The phosphorus cycle in Germiston Lake IV. The relationship between the absorption, accumulation and release of phosphorus and the metabolic rate and phosphorus contents of the tissues of *Potamogeton pectinatus* L.

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Abstract

A seasonal investigation was carried out to establish the possible relationship between metabolic rate and the phosphorus dynamics in the tissues of *Potamogeton pectinatus* L. Results showed that there is a direct relationship between metabolic rate and the absorption and accumulation of phosphorus. As was expected, fluctuations in phosphorus metabolism occurrred during the various seasons.

Introduction

A number of authors, e.g. Caines (1965), Denny (1966), Bristow and Whitcombe (1971), have shown that a variety of submerged hydrophytes absorb and accumulate nutrients from their aquatic environment. Most of these investigations concentrated on the absorption and accumulation of phosphorus. Some species, e.g. *Zostera marina* (Foehrenbach, 1969; McRoy and Barsdate, 1970), *Spartina alterniflora* and *Myriophyllum exalbescens* (De Marte and Hartman, 1974), *Nuphar luteum* (Twilley *et al.*, 1977) and *Potamogeton pectinatus* (Swanepoel and Vermaak, 1977; Vermaak *et al.*, 1982a and b) absorb phosphorus via their roots and shoots. Both the phosphorus absorption rate and phosphorus concentration of the plant tissues may vary temporally (e.g. Caines, 1965; Vermaak *et al.*, 1982b). Absorption and accumulation of phosphorus are also probably affected by factors such as the phosphorus concentration of the substrate and the limnetic water (Gerloff, 1975; Denny, 1966). Physiological as well as environmental factors are most probably decisive in determining nutrient levels in the tissues of aquatic plants (Boyd, 1970).

Considerable attention has recently been given to the possible role of submerged hydrophytes in the limnetic phosphorus cycle (e.g. Foehrenbach, 1969; McRoy and Barsdate, 1970; De Marte and Hartman; 1974; Twilley *et al.*, 1977; Vermaak *et al.*, 1981, 1982a and b), and some authors, notably McRoy and Barsdate (1970), are of the opinion that certain species, e.g. *Zostera marina* act as a phosphorus pump that returns mobilized phosphorus from the sediments to the limnion. However, Bristow and Whitcombe (1971) found that such a mechanism is probably absent in *Myriophyllum spicatum* and *Elodea densa*. Vermaak *et al.* (1982a and b) established that *Potamogeton pectinatus* does not perform such a function to any significant extent. The latter authors also found that absorption, accumulation and release of phosphorus by *P. pectinatus* varies seasonally (Vermaak *et al.*, 1982b).

In none of the above investigations has any attempt been made to relate the phosphorus absorption, accumulation or release rates of the species involved to their metabolic activities. However, the present authors are of the opinion that consideration of this aspect may assist in the better understanding of the possible effect of submerged hydrophytes in the phosphorus dynamics of an aquatic ecosystem.

Phosphorus compounds generally constitute the most important limiting nutrients in freshwater lakes (Hutchinson, 1957; Sawyer, 1966; Boyd, 1971; Wetzel, 1975). Furthermore, phosphorus is present in plant cells in the form of compounds that are intimately involved in metablism, e.g. ADP and ATP (e.g. Wetzel, 1975). Thus, the seasonal variation in the metabolic activities of aquatic plants may be expected to have some effect on the phosphorus pool in the plant, and probably also on the absorption, accumulation and release of phosphorus.

The aim of the present investigation was therefore to determine the metabolic rate of *P. pectinatus* on a seasonal basis, and to compare the latter with the seasonal trends in absorption, accumulation, and release of phosphorus by this species. Since the respiration rate of plant tissues provides a reliable indication of the metabolism of the plant (Siegelman, 1952), this rate was employed as criterion of metabolic activity in the present study. The possible relationship between the phosphorus contents of the tissues of *P. pectinatus* and the absorption and release of ^{31}P by the plant, was also investigated.

