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Decomposition of Leaves from *Amphibolis antarctica* (Labill.) Sonder et Aschers. and *Posidonia australis* Hook. f. the Major Seagrass Species of Shark Bay, Western Australia

D. I. Walker and A. J. McComb

Department of Botany, University of Western Australia, Nedlands, W. A. 6009, Australia

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Abstract

In situ decomposition studies were carried out using litter bags. Losses in dry weight, phosphorus, nitrogen and organic carbon were followed during two experiments, initiated at the times of highest and lowest water temperatures.

Initial nutrient concentrations were low for both species, at both times of year, $< 1 \text{ mg g}^{-1}$ total phosphorus, and $< 11 \text{ mg g}^{-1}$ total nitrogen, but were higher in winter than in summer. Rates of loss of all material for both species were similar, and were best described mathematically by a linear equation. The loss rate was $0.5\% \text{ day}^{-1}$, giving a time for complete decomposition of about 200 days. The significance of this fast rate is discussed in relation to the nutrient budget of seagrass meadows, in a nutrient poor environment.

Introduction

The extensive seagrass beds which occur in Shark Bay, Western Australia, have had an effect on the geomorphology of the area, by reducing current velocity and increasing rates of sedimentation, and because of the deposition of calcareous skeletal materials from epiphytes and infauna (Hagan and Logan 1974). They are also largely responsible for the marked reduction of carbon (as total CO_2) and phosphorus concentrations in the Bay, as compared with the waters of the adjacent open ocean (Smith and Atkinson 1983). They are of biological significance in supporting a variety of food chains as there are relatively high densities of turtles and dugongs and, perhaps of more significance, considerable numbers of particulate filter feeders, which presumably form the basis of the large amateur and commercial fish catches in the area (Anon 1982).

Two of the most common seagrasses in the area, *Amphibolis antarctica* and *Posidonia australis*, produce and discard large amounts of leaf material. The 'turnover' time for a leaf standing crop is about 65

days in *A. antarctica*, and 92 days in *P. australis* (Walker and McComb unpubl. data). Such discarded leaf material may act as an important source of material for detrital food chains (Klug 1976, Fenchel 1977). Another aspect of the decomposition of leaf material is its significance for the nutrient budgets of the seagrasses themselves. In Shark Bay, high rates of production (up to $17 \text{ g m}^{-2} \text{ d}^{-1}$) are maintained over large areas, in a nutrient-poor environment (Walker 1985); concentrations of phosphorus in the water are very low (typically $0.02\text{--}0.1 \text{ mmol m}^{-3}$, Smith and Atkinson 1983), and the meadows themselves represent a major bank of nutrients. Release of nutrients from plant material through decomposition may be important in nutrient retention within these meadows, and in recycling of nutrients in the Shark Bay ecosystem.

No information was available on rates of decomposition of seagrass leaf material anywhere on the Western Australian coastline. Although emphasis has been given to microbiological aspects of seagrass decomposition under laboratory conditions (eg. God-

shalk and Wetzel 1979a, b, c), it was felt that for our purposes it was more relevant to examine rates *in situ*. The litter bag technique was used because, although it is clearly not a perfect solution to understanding decomposition rates in the field (Godshalk and Wetzel 1979a, Marinucci 1982), it provided the most practicable method for obtaining the estimates required at this remote locality.

Materials and Methods

From the seagrass bed adjacent to Monkey Mia, Shark Bay (Fig. 1), large bags of intact plants of *A. antarctica* and *P. australis* were collected by snorkelling, and the older leaves were immediately separated. In *Amphibolis* these were the outer leaves from each leaf cluster, and in *Posidonia* the oldest leaf on each turion. Any large epiphytes were removed by hand, but no scraping was carried out, to prevent damage to the leaf surface. The leaves were left intact, as would occur in the natural process of decomposition.

Samples (20 g wet wt) of leaf material of each species were placed in nylon mesh bags (15 cm square, 2 mm mesh). The necks of the bags were tied and attached to buoyed ropes, one rope per species. The complete structure was taken to the experimental site near to the point of collection, with the seagrass bags remaining wet and in darkness during transport. After deployment the ropes were arranged so that the bags were free to follow changes in buoyancy of the seagrass material.

