

The Phosphorus Cycle in Germiston Lake. II The *in vitro* and *in situ* Absorption of ^{32}P by *Potamogeton pectinatus* L

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Abstract

The *in vitro* absorption of ^{32}P by the organs of intact and dissected plants of the submerged freshwater macrophyte, *Potamogeton pectinatus* L., was investigated. ^{32}P was absorbed by the roots, stems and leaves of intact and dissected plants under both light and dark conditions, and at both low and high phosphate concentrations. Absorption, translocation, and release of ^{32}P by this species were also investigated using compartmentalized containers separating foliage and roots. It was found that a higher P-concentration in the root compartment (simulating natural conditions) influences absorption, translocation and release of ^{32}P . An *in situ* study in Germiston Lake using ^{32}P confirmed that the roots of *P. pectinatus* can absorb phosphorus from the sediment followed by its translocation to the foliage.

Introduction

The cycling of inorganic nutrients in freshwater ecosystems, in particular the limnetic P-cycle, has been the subject of numerous investigations (cf. Lean 1973a,b,c; Rigler, 1973). Studies by Mortimer (1941, 1942) and Hayes and Phillips (1958), amongst others, showed that inorganic nutrients are exchanged between lake water and sediment. The existence and significance of an oxidised micro-zone at the sediment-water interface, under aerobic conditions, was emphasized by Mortimer (1941, 1942, 1971). When present, this zone can inhibit physico-chemical exchange of inorganic nutrients from the sediment to the limnion. Under aerobic conditions, the extent of the micro-zone is influenced by bioturbation (Davis, 1974; Davis *et al.*, 1975). The exchange equilibria across the sediment-water interface may also be affected by bacterial metabolism (Hayes, 1964; Pomeroy *et al.*, 1965), however, their overall effect appears to be negligible (Olsen, 1958a,b; Hayes, 1964).

Much work has been done on the absorption of inorganic nutrients by rooted submerged macrophytes. A number of investigators, notably Arber (1920), Arisz (1953) and Sutcliffe (1962), claimed that the roots of such plants only serve to anchor them to the substrate, whereas the foliage absorbs nutrients from the water. On the other hand, Rickett (1921), Wilson (1939), Moyle (1945) and Boyd (1971) found a definitive correlation between the chemical composition of the sediments and the distribution and proliferative growth of aquatic macrophytes. This was corroborated by several recent studies (Denny, 1966; McRoy and Barsdate, 1970; Bristow and Whitcombe, 1971; McRoy *et al.*, 1972; Reimold, 1972; De Marte and Hartman, 1974; Twilley *et al.*, 1977; amongst others) which established that the roots of some submerged macrophyte species do absorb nutrients from the substrate. Most of the

forementioned studies concentrated on the absorption of phosphorus. Foliar absorption and the bidirectional translocation of these nutrients were also confirmed by these investigations as well as by Foehrenbach (1969) and Gerloff (1975).

Gerloff (1975) predicted that the relative importance of the roots and shoots to the nutrition of an aquatic plant would depend upon ionic concentrations in the substrate and surrounding water. Denny (1966) suggested that the major absorption site in a species may alter, depending upon the relative nutrient levels in the substrate and the above-lying water.

A significant finding of some of the studies on the absorption and translocation of phosphorus is that some of this absorbed nutrient is released to the environment following translocation through the plant. Furthermore, this has led to some speculation as to the potential role of submerged macrophytes in the cycling of phosphorus in an aqueous environment. Foehrenbach (1969) and McRoy and Barsdate (1970) found that *Zostera marina* L. absorbs phosphorus from the sediments and translocates it to the foliage, which then releases some of it to the estuarine water. McRoy and Barsdate (1970) also determined that the roots release phosphorus which reaches it through translocation, following foliar absorption. However, foliar release exceeds the latter to such an extent that these authors postulated the existence in this species of a phosphorus pump-mechanism which replenishes the phosphorus of the estuarine water from soluble phosphorus found in the interstitium of the sediment. A similar mechanism is present in *Spartina alterniflora*, *Myriophyllum exalbescens* (De Marte and Hartman, 1974), and *Nuphar luteum* (Twilley *et al.*, 1977), but not in *M. spicatum*, *M. brasiliense*, or *Elodea densa* (Bristow and Whitcombe, 1971). As far as *Potamogeton* is concerned, *P. lucens* (Stemann-Nielsen, 1951) and *P. schweinfurthii* (Denny and Weeks, 1970) absorb ions through their submerged leaves. Acropetalous and basipetalous translocation of ^{32}P also occur in *P. schweinfurthii* (Denny, 1966). Swanepoel and Vermaak (1977) demonstrated that *P. pectinatus* absorbs ^{32}P *in vitro* through both roots and shoots, that some of the absorbed phosphorus is translocated bidirectionally, and, that the roots and shoots then release some of this phosphorus. However, they found that the foliar release is exceeded by that via the roots ($\mu\text{g P per plant per 24 h}$), so that a net movement of phosphorus from the water to the substrate, via the plant, is indicated. In their experiment, the initial soluble reactive phosphorus concentrations of the root and foliar compartments were identical — a situation which usually differs from that found under natural conditions (Holden, 1961; Olsen, 1964; Hopher, 1966). Consequently, the object of the present *in vitro* investigation was to determine:

