

## REVIEW

# The balance of nutrient losses and gains in seagrass meadows

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**ABSTRACT:** Seagrasses abound in the dynamic environment of shallow marine waters. From the often high annual biomass production it can be deduced that seagrass meadows have high requirements for inorganic nutrients, although the nutrient demands will be met to some extent by internal recycling. A series of processes lead to nutrient losses from the seagrass bed. Export of leaves and leaf fragments with currents, leaching losses from photosynthetically active leaves and from senescent and dead plant material, and nutrient transfer by mobile foraging animals, are processes specific to seagrass meadows; in addition, the nutrient losses are aggravated by 2 processes commonly occurring in marine sediments: denitrification and diffusion of nutrients from the sediments to the overlying water column. The persistence in time of most seagrass meadows points to an existing balance between nutrient losses and gains. Three processes may contribute to the replenishment of nutrients: nitrogen-fixation, sedimentation and nutrient uptake by the leaves. Nitrogen-fixation undoubtedly is important, but continued biomass production requires other nutrients as well. Crucial contributions, therefore, must come from sedimentation and/or leaf uptake. The concept of the seagrass meadow as an open system, with nutrient fluxes from and to the system varying in time, allows for imbalances between nutrient losses and gains. It is suggested that these imbalances may contribute to fluctuations in annual seagrass biomass production.

## INTRODUCTION

Seagrass meadows are the biological and physical foundation for many coastal marine ecosystems from the tropics to boreal regions. These meadows have a high nutrient demand, to support their high annual production, which ranks them among the most productive of submerged aquatic ecosystems (Zieman & Wetzel 1980, Hillman et al. 1989). The nutrients involved, however, are not all retained within the seagrass beds. In the dynamic environment of the shallow marine waters, a continual loss of nutrients may occur; the export of sloughed and decomposing leaves is only one of the more conspicuous processes contributing to this loss. If only export of nutrients occurred, the impoverishment of the biotope ultimately would lead to the disappearance of the seagrass vegetations. Obviously, their persistence in time will depend on mechanisms effecting a continuous replenishment of nutrients. In this paper, we examine the processes which contribute to either nutrient losses or gains (Table 1). The quantitative importance of the individual processes is indicated as much as the available data allow. We begin

with a discussion of the annual nutrient requirements for seagrass growth, offering a background against which the importance of the various processes can be assessed. The long-standing view that seagrass production is often nitrogen limited has resulted in a relatively large number of papers dealing with nitrogen dynamics in seagrass systems, and emphasis therefore will be on nitrogen in this review. However, it is obvious that nutrient losses and gains in seagrass meadows will not be restricted to nitrogen, but will also include

Table 1. Processes contributing to the loss or gain of nutrients in seagrass meadows (discussed in this paper)

### Losses

Exudation/leaching from living and dead plant material  
Export of sloughed leaves and leaf fragments  
Nutrient transfer by foraging animals  
Denitrification  
Diffusion from sediment

### Inputs

Nitrogen-fixation  
Sedimentation  
Nutrient uptake by leaves

other important nutrients such as phosphorus, which recently has been put forward as a limiting factor for seagrass vegetation on carbonate sediments (Short 1987, Short et al. 1990).

### ANNUAL NUTRIENT REQUIREMENTS FOR SEAGRASS GROWTH

Considering the high primary productivity of seagrasses and the chemical composition of the plant parts, it is easy to determine that seagrasses have high requirements for inorganic nutrients. For one widespread species, *Zostera marina* (eelgrass), short-term measurements of above-ground primary production during the time of peak growth give rates of 5 to 19 g dry wt  $m^{-2} d^{-1}$  (Sand-Jensen 1975, Jacobs 1979, Mukai et al. 1979, Thorne-Miller & Harlin 1984, Hamburg & Homan 1986, Kentula & McIntyre 1986, Ibarra-Obando & Huerta-Tamayo 1987, Roman & Able 1988, Umebayashi 1989). These values correspond to 150 to 574 mg N  $m^{-2} d^{-1}$  (Borum et al. 1989, Umebayashi 1989). Allowing for seasonal variation in rates of primary production and growth, on an annual basis the above-ground primary production of eelgrass growing in both the Atlantic and Pacific Ocean has been estimated as 440 to 1400 g dry wt  $m^{-2}$  (Sand-Jensen 1975, Jacobs 1979, Kentula & McIntyre 1986, Murray & Wetzel 1987, Roman & Able 1988). Assuming a range of nitrogen content of 1.5 to 3 % (Harrison & Mann 1975, Thayer et al. 1977), the annual nitrogen requirement for leaf growth will be somewhere between 6.6 and 42 g N  $m^{-2}$ . For tropical species similar requirements have been calculated; e.g. 9 g N  $m^{-2} yr^{-1}$  for *Posidonia australis* and 18 g N  $m^{-2}$  for *Amphibolis antarctica* (Walker & McComb 1988). The below-ground parts also require nitrogen, but their needs are small compared with those of the leaves, e.g. 7 % (Umebayashi 1989) to 11 % (Kenworthy & Thayer 1984) for eelgrass. Nonetheless, the range of annual requirement for nitrogen will extend to a somewhat higher value than 42 g N  $m^{-2}$ , but probably not higher than 50 g N  $m^{-2}$ , when below-ground biomass production is included.

