63	48.94	0.83	0.21
November	2.7484	4.77	46.36	1.19	0.23
December	2.0941	4.42	47.76	0.86	0.21

Table II. Seasonal changes in organic weight and in content of ash, C, N and P in *Phragmites* shoots. Average of 3 samples.

In this period the shoots grew at the cost of the roots since almost no leaf area was available for photosynthesis. The maximum shoot RGR was in the same range as the one found in Scottish lakes (0.05 - 0.06; HO, 1979) but much lower than the one found in the Czechoslovakian fish ponds (0.14; KVET, 1971). The present relative decay rates, however, were extremely high, and decay started earlier in the season than *e.g.* in Scotland. This might indicate regression of the vegetation in Lake Vechten.

sampling date	RGR		
	shoot	aerial	underground
April	0.036	0.057	0.001 *
May		0.027	0.012
June	0.012		
July	0.012	0.024	0.014
August	– 0.006		
September		– 0.029	– 0.014
October	– 0.005		
November	– 0.021	– 0.020	– 0.014

Table III. Seasonal RGR changes in biomass per unit biomass between harvests in the course of the year, calculated for shoots of the same age, shoots of different ages and underground organs.
(* Rate calculated as average over the winter period, omitting the first, probably faulty, value.

There were conspicuous differences in the RGR's of shoots which were tagged at the onset of the growing season and the shoots of the standing crop samples, the former being always lower than the latter (Table III). This might be explained by assuming that early shoots serve as initial light perceptors and apart from the root systems, as prime energy donors for the slightly later starting shoots. The latter grew consequently much faster by using these assimilates.

The number of full-grown shoots was counted in the aquatic as well as in the terrestrial reed zone in the period when maximum biomass occurred, being respectively 8,0 ± 5,5 and 3,5 ± 2,1.m^{-2}. This indicated, for instance, that in the aquatic vegetation the maximum shoot biomass of the early plants was 377 g ash-free dry weight.m^{-2}, and thus about 70 % (or 870 g.m^{-2}) of the shoot biomass development later in the year.

In using the relationship between shoot dry weight and plant height determined by HO (1979), the average height of the present *Phragmites* vegetation was estimated as about 1.5 m. HO concluded that only reed plants from eutrophic lakes have this low value, whereas it is much higher in plants from oligo- and mesotrophic lakes.

There were two periods in which most plant litter was present (Fig.2), namely in early spring when last years' stubbles fell largely apart, and in July-August when the lower parts of the vegetation were sloughing.

Chemical composition.

The changes in the nutrient concentrations in the tagged shoots are presented in Table II. The carbon concentrations varied between 44.13 and 50.94 % ash-free dr.wt. In May the highest value was found, which coincided with the highest N concentration (2.88 % org.wt.). C and N concentrations showed similar tendencies until mid-August, *i.e.* a sharp increase in the beginning of June followed by a slight decrease. This decrease continued steadily for the N concentration but not for the C concentration. The P concentration showed a different course; it decreased from the onset of the growing season, varying between 0.20 and 0.36 % ash-free dr.wt.

In Fig.3 the changes in nutrient concentrations in the standing crop samples are shown. In the shoots C and N showed a similar, only less clear, tendency as found in the tagged shoots. P showed a different course, in that its concentration increased until July and declined afterwards, possibly caused by the late emergence of a great number of shoots as discussed earlier. The C and N concentrations in the underground organs showed patterns which were similar to those of the tagged shoots. These indicated extensive mobilization of C- and, subsequently, N-containing compounds early in the season for growth. P fluctuated slightly with a minimum in August; this was also reported by MOCHNACKA-LAWACZ (1974a). The nutrient concentrations in the plant litter were considerable, at least when it is expected that initial leakage of the nutrients out of the plant material has occurred already. In October the C concentration was high whereas that of N was the same as in summer. Apparently N was either redistributed before the initiation of decay or it was lost by leakage. C, however, was still present in high concentration, possibly largely in the form of soluble carbohydrates (HUNTER, 1976). The P concentration was always low in the plant litter. Taking the enormous increase in biomass during the growing season into consideration,