Methods

During a study on the seasonal patterns in absorption and release of phosphorus by *P. pectinatus* in Germiston Lake (Vermaak *et al.*, 1982b), *P. pectinatus* plants were also collected from the same sampling localities for use in the present investigation.

Relationship between absorption of phosphorus and metabolic rate of the tissues

The plants used were thoroughly washed in tap water and the epiphytes removed (McRoy *et al.*, 1972). The plants were then again rinsed in distilled water, before being dissected into roots, stems and leaves. In order to exclude photosynthesis, respiration rate of a representative quantity of each type of organ (taken after thoroughly mixing the fragments of each type of organ) was conducted for one hour under dark conditions, with the aid of a Gilson differential respiro-meter, at the temperature prevalent in the sampling locality. Volumes of CO_2 released by the tissues were taken as criteria of the respiration rates, and the latter as indication of metabolic rate. The CO_2 released was absorbed with 0,2 mℓ 20% KOH solution, and the decrease in gaseous volume of the incubation flasks used to determine the actual volume of CO_2 released, according to Arditti and Dunn (1969). The various tissue samples were then dried for 24 h at 80°C, and their respective dry masses determined.

Phosphorus absorption by, and its contents in the tissues of *P. pectinatus*

The total phosphorus content of the roots, stems and leaves of *P. pectinatus* plants was determined by the isotopic dilusion method as described by Vermaak *et al.* (1982a).

Results of this study are summarized in Tables 1 and 2.

TABLE 1
RESPIRATION RATES OF THE ROOTS AND SHOOTS OF *P. PECTINATUS*

Organ	Spring x̄ (SEM)	Summer x̄ (SEM)	Autumn x̄ (SEM)	Winter x̄ (SEM)
	$\mu\ell$ CO_2 per mg dry mass per hour			
Roots	0,325 (0,19)	1,266 (0,29)	1,835 (0,31)	1,324 (0,13)
Shoots	1,110 (0,02)	0,627 (0,14)	1,592 (0,39)	0,753 (0,10)

x̄ = mean; SEM = standard error of the mean

TABLE 2
PHOSPHORUS CONTENTS OF THE TISSUES OF *P. PECTINATUS*

Organs	Spring	Summer	Autumn	Winter
	mg P per g dry mass x̄ (SEM)			
Roots	3,18 (0,14)	10,20 (2,45)	9,00 (2,37)	4,31 (1,28)
Shoots	5,14 (1,20)	2,34 (0,32)	7,95 (2,57)	3,71 (0,83)

x̄ = mean; SEM = standard error of the mean

TABLE 3
PHOSPHORUS ABSORPTION, ACCUMULATION AND RELEASE BY *P. PECTINATUS* TOGETHER WITH THE RESPIRATORY RATES OF THE DIFFERENT TISSUES

Season	Organs	μg ^{31}P per g dry mass per 24 h Absorbed	Released	Respiration rate $\mu\ell$ CO_2 per g per hour	Total phosphorus μg per g dry mass
Spring	Roots	94	5,35	235	3 180
	Shoots	127	1,45	1 110	5 140
Summer	Roots	2 474	10,00	1 260	10 200
	Shoots	87	1,94	627	2 340
Autumn	Roots	3 966	5,30	1 835	9 000
	Shoots	249	5,79	1 592	7 950
Winter	Roots	188	44,71	1 324	4 310
	Shoots	164	36,08	753	3 710

Results and Discussion

It is clear from Table 1 that the respiration rate ($\mu\ell\ CO_2 mg^{-1} h^{-1}$) of the roots increases from spring (235 $\mu\ell$) to atumn (1 835 $\mu\ell$), whereafter it decreases in winter (1 324 $\mu\ell$). The respiration rate of the shoots (stems and leaves) reaches a peak during spring (1 110 $\mu\ell$) and autumn (1 592 $\mu\ell$), while the values for summer (627 $\mu\ell$) and winter 753 $\mu\ell$) are much lower. Respective values for the leaves exceed those for the stems during all four seasons.