- the effect of the soluble reactive phosphorus concentration on the absorption of phosphorus by the different organs of *P. pectinatus*; and

- the effect of a higher soluble reactive phosphorus concentration in the root compartment on the absorption, translocation, and release of phosphorus by this species.

Additionally, the *in situ* absorption of phosphorus by the roots was also investigated.

Methods

The *in vitro* absorption of ^{32}P by intact and dissected *P. pectinatus* in media with high or low soluble reactive phosphorus (SRP) concentrations

P. pectinatus and water samples from a simulated stream ecosystem (Vermaak *et al.*, 1976) were used in this experiment. A 2 l water sample was collected, filtered through a 0,45 membrane filter and analysed for SRP ($185 \mu\text{g l}^{-1}$), according to the molybdenum blue method (APHA, 1971). Samples of the stream sediment were then collected with a core sampler (Welch, 1948) and the sediment interstitial water removed according to Reeburgh (1967).

This water was then filtered through a $0,45 \mu\text{m}$ membrane filter and its SRP concentration determined as $2\ 200 \mu\text{g l}^{-1}$. Due to the tediousness involved in collecting more than 25 ml interstitial water at a time, the SRP concentration of 1 l of the abovementioned 2 l water sample was adjusted to $2\ 200 \mu\text{g l}^{-1}$ through the addition of sufficient K_2HPO_4 . Twelve beakers were then prepared, six of which contained 75 ml of the low concentration SRP ($185 \mu\text{g l}^{-1}$) medium, with the remainder containing 75 ml of the high concentration SRP ($2\ 200 \mu\text{g l}^{-1}$) medium.

P. pectinatus plants, together with their substrate, were then dug out of the shallow littoral zone of the stream to the maximum depth of the sediment (established plants in this zone were of practical size). The sediment was carefully washed away under running tap water. Epiphytes, where visible, were carefully wiped away (McRoy *et al.*, 1972), after which the shoots were also rinsed with running tap water. In all these cases care was taken not to damage the plant tissues. The clean plants were temporarily stored in an aliquot of the low concentration SRP medium.

Twenty four undamaged plants were randomly selected and two plants, one intact and the other bisected into roots, stems, and leaves, placed into each of the twelve beakers. $5 \mu\text{Ci}$ carrier free ^{32}P , as phosphate, was then added to each of the twelve beakers and three beakers each of the high and low concentration of the SRP media, respectively, wrapped in aluminium foil. The twelve beakers were then placed in a Conviron growth cabinet for 6 h at 15°C (the existing environmental temperature) under 20 000 lx illumination (Swanepoel and Vermaak, 1977). Following incubation, the plants and plant organs from each beaker were separately rinsed in running tap water to remove adsorbed ^{32}P . The intact plants were then also divided into roots, stems, and leaves, and the individual samples dried at 80°C for 24 h, whereafter their individual dry masses were determined. Each sample was digested with $0,5 \text{ ml}$ of concentrated HNO_3 in stainless steel planchettes. Following digestion, the ^{32}P -activity of each sample was determined in a Beckman thin-window gasflow detector connected to the counter of a Beckman Beta Mate II liquid scintillation counter. The ^{32}P -activity of the incubation medium, following incubation, was determined by adding 1 ml water-soluble scintillation cocktail (Scintisol Complete, Isolab), and counted in a Phillips Model PW 4510 liquid scintillation spectrometer. Counting efficiency was determined