The annual nutrient requirements for primary production may to some extent be met by internal recycling processes. Senescence of seagrass leaves is accompanied by a decrease in certain chemical constituents, e.g. carbon (20 to 25 %: Harrison & Mann 1975; 36 %: Thayer et al. 1977) and nitrogen (20 to 25 %: Harrison & Mann 1975; 21 %: Thayer et al. 1977). Phosphorus content, too, declines with age by as much as 40 to 60 % (Walker & McComb 1988, Umebayashi 1989). These changes may be partly the result of conservation mechanisms operating in the plant, with selected components being removed from aging leaves

and transported to sites of growth and storage (Chapin 1980). Recent empirical support for this idea is found in the work of Borum et al. (1989). They found that older leaves did lose substantially more of their nitrogen (42 % and 57 % of the initial content from the fourth and fifth youngest leaves, respectively) than did younger leaves (e.g. only 3 % from the second leaf) during 1 wk, but translocation accounted for 92 % of the loss. Even when eelgrass shoots had adequate external supplies of nitrogen (i.e. 50  $\mu mol$  ammonium  $l^{-1}$ ), the youngest 2 leaves obtained about 2/3 of their new nitrogen via translocation from older leaves. Young rhizome segments were another sink for nitrogen mobilized from older leaves. Borum et al. (1989) used the difference between the maximum leaf nitrogen content (in the almost fully grown, third-youngest leaf) and the content of old leaves just before they were sloughed to estimate that 24 % of the nitrogen needed for new leaf growth in eelgrass is recycled internally. Umebayashi (1989) provided data on nitrogen content of mature and senescing leaves, growth rates, and defoliation rates for eelgrass in Japan during a short period of rapid growth from which we calculated that 17 % of the estimated 574 mg N  $m^{-2} d^{-1}$  needed for new leaf growth in May could be provided by recycling nitrogen from senescent leaves. Extending the calculation to cover a year's cycle for a perennial population is difficult. We estimate that conservation of nitrogen reduces the annual requirement for uptake of nitrogen by about 25 %, to somewhere in the range 5 to 35 g N  $m^{-2}$ .

### LOSSES OF NUTRIENTS FROM SEAGRASS BEDS

#### Leaching

Live seagrasses release up to 2 % of the carbon they fix in photosynthesis in the form of dissolved organic molecules (Brylinski 1977, Penhale & Smith 1977, Wetzel & Penhale 1979, Moriarty et al. 1986). The amounts of nitrogen or phosphorus released from healthy leaves are unclear but laboratory studies with  $^{32}PO_4$  suggested that eelgrass leaves excreted 1 to 3 % of the phosphorus that the roots had absorbed (Penhale & Thayer 1980). At least a part of the excreted nutrients will be captured by epiphytes on the leaves and bacteria in the rhizosphere and thus retained in the seagrass bed (Harlin 1973, Penhale & Smith 1977, Penhale & Thayer 1980, Moriarty et al. 1986), but another (unknown) portion will escape into the water (Jørgensen et al. 1981).

Nutrient losses from the leaves may continue during the phases of senescence and decay: increased leakiness of the leaves may be responsible for part of the

decrease in tissue concentrations of nutrients during senescence. Release of large amounts of soluble material from senescent leaves indeed has been demonstrated in *Posidonia australis* (Kirkman & Reid 1979), but the chemical composition of the leachate was not determined. Leaching is a process which probably will continue throughout the period of senescence and subsequent decay. Harrison & Harrison (1980) showed that even after aging 5 mo intertidally, *Zostera marina* leaves still contained 10 % of the dry weight in an easily extracted state.

### Export of sloughed leaves and leaf fragments

Transport of seagrass material followed by deposition outside the seagrass beds, in deeper waters or on the shore, is commonly observed (e.g. Gallagher et al. 1984, Suchanek et al. 1985, Newell et al. 1986, Whitfield 1988). This loss is not restricted to relatively nutrient-poor senescent or dead leaves. In an investigation of massive depositions of *Zostera noltii* wrack washed ashore on the Mauritanian coast, it was found that this material had the decomposition characteristics and the appearance of rather fresh leaves, and therefore probably consisted mostly of nutrient-rich leaves which were detached from the shoots while alive (Hemminga & Nieuwenhuize 1991).