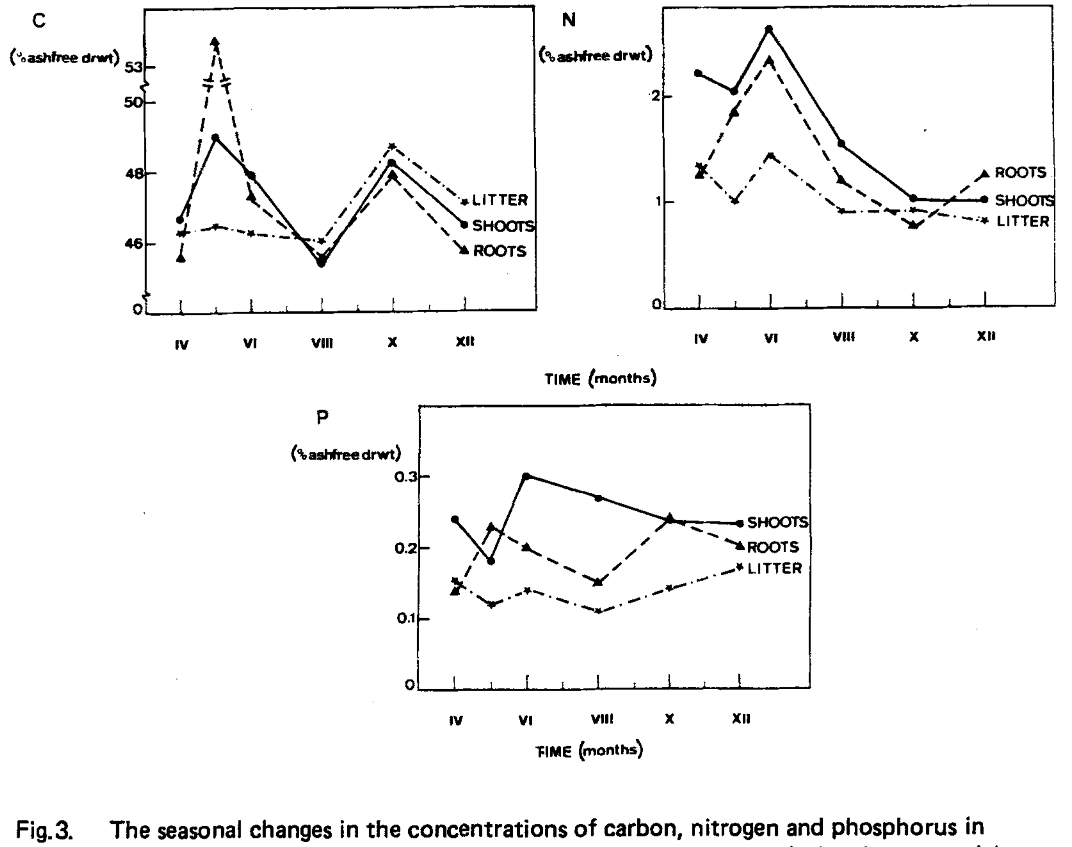

Fig.3. The seasonal changes in the concentrations of carbon, nitrogen and phosphorus in *Phragmites australis* during 1979; the standing crop was sampled; the plant material was divided into shoots, rootstocks + roots and litter.

the reed growth means a substantial increase in C, N and P fixed in biotic components as part of the nutrient cycles of the lake ecosystem, even though the nutrient concentrations in the plant material decrease substantially from summer towards autumn.

The ash concentrations in the shoots were mostly lower than in the underground organs (Table I). The relatively low ash value of the latter at the end of the season might indicate that then mainly rootstocks were sampled since rootstocks contain in general less ash than roots.

Production and nutrient budgets.

In order to calculate annual net production of macrophytes, the turnover time of both shoots and underground organs must be taken into account. For shoots the difference between the seasonal minimum and maximum biomass represents a fairly close estimate of annual net production (WESTLAKE, 1975). With rhizomes and roots, the turnover time is about four years (SCHIERUP, 1970; DYKYOVA, 1971; FIALA, 1976) and thus the difference between minimum and maximum biomass of underground organs should be divided by four. The minimum and maximum standing crop of both the terrestrial and aquatic *Phragmites* vegetation were calculated (Table IV). From these data it was derived that the net annual production for the whole lake was 655 kg organic weight in 1979, representing C, N and P values of, respectively, 336, 11 en 2 kg. Since about 50 % of the shoot biomass of the terrestrial vegetation was grazed by cattle, the actual values were 536 kg organic weight and, respectively, 282, 9 and 2 kg C, N and P. The contribution of the underground organs to the total production of the vegetation was relatively small (about 5 %), which is normal for areas with a fluctuating water level (DYKYOVA, 1971).

vegetation type	plant organs	biomass (kg ash-free dr.wt.lake $^{-1}$)		net annual production (kg.lake $^{-1}$)	C (kg.lake $^{-1}$)		N (kg.lake $^{-1}$)		P (kg.lake $^{-1}$)	
		min.	max.		min.	max.	min.	max.	min.	max.
terrestrial	shoots	7.0	245.3	238.3	3.27	111.41	0.15	3.80	0.02	0.66
	underground	12.8	56.4	10.9	5.83	25.67	0.16	0.67	0.02	0.08
aquatic	shoots	11.5	399.7	388.2	5.37	181.54	0.26	6.19	0.03	1.08
	underground	20.9	91.7	17.8	9.53	41.82	0.27	1.10	0.03	0.14
total				655.2	336.44		10.92		1.86	

Table IV. Calculation of standing crop for the whole lake. The vegetation is divided into aquatic and terrestrial belts, based on morphological criteria. The lake surface area is 4.715 ha.

In 1979 the production of *Phragmites*, calculated as described in this paper, comprised only 5.8 % of the lake's total annual primary production expressed in C (macrophytic, phytoplanktonic and periphytic). The contribution of the total macrophytic unit was 8.7 %. Total seasonal production of the lake was 24,2 kg.m^{-2}.day^{-1} (season 195 days, April 1 to October 15; BEST *et al.*, 1978).

The role of the contingent of nutrients (C, N and P) in lake metabolism lies largely in the nutrient release by leakage and decomposition. The latter process and the factors affecting it are discussed in another paper (BEST *et al.*, 1982).

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SUMMARY

A study was carried out on several production characteristics of *Phragmites australis* stands in Lake Vechten, the Netherlands. The aim was to quantify the role of this plant species in the lake's primary production and nutrient cycles (C, N and P).

Maximum biomass values of 1247 and 286 g org.wt.m^{-2} were measured in, respectively, shoots and underground organs in August. The shoot:root ratio was always > 1. Plant litter accumulated particularly in spring and autumn. The relative growth rates of early shoots differed from those determined for the whole vegetation, indicating shoots of different ages in the latter. This was confirmed by counting the number of plants.

The chemical composition of the plants changed with season. A carbon peak as high as 50.94 % org.wt. was found in spring, which coincided with a nitrogen peak of 2.88 % org.wt. At the end of the season N dissapeared faster from the shoots than C, whereas P declined from spring onwards.

The production of *Phragmites* contributed in 1979 for 5.8 % to the lake's total primary production expressed in C, whereas the share of the total macrophytic unit amounted to 8.7 %.

The potential role of *Phragmites* in the lake's nutrient cycles was largely due to nutrient leakage and decomposition.

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