by the internal standard method (Wang *et al.*, 1975) and activity converted to disintegrations per minute per gram dry plant tissue (dpm g^{-1}) or per ml medium (dpm ml^{-1}). A minimum of 10 000 counts were recorded in order to obtain an accuracy equivalent to 1% standard deviation. In order to calculate the quantities of stable phosphorus (^{31}P) absorbed by the plant organs, we converted the ^{32}P -activity values obtained for the plant tissues (dpm g^{-1} dry mass) to $\mu\text{g }^{31}\text{P}$ absorbed per gram dry mass ($\mu\text{g P g}^{-1}$), using the formula:

$$\mu\text{g }^{31}\text{P absorbed} = \frac{D \times C}{A} \quad \text{where}$$

D = dpm g^{-1} obtained for the samples; C = $\mu\text{g }^{31}\text{P}$ in the incubation medium; and A = dpm of tracer added to the incubation medium. The assumption was made that organs do not discriminate between ^{31}P and ^{32}P , and that the SRP concentration was equal to the $\text{PO}_4\text{-P}$ concentration.

The accumulation potential of the plant organs was also calculated, making use of the concentration factor (CF), i.e. the ratio of the activity in the plant to that in the incubation medium (Vermaak *et al.*, 1976; Swanepoel and Vermaak, 1977).

In all these experiments, the ^{32}P -activity (counts per minute) obtained for the individual samples, was converted to disintegrations per minute, after considering radio-active decay, quenching, and efficiency of the counting system.

The effect of a higher SRP concentration in the root compartment on the absorption, translocation, and release of phosphorus

Compartmentalized containers (Swanepoel and Vermaak, 1977) in which the roots are separated from the shoots, were used. *P. pectinatus* plants, together with their surrounding substrate were carefully dug out of the shallow littoral zone of the Natal-spruit system. The plants in this area were of adequate size to fit the experimental containers, and the depth of the soft bottom substrate of such an order that the root systems could be removed without undue damage. Simultaneously, a 5 l stream water sample, as well as substrate cores, were obtained from the sampling station, as previously described. The plants, embedded in substrate, were placed in plastic bags, together with sufficient stream water to cover them, whereas the core samples were transported in nitrogen-filled airtight vessels to prevent oxidation of the SRP contained within the cores.

In the laboratory, the plants were cleaned and the stream and interstitial water filtered and their respective SRP concentrations (975 and $4\ 480 \mu\text{g SRP l}^{-1}$) determined. The SRP concentration of $1,25 \text{ l}$ of the stream water collected was adjusted through the addition of K_2HPO_4 , to that of the interstitial water. Twelve compartmentalized containers, each containing a randomly selected intact plant, were prepared as described by Swanepoel and Vermaak (1977), with the exception that the incubation medium of all the upper compartments was filtered ($0,45 \mu\text{m}$) stream water; the lower compartments of all the containers were filled with the adjusted stream water ($4\ 480 \mu\text{g SRP l}^{-1}$); and the lower compartments of all the containers destined for light incubation, were wrapped in aluminium foil.

Henceforth reference will be made to this set-up as Experiment B. A further 12 containers were prepared in the same way, with the exception that both compartments of each contained the $975 \mu\text{g SRP l}^{-1}$ solution — Experiment A.

In each experiment, three containers with no SRP concentration gradient between the foliar and root compartments, as well as three with such a gradient, were then incu-

bated in the dark. Simultaneously, the remaining six containers per experiment, i.e. three with and three without such a concentration gradient, were incubated in the light. Incubation was carried out in a Conviron Growth Cabinet for 24 h under 20 000 lx illumination (Swanepoel and Vermaak, 1977) at the prevalent temperature of the sampling station (20°C). Following incubation, the ^{32}P activity of both plant tissue and incubation media was determined as described above.

In situ ^{32}P absorption by the roots

Six millilitres interstitial water, obtained as described in the previous experiment, with an activity of 0.03 mCi ^{32}P , as phosphate, was injected into a *Potamogeton*-bed at a depth of 6 cm, using a syringe. The syringe was left undisturbed in order to identify the exact locality. After 72 h some plants surrounding the syringe were removed, as previously described, and rinsed in tap water. The plants were then dissected into roots, stems, and leaves, dried at 80°C for 24 h, and their dry mass recorded. The ^{32}P -activity of the plant organs were determined in a gasflow detector, as described.

In all the above experiments, the ^{32}P -activity (counts per minute) obtained for the individual samples, were converted to disintegrations per minute, after considering radioactive decay, quenching, and efficiency of the counting system.