At zero time and thereafter at approximately 6-week intervals, 5 bags were removed for each species, the contents dried to constant weight and concentrations of organic carbon, total phosphorus, and total nitrogen determined. Organic carbon was obtained by ashing (600 °C, 2 h) and multiplying the ash-free dry weight by 0.44 (Westlake 1963). Total nitrogen was obtained by Kjeldahl digestion, the ammonia determined colorimetrically using a Technicon Autoanalyser II (Technicon Method 334-74w/B, Technicon Industrial Systems, New York). Total phosphorus was determined by the single solution method, following perchloric digestion (Major *et al.* 1972). Regression analyses were carried out on the results for each species, nutrient and time combination, and also including or excluding the result obtained at the final collection (0 in all cases).

Litter bags were deployed in March 1982, the time of highest water temperature (26 °C), and again in August, when temperature was lowest (17 °C) (Logan *et al.* 1970, and pers. obs.).

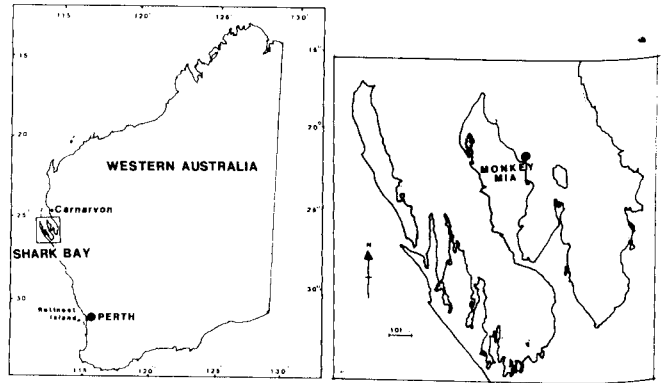


Fig. 1. Location Map, showing the position of Shark Bay on the West Australian Coastline, and the study site (●) Monkey Mia.

Results

Observations

Amphibolis leaves are negatively buoyant when shed, so that most leaf litter is usually found in or adjacent to the beds in which it is produced. In contrast, older leaves of *Posidonia* have some positive buoyancy, and may float on the water surface for a few days. Following storm events, beaches facing the prevailing wind usually accumulate large banks of drift; these are normally composed only of *Posidonia* leaves, despite the dominance of *Amphibolis* in the Bay on a cover basis. However under calmer conditions, when tidal movements are more important, considerable amounts of *Posidonia* drift are trapped in the seagrass beds.

When the litter bags were deployed, those containing *Amphibolis* sank to the bottom, whereas those with *Posidonia* floated. When the first samples were recovered 8 days later, the *Posidonia* bags had also sunk; thus the technique allowed for the difference in buoyancy between the species.

On subsequent collections, apart from the last, the leaf structures were still apparent, although the material was blackened and there was an obvious decrease in the amount present. At the time of the final sampling (*ca.* 200 days) no material of either species remained in the bags.

Initial nutrient concentrations

Concentrations were initially similar in the leaves of *Amphibolis* and *Posidonia* (Table I), but there were seasonal differences; carbon, nitrogen and phosphorus were some 30% higher at the commencement of the second, winter, experiment. The N:P ratios were also similar at about 10.5–11.6:1; tissue concentrations of these nutrients were below the levels of 1.3 mg g⁻¹ dry wt for phosphorus and 13 mg g⁻¹ dry wt for nitrogen, found by Gerloff and Krombholz

Table I. Concentrations in starting material

	°C	Carbon (mg g ⁻¹)	Phosphorus (mg g ⁻¹)	C:P	Nitrogen (mg g ⁻¹)	C:N	N:P ratio
<i>Posidonia</i>	26°	222.83	0.76	293:1	8.49	26:1	11.2
	17°	284.03	0.95	299:1	10.99	26:1	11.6
<i>Amphibolis</i>	26°	244.10	0.67	364:1	7.68	32:1	11.46
	17°	257.90	0.92	280:1	9.61	27:1	10.45

(1966) to be critical for supporting maximum growth in a number of aquatic plants.

Decomposition

Loss rates are shown in Figs 2 and 3, where the small standard errors indicate the usefulness of using wet weights as a technique for obtaining replicates in such experiments. In both species, there was little change during the first 8 days, followed by a rapid decrease in the weight remaining in the bags. Nutrient concentrations remained relatively constant, indicating similar loss rates (Fig. 3). An exception is the fall in phosphorus concentration in the tissue of *Posidonia* in winter, and the suggestion of a similar trend in *Amphibolis*.

