

The Phosphorus Cycle in Germiston Lake

III Seasonal Patterns in the Absorption, Translocation and Release of Phosphorus by *Potamogeton pectinatus* L.

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Abstract

The seasonal fluctuation in the phosphorus absorption, translocation, and release by the roots and shoots of *Potamogeton pectinatus* L. in Germiston Lake, is discussed. Shoot absorption exceeds that by the roots during spring and winter, while the reverse applies for summer and autumn. The shoots consistently release more phosphorus per plant than the roots. Both shoots and roots absorb considerably more phosphorus than what they release to the environment. This macrophyte, therefore, mainly acts as a phosphorus reservoir in Germiston Lake.

Introduction

The absorption of nutrients, especially phosphorus, by the roots and shoot systems of some submersed rooted aquatic macrophytes, as well as the bidirectional translocation thereof, were previously studied by Denny (1966), Föehrenbach (1969), McRoy and Barsdate (1970), Bristow and Whitcombe (1971), McRoy *et al.* (1972), Reimold (1972), De Marte and Hartman (1974), Gerloff (1975), Twilley *et al.* (1977), and others. Some of these authors observed that a fraction of the translocated phosphorus was released to the surrounding environment. In certain cases, the acropetalous translocation and concomitant release of phosphorus exceeds its basipetalous equivalent. In the latter instances, therefore, the role of a phosphorus pump mechanism for the transport of soluble reactive phosphorus (SRP) from the interstitial water of the anaerobic sediment to the limnetic water probably is an important ecological function of such hydrophyte species (McRoy and Barsdate, 1970; McRoy *et al.* 1972). Swanepoel and Vermaak (1977) and Vermaak *et al.* (1982) recorded similar phenomena involving *Potamogeton pectinatus* L. However, their results did not substantiate the concept of a phosphorus pump mechanism, but rather emphasize the significance of phosphorus concentration gradients between the plant and its environment in the actual processes of absorption, translocation and release of this nutrient.

Penfound (1956), Westlake (1963), and Boyd (1968, 1969), stressed the limnological importance of large standing crops and extensive aquatic macrophyte infestations in water bodies. In such cases the plant material contains large percentages of mineral nutrients and organic material (Boyd, 1967, 1968), so that aquatic macrophytes play a significant role in the biogeochemical cycles of lakes (Boyd, 1969). Caines (1965) demonstrated that the phosphorus concentration in the tissues, especially the meristems, of *Myriophyllum alterniflorum* and *Potamogeton praelongus*, varies in a cyclic fashion during the growing season. Likewise, Stake (1967, 1968), and Boyd (1970) found that the mineral composition of certain freshwater macrophytes varies temporally. Boyd (1970) further observed

fluctuating net uptake rates for phosphorus, amongst other nutrients, in *Typha latifolia*. Caines (1965) also recorded fluctuations in phosphorus concentrations of *M. alterniflorum* and *P. praelongus*, which may vary from year to year. Annual variation in ^{32}P uptake is also described by Ball and Hooper (1963) and Ball *et al.* (1963) for *Potamogeton pectinatus*, *Chara* sp., and the moss *Fontinalis antipyretica*. Boyd (1969) indicated that various species of aquatic plants are able to absorb large amounts of nutrients prior to the period of maximal growth. This might have an ecological advantage, as the plants can accumulate these nutrients for utilization during optimal conditions for growth and development (MacKenthun, 1964, 1965; Boyd, 1969). However, despite the knowledge accrued on this subject, the literature offers very little information concerning the seasonal patterns and ecological significance of absorption and accumulation of nutrients by submersed (and other) aquatic macrophytes (Stake, 1967; Boyd, 1970; Wetzel, 1975; Twilley *et al.*, 1977). Little is known about the release of absorbed nutrients and the ecological significance thereof.

P. pectinatus has colonized the littoral zone of Germiston Lake extensively, and it exhibits an active growth phase and resultant increase in biomass in the lake during spring and summer (Vermaak *et al.*, 1981). Consequently, the aim of the present experiment was primarily to investigate possible seasonal patterns in phosphorus absorption, translocation, and release phenomena by this species.