Results and Discussion

The *in vitro* absorption of ^{32}P by intact and dissected *P. pectinatus* in media with high or low soluble reactive phosphorus (SRP) concentrations

Laboratory experiments to study the possible sites of nutrient absorption by tissues and cellular preparations of aquatic plants are not unusual (Denny, 1971). Thus, excised shoots and leaves of certain species were used by Arens (1933),

Rosenfels (1935), Ingold (1936), Steemann-Nielsen (1951), Lowenhaupt (1956) and Arisz (1960, 1964). McRoy *et al.* (1972) investigated the effect of the phosphorus concentration on the *in vitro* absorption of ^{32}P by intact and dissected *Z. marina*. They also established that phosphate was taken up by leaves, roots, and rhizomes, whether these organs were detached from the plant or not. Furthermore, a higher phosphorus concentration in the incubation medium increased phosphorus uptake in general, whilst uptake by detached organs exceeded that by intact plants at all the concentrations used. The results of our *in vitro* experiment on intact and dissected *P. pectinatus* in this regard are given in Table 1. Light and dark incubations were used to simulate day and night conditions for the shoots, whilst incubation of the roots in darkness simulates the darkness within the sediments.

Although excised organs would probably be more subject to ^{32}P penetration and/or leaching through cut surfaces, they were nevertheless included for comparison with the findings of McRoy *et al.* (1972). In order to compile Table 1, all activities (dpm) were converted to $\text{mg } ^{31}\text{P g}^{-1}$ dry mass absorbed.

It follows from Table 1 that all plant organs absorb ^{32}P under these experimental conditions, whether the plants were intact or not. Furthermore, a higher phosphorus concentration in the incubation medium increased the quantity of phosphorus ($\mu\text{g } ^{31}\text{P g}^{-1}$ dry mass) absorbed in all instances. Both these observations support the findings of McRoy *et al.* (1972). On the other hand, we did not find any consistently higher absorption values for detached organs as was the case with *Z. marina* (McRoy *et al.*, 1972). This may indicate the possibly unpredictable effect of leaching and/or easier penetration of ions through the cut surfaces.

When phosphorus absorption values ($\mu\text{g } ^{31}\text{P g}^{-1}$ dry mass) obtained for intact plants at low phosphate concentration (185 μg) under light conditions are compared with those following incubation in darkness, it seems that the roots absorb more phosphorus per equivalent dry mass than the leaves.

However, this situation is reversed when incubation oc-

TABLE 1
AVERAGE $\mu\text{g } ^{31}\text{P g}^{-1}$ DRY MASS ABSORBED BY INTACT AND DISSECTED *P. PECTINATUS* IN LOW (185 $\mu\text{g l}^{-1}$) AND HIGH (2 200 $\mu\text{g l}^{-1}$) SRP CONCENTRATIONS, IN THE LIGHT AND IN THE DARK

		Dissected Plants			Intact Plants		
		Roots	Stems	Leaves	Roots	Stems	Leaves
185 $\mu\text{g } ^{31}\text{P l}^{-1}$	$\mu\text{g } ^{31}\text{P g}^{-1}$	147	19	56	115	39	82
Light	CF*	2 450	317	933	1 917	650	1 367
185 $\mu\text{g } ^{31}\text{P l}^{-1}$	$\mu\text{g } ^{31}\text{P g}^{-1}$	73	25	79	80	47	75
Dark	CF	1 100	417	1 317	1 330	783	1 250
2 200 $\mu\text{g } ^{31}\text{P l}^{-1}$	$\mu\text{g } ^{31}\text{P g}^{-1}$	440	199	1 390	367	708	1 780
Light	CF	614	278	1 939	512	988	2 483
2 200 $\mu\text{g } ^{31}\text{P l}^{-1}$	$\mu\text{g } ^{31}\text{P g}^{-1}$	90	164	743	106	66	668
Dark	CF	125	229	1 036	148	92	932

*CF = Concentration factor.

curs under corresponding light and dark conditions but at high phosphate concentration ($2\ 200\ \mu\text{g}\ \ell^{-1}$). In natural water bodies, the phosphate concentration of the limnetic water is substantially lower than that of the bottom sediments (Holden, 1961; Hepher, 1966). It therefore follows that the roots of *P. pectinatus* are usually exposed to relatively higher phosphate concentrations (in the dark) than the foliage (in the light and in the dark). In order to equate the phosphorus absorption ability of the foliage with that of the roots, the leaf absorption values ($\mu\text{g}\ ^{31}\text{P}\ \text{g}^{-1}$ dry mass) at low phosphate concentrations (in the light and in the dark) should be compared with the values obtained for the roots at a high phosphate concentration; following incubation in the dark. When this is done, phosphate absorption ratios of 1:1,29 and 1:1,41 (shoots:roots) for these comparisons respectively, are obtained. The results indicate that under natural conditions, the roots may absorb more phosphorus than the foliage, although this difference is not substantial. However, this trend generally corresponds with that found in *Z. marina* (McRoy and Barsdate, 1971; McRoy *et al.*, 1972), and in *Egeria densa*, *Hydrilla verticillata*, and *Myriophyllum spicatum* (Barko & Smart, 1980), although not nearly to the same order of magnitude.