During decay, the ratios of C:N therefore remained approximately constant, but C:P ratios for *Posidonia* rose in winter because of the preferential loss in phosphorus; this resulted in an increase in the N:P ratio from 11.0 initially, to 12.3, 18.0 and 37.4 at the different harvests. The reason for the preferential loss of phosphorus, not seen for *Amphibolis* (though the N:P ratio rose to 14.0 on the third winter harvest), remains obscure, although phosphorus was at a higher initial concentration in the winter period.

Wieder and Lang (1982) discussed the different equations which have been used to analyse such data, and pointed out the usefulness of single exponential curves. They suggested that an important criterion for the validity of an equation used to describe decomposition rates is that it should predict the mass of material at time 0 (M_0). Highest correlation coefficients were obtained by including the final data point, and using a linear equation to describe the data. A linear equation also gave a closer approximation to M_0 than did an exponential function which produced over-estimates of M_0 . All r values were highly significant ($p < .01$). Where the final point was omitted, the predicted time of total loss from the bags (Table II) was close to that observed. However, the time predicted was shorter than that observed, suggesting that total loss of material from the litter bags occurred prior to the time of final collection.

Table III summarizes the results obtained for the rates of loss (regression coefficients) for each nutrient and species. There are no consistent or significant trends at different times, and no significant change in decomposition rate when integrated over the time of the experiments.

Table II. Theoretical time (days) for complete decomposition, calculated from the appropriate regression coefficients for the first 4 harvests. All material had been lost from the litter bags by 200 days.

	<i>Posidonia</i>				<i>Amphibolis</i>			
	Experiment 1		Experiment 2		Experiment 1		Experiment 2	
	\bar{x}	Range (SE)	\bar{x}	Range (SE)	\bar{x}	Range (SE)	\bar{x}	Range (SE)
Dry wt	176	170-182	321	285-366	233	212-257	169	156-184
TP	232	198-279	153	142-165	253	225-288	161	143-184
TN	189	175-204	376	323-450	267	241-298	156	143-171
Org. C	178	172-186	229	212-249	205	193-220	161	149-175

Table III. Loss rates (percent day⁻¹) of all material from *P. australis* and *A. antarctica* during the two experiments ($\bar{x} \pm$ s.e.)

	<i>Posidonia</i>		<i>Amphibolis</i>	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2
Dry wt.	.487 ± .018	.486 ± .033	.450 ± .024	.519 ± .027
TP	.455 ± .041	.508 ± .033	.436 ± .029	.492 ± .045
TN	.482 ± .025	.464 ± .057	.434 ± .025	.520 ± .034
Carbon	.458 ± .022	.505 ± .021	.461 ± .019	.521 ± .023