The values obtained by Vermaak *et al.* (1982b) for phosphorus absorption and release, converted to diurnal values for each respective season, are given in Table 3, together with the total phosphorus values of the tissues, as determined in the present investigation.

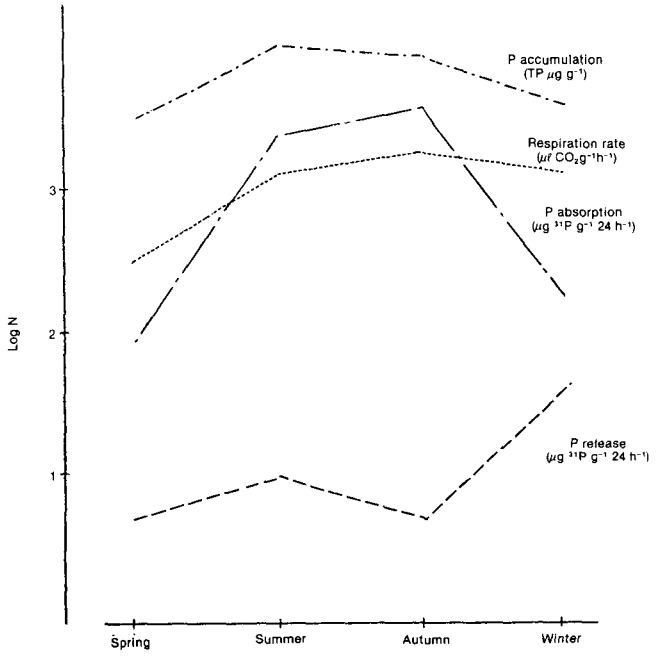

Figure 1
Comparison of total phosphorus contents, respiration rate, phosphorus absorption and release by the roots of P. pectinatus *during the four seasons.*

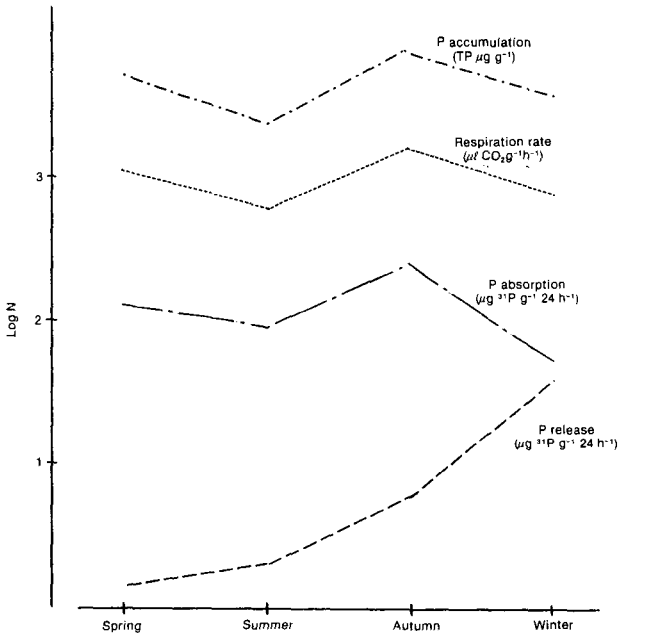

Figure 2
Comparison of total phosphorus contents, respiration rate, phosphorus absorption and release by the shoots of P. pectinatus *during the four seasons.*

Results from Table 3, plotted on logarithmic scale in Figures 1 and 2 show that a distinct relationship exists between respiration rate and ^{31}P absorption by the roots and shoots, respectively. Furthermore, with regard to the roots, both absorption and respiration rates increase from spring to autumn, but decline towards winter (Fig. 1). By comparision, there is a more direct relationship between respiration rate and ^{31}P absorption values of the shoots (Fig. 2). There are two peaks in both cases, viz. during spring and autumn, with the autumn values being higher than those obtained for spring.