Materials and Methods

Samples of *P. pectinatus* plants, water and substrate were collected seasonally from the same *Potamogeton* bed in Germiston Lake. Materials and methods employed for collection of samples as well as for investigating ^{32}P absorption, translocation, and release by the plants, have been described elsewhere (Swanepoel and Vermaak, 1977; Vermaak *et al.* (1982)). For each seasonal experiment, twelve containers (four in triplicate) were prepared and each provided with a *P. pectinatus* plant obtained from the lake.

In order to simulate natural conditions, the SRP concentration of the root compartment of the experimental containers were adjusted to that of the interstitial water of the sediments from which the plants were removed according to the techniques described by Vermaak *et al.* (1982). Consequently, the SRP concentration of the root compartment of each container was in all instances substantially higher than that of each corresponding shoot compartment. To six of these containers $5\ \mu\text{Ci}$ ^{32}P , as phosphate, was added to the shoot compartment, whilst the root compartment of the other six received the same activity of the radio-isotope. The root compartments of all the culture vessels were wrapped in aluminium foil, whilst the shoot com-

partments of three of each set were also darkened (Vermaak *et al.* 1982). All the containers were then incubated for 24 h in a Conviron growth cabinet at 20 000 lx (Swanepoel and Vermaak, 1977) at prevailing water temperatures of the habitat from which the plants were removed during a particular season. The relative humidity in the cabinet was adjusted to 80% to minimize evaporation of the incubation media. After incubation, the activities of the incubation media, as well as those of the plant tissues, were determined according to the procedures followed by Swanepoel and Vermaak (1977) and Vermaak *et al.* (1982). It must be emphasized that the SRP concentration of the root compartments were substantially higher than that in the shoot compartments, which usually is the case under natural conditions (Holden, 1961; Olsen, 1964; Hopher, 1966; amongst others). For this reason, and since it was assumed that the plants do not discriminate between ^{31}P and ^{32}P (Swanepoel and Vermaak, 1977; Vermaak *et al.*, 1982), the ^{32}P activity was converted to ^{31}P absorbed and/or released per g dry mass of plant tissue. The results are given in Table 1.

Results and Discussion

The mean values pertaining to the $\mu\text{g } ^{31}\text{P g}^{-1}$ dry mass absorbed and released by *P. pectinatus* for the period: spring 1977 – winter 1978, are given in Table 1.

According to the results obtained, similar quantities of $^{31}\text{P g}^{-1}$ dry mass are respectively absorbed by the shoots and roots during spring (166 μg and 158 μg) and winter (101 μg and

102 μg) light incubations (Table 1). By comparison, the roots of plants collected during summer and autumn absorb approximately 25 and 23 times more $^{31}\text{P g}^{-1}$ than their shoots. The greatest quantity of $^{31}\text{P g}^{-1}$ dry mass is absorbed by the roots of the plants during autumn (4 525 μg and 3 407 μg), followed by summer (1 203 μg and 1 105 μg). Absorption via the roots clearly declines during spring and winter (166 μg and 22 μg ; 101 μg and 83 μg , respectively). The highest absorption values obtained for the shoots are during autumn (198 μg and 300 μg), with the values for summer (49 μg and 25 μg) being the lowest. Thus, when phosphorus absorption is expressed in terms of $\mu\text{g } ^{31}\text{P g}^{-1}$ dry mass absorbed, the roots evidently appear to be the major organs of absorption, particularly so during summer and autumn. The results obtained for the simulated day conditions further suggest that, with the exception of winter, the roots of *P. pectinatus* absorb more $^{31}\text{P g}^{-1}$ than the shoots. This is especially noticeable for summer and autumn periods (Table 1). In comparing the day and night absorption of ^{31}P by the roots, indications are that more P is absorbed during the light phase. This phenomenon also applies to the shoots of *P. pectinatus* for all seasons except autumn, during which the reverse was recorded.

The release of phosphorus by the roots and shoots is always higher for the roots, with the exception of the autumn and winter dark incubations, where the reverse was recorded (Table 1).