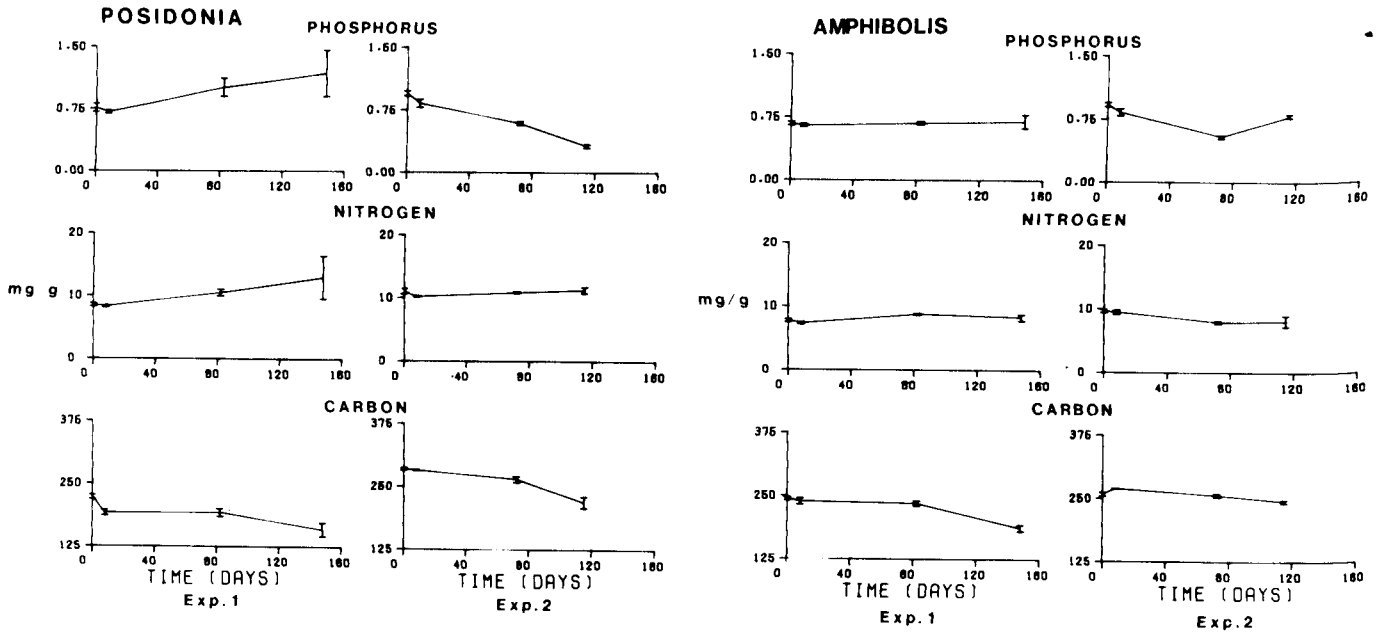


Fig. 2. The concentrations of each component for both species during both experiments. (Exp. 1, 26 °C; Exp. 2, 17 °C)