From the results in Figs. 1 and 2, it is also clear that the total phosphorus concentration of the roots and shoots closely follows the respiration rate and phosphorus absorption values, respectively. This is especially so for the shoots (Figs. 1 and 2).

The phosphorus release rate of the roots correlates well with the total phosphorus (TP) values of the same tissues, i.e. with increasing TP, more phosphorus is released to the surrounding water, and *vice versa* (Fig. 1). An exception, however, is the values for winter, where the decline in TP of the tissues is accompanied by a sharp increase in the rate of phosphorus release (Fig. 1). It must be noted, however, that the quantity of phosphorus released is much less than the decrease in TP of the root tissues during the autumn to winter period (Vermaak *et. al.*, 1982b).

There is no clear relationship between the TP contents of the shoot tissues and their phosphorus release rates. However, it should be noted that the rate of release increases towards winter when it reaches a peak. As in the case of the roots, the amount of phosphorus released by the shoots cannot fully account for the fluctuations in TP values (Vermaak *et al.*, 1982b).

During each of the seasonal investigations, the absorption of phosphorus occurs against a concentration gradient (Tables 3 and 4) by active absorption processes (Boyd, 1969; 1970). The involvement of active absorption, which is an energy-requiring process, is confirmed by the findings that the respiration rates of both roots and shoots, respectively increase or decrease with greater or lesser absorption rates (Figs. 1 and 2). However, there is no clear relationship between the respiration rates of the roots or shoots and the extent to which phosphorus is released to the environment. This seems to preclude the possibility of an energy-dependent mechanism which may actively release translocated phosphorus to the environment by this species in Germiston Lake. Furthermore, no relationship exists between the concentrations of accumulated phosphorus (μg TP per g dry mass, Table 3) nor the phosphorus absorption rates (μg ^{31}P per g per 24 h, Table 3) and the quantities of phosphorus released by the test plants to the environment (μg ^{31}P per g dry mass per 24 h (Table 3), as might have been expected in view of the results obtained with *Zostera marina* (McRoy and Barsdate, 1970; McRoy *et al.*, 1972), *Spartina alterniflora* and *Myriophyllum exalbescens* (De Marte and Hartman, 1974), and *Nuphar luteum* (Twilley *et al.*, 1977). The exceedingly small quantities of phosphorus released during a 24 h period, in the present investigation, further indicate that *P. pectinatus*, in Germiston Lake, does not release phosphorus to an extent that may be of ecological significance in resupplying phosphorus from the sediments to the open waters. It seems probable that phosphorus is released to the environment solely through leaching from the plant surfaces (Boyd, 1970). The very low quantities released in this way probably does not have any significant impact on the phosphorus levels in the surrounding waters (Table 4).

The roots of the test plants absorb phosphorus at increasing rates from spring to autumn and this is accompanied by an increase in TP in the root tissues from spring to summer, but TP declines in autumn and winter (Table 3). The declining autumn TP value in spite of an increased absorption rate in autumn may be attributed to the translocation of phosphorus from the roots to the reproductive bulbs in the plant which develop from summer towards winter. This is consistent with the findings of Caines (1965) and Boyd (1970) that nutrients are translocated from vegetative parts to reproductive structures. Vermaak *et al.* (1982b) found that the roots of *P. pectinatus* are the major organs of phosphorus absorption during summer and autumn when their absorption rates exceed that of the shoots by several-fold (Table 3). However, the TP concentration of the shoots reaches a peak during autumn and it follows that another possible reason for the decline in TP concentration of the root tissues from summer to autumn, may be due to translocation of phosphorus to the shoots.

The values obtained for the winter investigation of the phosphorus contents, phosphorus absorption rate, and respiration rate, all show and expected decline during winter when the vitality of the roots decreases.