The possible importance of the roots in the absorption of phosphorus, found by the present authors for *P. pectinatus*, is also indicated for other aquatic macrophytes, e.g. Twilley *et al.* (1977) for *Nuphar luteum*. Although the latter authors found

TABLE 1
MEAN $\mu\text{g } ^{31}\text{P g}^{-1}$ DRY MASS ABSORBED AND RELEASED BY *P. PECTINATUS* DURING THE FOUR SEASONS,
SPRING 1977 TO WINTER 1978

Season	^{32}P administered to:	Incubation	$\mu\text{g } ^{31}\text{P g}^{-1}$ dry mass absorbed		$\mu\text{g } ^{31}\text{P g}^{-1}$ dry mass released	
			Roots	Shoots	Roots	Shoots
Spring	Shoots	L	0,07	158	5,3	—
	Roots	(L)	166	0,09	—	0,2
	Shoots	D	0,07	96	5,4	—
	Roots	D	22	0,29	—	2,7
Summer	Shoots	L	0,02	49	4,9	—
	Roots	(L)	1 203	0,79	—	0,6
	Shoots	D	0,15	25	4,4	—
	Roots	D	1 105	2,84	—	1,54
Autumn	Shoots	L	1	198	2,8	—
	Roots	(L)	4 525	0,12	—	0,57
	Shoots	D	0,67	300	7,8	—
	Roots	D	3 407	7,2	—	11,0
Winter	Shoots	L	0,2	102	28,1	—
	Roots	(L)	101	8,2	—	7,0
	Shoots	D	0,12	65	17,6	—
	Roots	D	83	12,35	—	22,2

L = Light incubation

D = Dark incubation

(L) = Light incubation; roots in darkness

only slight seasonal variation in the phosphorus absorption rates of the roots, the trend in absorption was summer > spring > winter, suggesting a possible temperature-dependent phenomenon. The studies of Bristow and Whitcombe (1971) on *Myriophyllum brasiliense*, *M. spicatum*, and *Elodea densa*, as well as those by McRoy and Barsdate (1970) and McRoy *et al.* (1972) on *Zostera marina*, also indicate the significance of the roots in the P absorption of some aquatic species.

In the foregoing discussion, a certain bias is introduced, since the actual biomass ratio of roots and shoots were not considered. Consequently, a true perspective of the P dynamics involving roots and shoots under natural conditions for *P. pectinatus* is not perceived. Thus, in order to obtain a more realistic picture of the movement of P through *P. pectinatus*, the data in Table 1 were converted to take into account the actual ratio between the biomass of roots and shoots for the various seasons. Values obtained are presented in Table 2, with the root dry mass taken as 1 g. Since the root : shoot dry mass ratio for *P. pectinatus* varied seasonally, a correction factor was introduced for each respective season.

According to these results (Table 2), the shoots clearly absorb considerably more phosphorus than the roots, during both light and dark incubations in spring and winter. The reverse situation exists during summer and autumn.

A comparison of these findings with those where results are purely expressed per g dry mass (e.g. McRoy and Barsdate, 1970; McRoy *et al.*, 1972) show the possible discrepancy that can be introduced if data of this nature is considered without

taking into account the relative biomass of these organs of aquatic macrophytes. Phosphorus is mainly absorbed through the shoots of *P. pectinatus* in Germiston Lake during spring and to a lesser extent, winter. This trend, however, is reversed during summer and autumn. This is in agreement with the basic assumption that the actual site of P absorption and the rate at which it occurs may vary during the different seasons (Denny, 1966).

The results in Table 2 also suggest that with the exception of spring, phosphorus is released mainly by the shoots, especially so during the night. For instance, the ratios of ³¹P released by the shoots : roots for the four seasons are 3,4:1, 4:1, 4,5:1 and 9:1. Nevertheless, the quantity of phosphorus released is only a small fraction of that absorbed (Swanepoel and Vermaak, 1977; Twilley *et al.*, 1977; Vermaak *et al.*, 1982). In the present experiments this species never translocated significant quantities of ³¹P from the root to the shoot compartments, as did *Zostera marina* (McRoy and Barsdate, 1970; McRoy *et al.*, 1972). Twilley *et al.*, (1977) state that secretion of P by the roots and shoots alike is a means whereby steady state levels of this nutrient can be maintained within the plant. They further consider it likely that secretion of this nutrient only occurs after a certain threshold level is reached. In *N. luteum* this only occurs, for the shoots, during summer.