Although this experiment does not provide a direct indication of internal translocation of absorbed phosphate, certain deductions can however be made when the values obtained for intact plants are compared with those for dissected plants. Table 1 shows that at low and high phosphate concentrations and under light incubation, the concentration factor values (i.e. the ratio between the radio-activity of the plant ($\text{dpm}\ \text{mg}^{-1}$) and that of the incubation medium ($\text{dpm}\ \text{ml}^{-1}$) obtained for the leaves of the intact plants are higher than those for the dissected leaves. The corresponding values for the dissected roots are higher than those obtained for the intact roots. When the potential effects of leaching and/or easier penetration through the cut surfaces are discounted, a possible explanation for this phenomenon may be that some of the phosphate absorbed by the roots of the intact plants, was translocated to the stems and

leaves. Similarly, some of the phosphate absorbed by the foliage of intact plants was translocated to the roots during dark incubation. These assumptions seem reasonable, especially in view of the findings of McRoy and Barsdate (1970), McRoy *et al.* (1972); and Barko and Smart (1980).

It may thus be concluded that phosphorus is absorbed by the roots, stems and leaves of both intact and dissected plants; that the quantity of phosphorus thus absorbed is dependent upon the phosphate concentration of the medium; and, that translocation of absorbed phosphorus may possibly occur, i.e. basipetal translocation in the light (day), and acropetal in the dark (night). However, no definite conclusions could be drawn with regard to the possible release of absorbed phosphorus.

The effect of a higher SRP concentration in the root medium on the ^{32}P absorption and release of *P. pectinatus*

Swanepoel and Vermaak (1977) incubated *P. pectinatus* from a laboratory stream ecosystem in compartmentalised containers which were identical to the ones used for the present investigation. However, in their experiment there was no concentration gradient with regard to the SRP concentration of the incubation media of the foliar or root compartments. As has been pointed out above, this situation is unlikely to exist under natural conditions. Since Denny (1966) and Gerloff (1975) suggested that the prevalent nutrient concentrations may influence absorption by the roots and/or foliage, the present investigation was carried out to determine whether this applies to *P. pectinatus*. During the light incubations of their experiment, Swanepoel and Vermaak (1977) did not darken the root compartments of the containers, and it is therefore possible that illumination of the roots could well have affected the ^{32}P absorption and its release by these organs.

The data with regard to the ^{32}P activity of the incubation media and plant tissues for both Experiments A and B were converted to $\mu\text{g}\ ^{31}\text{P}\ \text{g}^{-1}$ dry mass absorbed and released, and is presented in Table 2.

AVERAGE $\mu\text{g}\ ^{31}\text{P}$ ABSORBED AND RELEASED (PER g DRY MASS) BY THE ROOTS AND SHOOTS OF *P. PECTINATUS* WITH AN INDICATION OF THE INCUBATION PROCEDURE

Exp.	^{32}P addition	Incubation	$\mu\text{g}\ ^{31}\text{P}\ \text{g}^{-1}$ absorbed		$\mu\text{g}\ ^{31}\text{P}\ \text{g}^{-1}$ translocated		$\mu\text{g}\ ^{31}\text{P}\ \text{g}^{-1}$ released	
			roots	shoots	roots	shoots	roots	shoots
A	^{32}P added to shoots	L	—	720	5	—	46	—
	^{32}P added to roots	L	2 413	—	—	5,3	—	2,2
	^{32}P added to shoots	D	—	723	0,35	—	45	—
	^{32}P added to roots	D	3 010	—	—	4	—	0,7
B	^{32}P added to shoots	L	—	954	1,1	—	82	—
	^{32}P added to roots	L	9 686	—	—	137	—	43
	^{32}P added to shoots	D	—	563	0,7	—	66	—
	^{32}P added to roots	D	2 447	—	—	39	—	30

*L = light incubation

D = dark incubation

According to these results the roots absorb four times as much ^{31}P g^{-1} during incubation in the light than in the dark. Although the shoots also absorb more ^{31}P g^{-1} during light incubation (954 compared to 563), the absorption values are respectively 10 and 4,4 times lower than the corresponding values for the roots. During light incubation, more ^{31}P is translocated from the roots to the shoots than during dark incubation (137 compared to 39). A similar tendency also applies with regard to translocation from the shoots to the roots. However, in this case, the values are significantly lower (1,1 in contrast with 0,7). Both the roots and shoots liberate more ^{31}P g^{-1} during light incubation than during dark incubation.