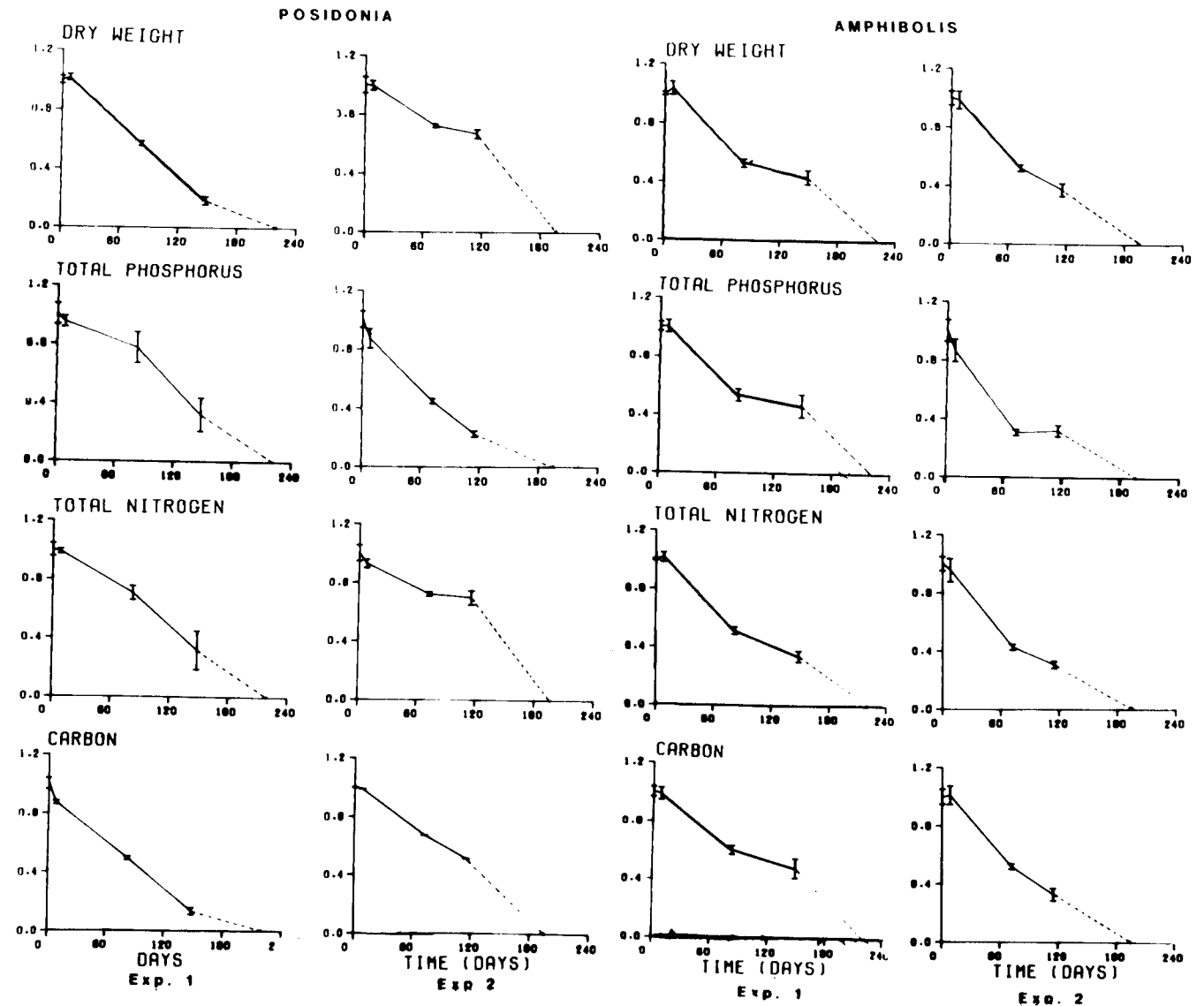


Fig. 3. Relative proportions of the initial mass of each component, for both species, during both experiments.

Discussion and Conclusions

Although no significant differences in nutrient concentrations were observed during the first 8 days, the alteration in buoyancy of *Posidonia* suggests a marked change in leaf physiology. In *Amphibolis*, similar physiological changes may have already taken place during the last phases of leaf maturation, as although the leaves used here were negatively buoyant, leaf clusters of the intact plant are positively buoyant. Although under storm conditions *Posidonia* drift is deposited on beaches, under calmer conditions relatively little *Posidonia* is found in beach drift, compared with the amount produced in the meadow. Kirkman and Reid (1979) found that most leaves of *Posidonia australis* in an estuary in new South Wales remained to decay within the seagrass beds.

Material was lost at a linear rate, with all components having a similar loss rate of $0.5\% \text{ d}^{-1}$. Few data are available for comparison. Klumpp and van der Valk (1984) provide the first published account of seagrass decomposition in Australia for the species *Heterozostera tasmanica* and for *Posidonia australis* in Victoria. They found rates of $0.4\% \text{ day}^{-1}$ for *Heterozostera*, but only $0.13\% \text{ day}^{-1}$ for *Posidonia*, a much lower rate than in the present study. However, in comparison to Shark Bay, water temperatures were generally lower during their study and the sites were not subjected to a high current regime.

Comparisons with other decomposition experiments are difficult. Much work has been done on emergent salt-marsh plants which have much higher proportions of structural tissue, giving correspondingly lower decomposition rates. These resemble those of terrestrial plants; for example, a rate of $0.14\% \text{ d}^{-1}$ has been given for *Spartina* (White and Trapani 1982). Most seagrass studies have been carried out on material which has been dried and/or frozen (eg.

Rice and Tenore 1981), and this gives rise to a rapid initial leaching phase due to the rupture of cell membranes during tissue preparation; there may then be a lag before the remaining material begins to decay. For example, Rogers and Breen (1982) found that drying has a significant effect on the rate of decomposition of *Potamogeton*. Harrison and Mann (1975) discuss the relative importance of leaching, fragmentation and microbial decay in decomposition of *Zostera* leaves. In laboratory experiments, they attributed most of the initial loss to leaching, but at a faster rate if the leaves were dried first. Other problems include the use of complete seagrass plants, including the younger leaves which have not been subjected to the natural processes of senescence on the plant, and may decompose at a different rate.

Decomposition rates for some aquatic angiosperms are given in Table IV. The rates obtained in this experiment are similar to, or slightly lower than, other data obtained in field experiments, but higher than those from laboratory conditions.

Mean rates of decomposition (Table III) were similar during the two experiments here, despite the difference in temperature of about 10°C . Comparing the mean rate of carbon loss (all harvests), the results were 10–11% higher for both species at the lower temperature. This may be related to the presence of different suites of microorganisms on the two occasions, with different temperature optima, and emphasises the value of *in situ* studies at appropriate times of year.

Loss rates from other decomposition experiments have mainly been analyzed using at least a single exponential relationship, but the losses observed here were generally linear. A linear loss rate was also found by Rogers and Breen (1982) for *Potamogeton* and by Hillman (pers. comm.) for *Halophila*. An exponential rate is not apparent in the data of Schmidt

Table IV. Comparison of Rates of Decomposition of Aquatic Angiosperms (F = in situ experiments; L = laboratory experiments; D = dried material)