The TP concentration of the shoots, as well as their phosphorus absorption values, decline from spring to summer. Boyd (1969) and Caines (1965) state that nutrient absorption during the early part of the growing season may be followed by a period during which the accumulated nutrients are translocated to the more actively growing parts. Boyd (1970) also found that N, P, and Mg were concentrated in the reproductive structures and that this accrual of nutrients could not, in the case of *Typha latifolia*, be accounted for by the net uptake rates of these nutrients by the plants during flowering and fruiting. He concluded that a considerable amount of translocation of nutrients occurs from the foliage to the reproductive tissues at the expense of foliage nutrient levels. This may also apply to *P. pectinatus* which grows actively (cf. dry mass values, Table 4) from spring to summer, while flowering structures also develop during the latter season. It is however not certain to what factors the declining

TABLE 4

P. PECTINATUS DRY MASS AND ESTIMATED TP CONTENTS, TOGETHER WITH THE SRP LEVELS IN THE WATER OF GERMISTON LAKE, AND THE ^{31}P ABSORPTION AND RELEASE VALUES, DURING THE PRESENT INVESTIGATION

Season	*Potamogeton* dry mass	TP in plants	SRP (water)	^{31}P absorption/plant		^{31}P release/plant/24 h	
				Roots	Shoots	Roots	Shoots
	kg	kg	$\mu g\ \ell^{-1}$	$\mu g\ ^{31}P$	$\mu g\ ^{31}P$	$\mu g\ ^{31}P$	$\mu g\ ^{31}P$
Spring	3 279	12,9	52	94	1 849	5	21
Summer	23 880	140,9	196	1 162	578	5	15
Autumn	11 516	98,7	59	3 966	1 992	5	47
Winter	5 955	26,4	51	91	562	110	110

respiration values, measured during the summer investigation, can be ascribed. A possible reason may be that the extensive proliferation of the plants to form an extremely dense growth in the littoral zone may result in attenuation of light so that those portions of the plants that do not lie at or close to the surface, may be inhibited. The leaves most probably become unhealthy and their phosphorus absorption and accumulation capacities depressed (Caines, 1965).

As is obvious in Table 4 a sharp decrease in *P. pectinatus* dry mass occurs from summer to autumn. The abovementioned light attenuation may be the causal factor and lead to the eventual dying off of many plants. This in turn will eliminate the inhibition of shoot metabolism and lead to increased metabolic activity of the surviving stronger shoots. The markedly higher respiration and absorption rate and TP concentration measured during autumn may be evidence thereof. This is also the period when seed formation is completed, and as Boyd (1970) pointed out, adequate levels of nutrients probably are essential for survival immediately following seed germination, so that the net translocation of nutrients into seeds occurs. This may be a further reason why shoot absorption and accumulation of phosphorus is at its greatest during autumn. Phosphorus will then be available for translocation to the seeds whose formation is completed during late summer and autumn.

Conclusions

- There is a distinct relationship between the respiratory rate of the roots and shoots of *P. pectinatus* and their respective phosphorus absorption rates.
- The respiratory rate and P absorption of the shoots are higher during spring and autumn than during summer and winter. This increased metabolism and P absorption can possibly be correlated with an active growth phase during spring and production of seeds during late summer and autumn.
- Respiration rate and P absorption of the roots reach a peak during autumn and this is possibly due to the active production of bulbs during this period, and also as a means of augmenting the P concentration of the shoots through translocation.
- The highest phosphorus concentrations in the tissues of *P. pectinatus* occur during autumn when the roots and shoots also exhibit highest absorption values.
- Release of phosphorus from the plant surfaces probably occurs through leaching. The very small quantities thus released to the environment can hardly have any effect on the phosphorus level of the water environment.

The results provided in this paper, as well as those incorporated in preceding papers on the role of *P. pectinatus* in Germiston Lake, will be reviewed and integrated in a separate paper, which will conclude this series of publications on this topic.

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