By using the results in Table 2, and by further extrapolation of the information on root and shoot P absorption and release to the actual day : night ratios for the various seasons, the following results were obtained (Table 3):

TABLE 2
 $\mu\text{g } ^{31}\text{P}$ PER PLANT ABSORBED OR RELEASED DURING THE FOUR SEASONS IN GERMISTON LAKE.
 THE ROOT MASS IS TAKEN AS 1 g

Season	³² P administered to:	L/D	$\mu\text{g } ^{31}\text{P}$ dry mass ⁻¹ absorbed		$\mu\text{g } ^{31}\text{P}$ dry mass ⁻¹ released	
			Roots	Shoots	Roots	Shoots
Spring	Shoots	L	0,07	2 301	5,3	—
	Roots	(L)	166	1,3	—	3,0
	Shoots	D	0,07	1 396	5,4	—
	Roots	D	22	4,2	—	39
Summer	Shoots	L	0,02	725	4,9	—
	Roots	(L)	1 203	11,7	—	9
	Shoots	D	0,15	372	4,4	—
	Roots	D	1 105	42	—	23
Autumn	Shoots	L	1,0	1 581	2,8	—
	Roots	(L)	4 525	1,0	—	5
	Shoots	D	0,7	2 402	7,8	—
	Roots	D	3 407	58	—	88
Winter	Shoots	L	0,2	710	28,1	—
	Roots	(L)	101	57	—	49
	Shoots	D	0,12	456	17,6	—
	Roots	D	83	87	—	155

L = Light incubation
 D = Dark incubation
 (L) = Light incubation, roots in darkness

TABLE 3
 ABSORPTION AND RELEASE OF ^{32}P PER 24 h BY
P. PECTINATUS IN GERMISTON LAKE AFTER
 ADAPTING THE DURATION OF THE LIGHT AND
 DARK INCUBATION PERIODS TO STANDARD
 DAY AND NIGHT LENGTHS OF THE RESPECTIVE
 SEASONS

	Absorption		Absorption ratio		Release		Release ratio
	Root	Shoot	R/S*	S/R**	Root	Shoot	S/R**
Spring	94	1 849		20	5	21	4
Summer	1 162	578	2		5	15	3
Autumn	3 966	1 992	2		5	47	9
Winter	91	562		6	22	110	5

*R/S = Root to shoot ratio

**S/R = Shoot to root ratio

P. pectinatus apparently removes more P day⁻¹ from the limnion during spring and winter than from the sediments. Furthermore, twice as much P is removed from the sediments than the limnion during summer and autumn. Also, the plant releases more P to the surrounding water during autumn. In the latter instance, the shoot/root value was the highest. Even more important, however, is the fact that considerably more P is retained by the plant than the quantity which is again released to the environment. This contrasts sharply with the findings for *Z. marina* (McRoy and Barsdate, 1970; McRoy et al. (1972).

Conclusions

P. pectinatus from Germiston Lake exhibits distinctly changing P absorption, translocation, and release patterns during the different annual seasons. The following characteristics are pertinent:

- The shoot system is mainly responsible for P absorption during spring and winter. This function is performed chiefly by the roots during summer and autumn.
- After translocation of P, the shoot system releases more P than the roots. This occurs during all seasons.
- Both shoots and roots absorb much more P than what they release.

From the results indications are that live and actively growing *P. pectinatus* primarily acts as a P reservoir and not as a P pump, as referred to by McRoy and Barsdate (1970) for *Zostera marina*. Possible explanations for the above tendencies as well as their impact on the P cycle of Germiston Lake will be dealt with in a later paper.

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