Taxon	Type	Rate (% day^{-1})	Reference
<i>Potamogeton</i>	F	4.0	Rogers and Breen 1982
<i>Potamogeton</i>	F, D	18.0, 2.0	Rogers and Breen 1982
<i>Potamogeton</i>	F	2.0	Howard-Williams and Davies 1979
<i>Thalassia</i>	F	1.5	Zieman 1975
<i>Halophila</i>	F	1.5	Hillman (unpubl. data)
<i>Zostera</i>	F	0.8	Nienhuis 1980
<i>Zostera</i>	F	0.4	Schmidt 1980
<i>Zostera</i>	L	0.5	Harrison and Mann 1975a
<i>Zostera</i>	F, D	0.2	Mann 1976
<i>Thalassia</i>	L	1.1	Knauer and Ayers 1977
<i>Thalassia</i>	L	0.12	Rice and Tenore 1981
<i>Syringodium</i>	L	0.07	Rice and Tenore 1981

(1980) for *Zostera marina in situ*, nor is an exponential rate strongly supported by the data of Knauer and Ayers (1977) for *Thalassia* or of Rice and Tenore (1981) for *Syringodium* and *Thalassia*. Although Wieder and Lang (1983) suggest that linear rates are biologically unrealistic, two factors may be important. Seagrass leaves have large amounts of cellulose, rendering the leaves sufficiently robust to withstand considerable mechanical stress, but in contrast to many other plants there is little lignification, presumably to maintain flexibility (Kuo 1978). Thus as decomposition proceeds there will not be an increasingly significant residue of intractable material. The second factor is that the ultimate stages of decomposition are not measured in experiments of the type described here – what is observed is loss of material < 2 mm, much of which would be suitable for filter-feeding organisms. These smaller particles may also have faster rates of decomposition. Harrison and Mann (1975a) found that particles less than 1 mm had rates of loss of 1% day⁻¹, whereas the rate for whole leaves was 0.5% day⁻¹.

The nutritional quality of such particles, and the changes which occur as decomposition proceeds are open to debate. No consistent trends were observed in the value of the C:N ratios. All C:N ratios were greater than the 17:1 value proposed by Russell-Hunter (1970) as adequate for animal nutrition, except for that of the final sample of *Posidonia* detritus in the summer experiment (C:N = 12.3). Knauer and Ayers (1977) found a similar trend with variable C:N ratios in the later stages of decomposition of *Thalassia* and suggested that the seagrass plus bacterial assemblage was actually a poorer source of nutrition than the seagrass alone. In contrast, Harrison and Mann (1975a) observed decreases in the C:N ratios and attributed them to increases in microbial numbers. However, in their 1975b paper they suggested the C:N ratio was an unreliable indicator of nutritional quality as the material was so seasonally variable. Thayer *et al.* (1977) also found high C:N ratios and proposed that a C:N ratio of 17:1, derived from terrestrial mammalian studies may not apply to marine herbivores and detritivores. Given the extremely high C:N ratios for fresh and detrital material of both seagrass species here, it would seem that this must be the case for the seagrass in Shark Bay to support the large animal populations present in the bay.

Loss rates for all components examined were about 0.5% d⁻¹, giving a time of reduction to particles < 2 mm of 200 d. Leaf turnover times (i.e. the average life span of a leaf) are 65 d for *Amphibolis* and 92 d for *Posidonia* (Walker and McComb, unpubl. data). That is, *Amphibolis* leaves take about 3 times as long to decay as they do to grow and function in the head, while for *Posidonia* the value is 2 times. As a first approximation, we might therefore expect there to be on average about 3 times (for *Amphibolis*) and twice (for *Posidonia*) as much leaf material in various stages of dissolution in the ecosystem, as there are leaves on the seagrass plants. This represents a large input to the detrital pathways, as well as a considerable pool of nutrients.

Since a large proportion of decomposition occurs within the seagrass beds, it may be assumed that at least part of the nutrient pool released during decomposition becomes available for seagrass growth. The pathway for such recycling would be complex, but might involve trapping by leaves and epiphytes, remineralization within the sediments, and uptake by roots as well as leaves. However, the proportion of nutrients derived from decomposition of shed material would be considerable; a single leaf standing crop would release the equivalent of 33% of the nutrients required during the growth of a new leaf crop in *Amphibolis*, and 46% for *Posidonia*. Nutrient recycling within the plants by withdrawal and redeployment of nutrients within the parent plant as leaves senesce has been discussed elsewhere (McComb *et al.* 1981) and would supplement the external nutrient recycling mentioned here. The present work emphasises the possible magnitude of nutrient cycling through decomposition, and its potential significance in a nutrient-poor environment.

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