Comparing the results of Experiment B with those of Experiment A in which the SRP concentration of both compartments was the same as that of the shoot compartment of Experiment B, the following is revealed:

- The roots in Experiment B absorbed four times more ^{31}P during light incubation than those in Experiment A. However, the Experiment A roots absorbed 1,2 times more ^{31}P during dark incubation than those in Experiment B.
- The shoots in Experiment B absorbed more ^{31}P g^{-1} dry mass during light incubation than those in Experiment A (954 as opposed to 720). The situation is reversed during dark incubation (563 as against 723).
- With regard to the translocation of the absorbed ^{31}P , respectively 26 and 9,7 times more ^{31}P g^{-1} is translocated to the shoots in Experiment B during light and dark incubation than that occurring in Experiment A. Translocation from the shoots to the roots in Experiment B, during light and dark incubations, is respectively five times less and two times more than in Experiment A.
- The shoots in Experiment B release respectively 19 and 44 times more ^{31}P g^{-1} dry mass during light and dark incubations than those in Experiment A, while the roots release 1,8 and 1,5 times more ^{31}P g^{-1} dry mass respectively.

Evidently in this experiment, the concentration of SRP in the medium did affect absorption, translocation and release of ^{31}P by *P. pectinatus*. A higher SRP concentration in the medium surrounding the roots, is followed by an increased ^{31}P absorption by the roots during light incubation (day conditions). There is also an increased translocation of ^{31}P to, and increased release of ^{31}P by the foliage. However, for the same SRP concentration, but during dark incubation, less ^{31}P g^{-1} dry mass is absorbed by the roots; nevertheless, a larger fraction of the latter is translocated to and released by the foliage than is the case when there is no SRP concentration gradient between the root and foliar compartments.

A higher SRP concentration in the root compartment does affect the ^{31}P absorption by the foliage, translocation to the roots and concomitant release of ^{31}P by the roots. This applies to both light and dark incubations. However, according to the results, the latter phenomenon is negligible.

The *in situ* absorption of ^{32}P by *P. pectinatus*

The ^{32}P activity of the roots, stems, and leaves of *P. pectinatus*, 72 h after radio-active phosphorus was injected into the sediment in a *Potamogeton* bed, is shown in Table 3. It is evident from these data that ^{32}P was absorbed by the roots of this macro-

TABLE 3
AVERAGE DRY MASS (g) AND ^{32}P -ACTIVITY (dpm) OF THE ROOTS, STEMS AND LEAVES OF *POTAMOGETON PECTINATUS* 72 HOURS AFTER INJECTING ^{32}P INTO THE SUBSTRATE

Organ	Dry mass	dpm	dpm g^{-1}
roots	13	6 047 132	465 164
stems	27	259 473	9 610
leaves	21,73	506 243	23 297

phyte, followed by translocation to the foliage. This supports the findings of Bristow and Whitcombe (1971), amongst others, on similar investigations in some submerged aquatic macrophytes. It was assumed that the radio-isotope, due to chemical exchange processes in the sediment, would not become homogeneously mixed with the phosphate of the interstitial water. Consequently, the data in Table 3 is expressed only in terms of the ^{32}P activity although the mass of ^{32}P added and the SRP concentration of the interstitial water was known.

Conclusions

The experiments described above demonstrate that (i) the roots of *P. pectinatus* absorb ^{32}P *in situ*; (ii) both the roots and foliage of this species absorb ^{32}P from their respective environments; and (iii) both the roots and foliage release a small fraction of the absorbed ^{32}P , after translocation.

On the basis of the above-mentioned findings as well as that by Swanepoel and Vermaak (1977), it was decided to use the compartmentalized container method to study the uptake and release of ^{32}P by *P. pectinatus* in Germiston Lake, on a seasonal basis. The results of this experiment which showed the existence of a seasonal variance in phosphorus uptake, translocation, and release, will be dealt with in a separate paper.

References

- A.P.H.A. (1971) Standard Methods for the examination of water and waste water. American Public Health Association. Washington D.C. 13th Edition.
- ARBER, A. (1920) *Water plants*. Cambridge. 436 pp.
- ARENS, K. (1933) Physiologisch polarisierter Massenaustausch und Photosynthese bei submersen Wasserpflanzen, 1. *Planta* **20** 621–58.
- ARISZ, W.H. (1953) Active uptake, vacuole secretion and plasmatic transport of chloride ions in leaves of *Vallisneria spiralis*. *Acta. Botan. Neerl.* **1** 506–515.
- ARISZ, W.H. (1960) Translocation of salts in *Vallisneria* leaves. *Bull. Res. Coun. Israel* **8**(d) 247–57.
- ARISZ, W.H. (1964) Influx and efflux of electrolytes. II. Leakage out of cells and tissues. *Acta. bot. Neerl.* **13** 1–58.
- BARKO, J.W. and SMART, R.M. (1980) Mobilization of sediment phosphorus by submersed freshwater macrophytes. *Freshwater Biology* **10** 229–238.
- BOYD, C.E. (1971) The limnological role of aquatic macrophytes and their relationship to reservoir management. In: Hall, E.G. (Ed). *Reservoir fisheries and limnology*. Am. Fish. Soc. Special Publ. No. 8, Washington. pp.153–166.

- BRISTOW, J.M. and WHITCOMBE, M. (1971) The role of roots in the nutrition of aquatic vascular plants. *Amer. J. Bot.* 58(1) 8-13.
- DAVIS, R.B. (1974) Stratigraphic effects of tubificids in profundal lake sediments. *Limnol. Oceanogr.* 19 466-488.
- DAVIS, R.B., THURLOW, D.L. and BREWSTER, F.E. (1975) Effects of burrowing tubificid worms on the exchange of phosphorus between lake sediment and overlying water. *Verh. Int. Verein. Limnol.* 19 382-394.
- DE MARTE, J.A. and HARTMAN, R.T. (1974) Studies on absorption of ^{32}P , ^{59}Fe and ^{45}Ca by water-milfoil (*Myriophyllum exalbescens* Fernald) *Ecology* 55 188-194.
- DENNY, P. (1966) A study of some factors affecting the distribution of aquatic macrophytes. Ph.D. thesis, University of St. Andrews.
- DENNY, P. (1971) Zonation of aquatic macrophytes around Habukara Island, Lake Bunyonyi, S.W. Uganda. *Hidrobiologia* 12 249-57.
- DENNY, P. and WEEKS, D.C. (1970) Effects of light and bicarbonate on membrane potential in *Potamogeton schweinfurthii* (Benn.) *Ann. Bot. N.S.* 34 438-476.
- FOEHRENBACH, J. (1969) Pollution and eutrophication problems of Great South Bay, Long Island, New York. *J. Water Pollut. Control. Fed.* 41 1456-1466.
- GERLOFF, G.C. (1975) Nutritional ecology of nuisance aquatic plants U.S., EPA., EPA - 660/3-75-027.
- HAYES, F.R. (1964) The mud-water interface. *Oceanogr. Mar. Biol. Rev.* 2 121-145.
- HAYES, F.R. and PHILLIPS, J.E. (1958) Lake water and sediment. IV. Radiophosphorus equilibrium with mud, plants, and bacteria under oxidized and reduced conditions. *Limnol. Oceanogr.* 3 459-475.
- HEPHER, B. (1966) Some aspects of the phosphorus cycle in fish ponds. *Verh. Int. Ver. Limnol.* 16 1293-1297.
- HOLDEN, A.V. (1961) The removal of dissolved phosphate from lake waters by bottom deposits. *Verh. Int. Ver. Limnol.* 14 247-251.
- INGOLD, C.T. (1936) The effect of light on the absorption of salts by *Elodea canadensis*. *New Phytol.* 35 132-141.
- LEAN, D.R.S. (1973a) Phosphorus compartments in lake water. Ph.D. Thesis, University of Toronto, Canada, 192 pp.
- LEAN, D.R.S. (1973b) Phosphorus dynamics in lake water. *Science N.Y.* 179 678-680.
- LEAN, D.R.S. (1973c) Movements of phosphorus between its biologically important forms in lake water. *J. Fish. Res. Bd. Can.* 30 1525-1536.
- LOWENHAUPT, B. (1956) The transport of calcium and other cations in submerged aquatic plants. *Biol. Rev.* 31 371-395.
- McROY, C.P. and BARSDATE, R.J. (1970) Phosphate absorption in eelgrass. *Limnol. Oceanogr.* 15 6-13.
- McROY, C.P., BARSDATE, R.J. and NEBERT, M. (1972) Phosphorus cycling in an eelgrass (*Zostera marina* L.) ecosystem. *Limnol. Oceanogr.* 17 58-67.
- MORTIMER, C.H. (1941) The exchange of dissolved substances between mud and water in lakes (Parts I and II). *J. Ecol.* 29 280-329.
- MORTIMER, C.H. (1942) The exchange of dissolved substances between mud and water in lakes (Parts III, IV, summary and references). *J. Ecol.* 30 147-201.
- MORTIMER, C.H. (1971) Large-scale oscillatory motions and seasonal temperature changes in Lake Michigan and Lake Ontario. Spec. Rept. No. 12., Center for Great Lakes Studies, University of Wisconsin, Milwaukee. Part I, Text III pp. Park II, Illustrations, 106 pp.
- MOYLE, J.B. (1945) Some chemical factors influencing the distribution of aquatic plants in Minnesota, *Amer. Midl. Nat.* 34 402-420.
- OLSEN, S. (1958a) Phosphate absorption and isotopic exchange in lake muds. Experiments with ^{32}P . *Verh. Int. Verein. Limnol.* 13 915-922.
- OLSEN, S. (1958b) Fosfatbalancen mellom bund og vand i Furesø. Forsøg med radioaktivt fosfor. *Folia Limnol.* 10 39-96.
- OLSEN, S. (1964) Phosphate equilibrium between reduced sediments and water. Laboratory experiments with radioactive phosphorus. *Verh. Int. Verein. Limnol.* 15 333-341.
- PEARSALL, W.H. (1920) The aquatic vegetation of the English Lakes. *J. Ecol.* 8 163.
- POMEROY, L.R., SMITH, E.E. AND GRANT, C.M. (1965) The exchange of phosphate between estuarine water and sediments. *Limnol. Oceanogr.* 10 167-172.
- REEBURGH, W.S. (1967) An improved interstitial water sampler. *Limnol. Oceanogr.* 12 163-165.
- REIMOLD, R.J. (1972) The movement of phosphorus through the salt marsh cord grass, *Spartina alterniflora* Loisel. *Limnol. Oceanogr.* 17 606-611.
- RICKETT, H.W. (1921) A quantitative study of the larger aquatic plants of Lake Mendota, Wisconsin. *Trans. Wis. Acad. Sci. Arts Lett.* 20 501-527.
- RIGLER, F.H. (1973) A dynamic view of the phosphorus cycle in lakes. In: E.J. Griffith, A. Beeton, J.M. Spencer and D.T. Mitchell, (Eds). *Environmental Phosphorus Handbook*. John Wiley and Sons, N.Y., pp.539-572.
- ROSENFELS, R.S. (1935) The absorption and accumulation of potassium bromide by *Elodea* as related to respiration. *Protoplasma* 23 503-519.
- STEMANN-NIELSEN, E. (1951) Passive and active ion transport during photosynthesis in water plants. *Physiologia Pl.* 4 189-198.
- SUTCLIFFE, J.F. (1962) *Mineral salts absorption in plants*. Pergamon Press, Oxford.
- SWANEPOEL, J.H. and VERMAAK, J.F. (1977) Preliminary results on the uptake and release of ^{32}P by *Potamogeton pectinatus*. *J. Limnol. Soc. Sth. Afr.* 3(2) 63-65.
- TWILLEY, R.R., BRINSON, M.M. and DAVIS, G.J. (1977) Phosphorus absorption, translocation and secretion in *Nuphar luteum*. *Limnol. Oceanogr.* 22(6) 1022-1032.
- VERMAAK, J.F., SWANEPOEL, J.H. and SCHOONBEE, H.J. (1976) Absorption and accumulation of ^{32}P by *Oedogonium* and some aquatic macrophytes. *Water SA* 2(1) 7-12.
- WANG, D.H., WILLIS, D.L. and LOVELAND, W.D. (1975) *Radio-tracer methodology in the biological, environmental and physical sciences*. Prentice-Hall, New Jersey, 480 pp.
- WELCH, P.S. (1948) *Limnological Methods*. Blakiston Co., Philadelphia, 381 pp.
- WILSON, L.R. (1939) Rooted aquatic plants and their relation to the limnology of freshwater lakes. pp. 107-122. In: *Problems of lake biology*. Publ. Amer. Assoc. Adv. Sci. No. 10.