Estimates of the losses due to leaf export from seagrass beds range from <1 % of primary production for *Thalassia testudinum* (Zieman et al. 1979), and 12 % for *Posidonia australis* (Kirkman & Reid 1979), to 1 and 30 % for *Zostera marina* (Josselyn et al. 1983, Bach et al. 1986), 2 to 74 % for *Halodule wrightii* (Bach et al. 1986), and 27 to 79 % for *Syringodium filiforme* (Fry & Virnstein 1988). Morphological characteristics such as the dimensions of lacunal spaces, susceptibility to grazing by larger herbivores such as fish and turtles, which sever blades and allow large fragments to float away (Zieman et al. 1979, Bjorndal 1980), and environmental conditions, e.g. wind and currents (Bach et al. 1986), determine the extent of leaf loss from seagrass beds. In cases where the canopy is dense and water currents are slow, seagrass beds act as traps for particulate matter in the water (Fonseca et al. 1982) and a larger proportion of the sloughed leaves will decay in the bed.

It is more difficult to assess the export of smaller particles from seagrass beds. Bach et al. (1986) conjectured that the loss of small particles from eelgrass beds in the southeastern USA could exceed the export of surface-floating leaf material which was up to 30 % of the production. A comprehensive study of eelgrass growth and decay in the Netherlands suggested that almost half of the nitrogen incorporated into a year's

growth of leaves in Lake Grevelingen was subsequently lost from the seagrass bed when it was deposited as very small particles in the sediment of the deepest part of the Lake (Pellikaan & Nienhuis 1988). In conclusion, export of particulate material, either whole leaves or small particles, is likely to result in ongoing nutrient losses. In view of the data presented above, these losses will strongly vary between sites and, following our estimates of annual requirements for nitrogen uptake, may fall anywhere in the range 0 to  $30 \text{ g N m}^{-2} \text{ yr}^{-1}$ .

### Nutrient transfer by foraging animals

There are a number of mobile, larger animals, particularly herbivores, which may be involved in the transfer of nutrients from seagrass meadows, by tapping the resources of the beds and producing fecal matter outside the meadow when the animals have moved from their feeding ground. Potentially important in this respect are fishes, turtles, manatees and dugongs, and birds (see reviews by Thayer et al. 1984, Lanyon et al. 1989). Direct consumption of fresh, growing seagrasses, however, is generally considered to be limited, although the frequently cited paper of Greenway (1976) shows that, locally, grazing pressure may be very high. In the Caribbean, which is noted for a relatively high number of seagrass herbivores, Zieman et al. (1979) found that only 5 to 10 % of the productivity of *Thalassia testudinum* was consumed. Even lower values have been estimated for direct seagrass consumption in temperate regions, where waterfowl species are the dominant larger herbivores (Thayer et al. 1984, Nienhuis & Groenendijk 1986). Considering the fact that fecal production may also occur during foraging in the meadows, and part of the nutrients ingested therefore potentially returns to the seagrass system, it can be assumed that this type of nutrient loss represents only a relatively minor flux from the seagrass meadows. Detailed discussion of this topic, therefore, will be omitted here.

### Denitrification

The microbial reduction of nitrate to gaseous nitrogen ( $\text{N}_2\text{O}$  and  $\text{N}_2$ ) makes nitrogen essentially unavailable for biological production, except for diazotrophs (see below). Nitrate in the sediment usually is supplied either by diffusion from the overlying water or by bacterial nitrification occurring in the sediment (Koike & Sørensen 1988), the latter process generally being the more important (e.g. Seitzinger 1987). In contrast to denitrification, which is a strictly

anaerobic process, the transformation of ammonium to nitrate in the process of nitrification requires aerobic conditions. Nonetheless these processes may be tightly coupled (Jenkins & Kemp 1984). Vegetated aquatic sediments offer an environment where nitrification and denitrification may coincide deep in the sediment. Via the roots of macrophytes, oxygen diffuses into the sediment, creating a mosaic of oxic and anoxic microenvironments throughout the root zone. Furthermore, the relatively high organic content of vegetated sediments, due to input of organic particulate material and root exudation processes, provides abundant substrate both for  $\text{NH}_4^+$  regeneration, which would in turn enhance nitrification, and for denitrification (cf. Nixon 1981, Kemp et al. 1982). Christensen & Sørensen (1986) indeed found that the root zone accounted for a major part of the annual denitrification in a stand of the freshwater macrophyte *Littorella uniflora*. The importance of rhizosphere processes is also well demonstrated in a recent study of Reddy et al. (1989), who performed growth chamber experiments with various aquatic plant species. Mass balance calculations of  $^{15}\text{NH}_4^+$  added to the soil indicated that 34 % of the added ammonium was denitrified in soil columns with rice plants, whereas the corresponding figure in columns without plants was only 11 %.

Few studies have addressed nitrification and denitrification in seagrass beds, but the processes mentioned above undoubtedly operate in these marine meadows. Nitrate and nitrite are present in tropical (Boon 1986a) and in temperate sediments of seagrass beds, even below 30 cm depth (Iizumi et al. 1980), indicating nitrification in the root zone. The latter authors measured in situ rates of denitrification in the upper 7 cm of the sediments equivalent to a daily loss of 0.3 to 3  $\text{mg N m}^{-2}$ . As denitrification was also found below 20 cm depth, this most probably is a conservative estimate. In situ denitrification rates in the top 10.5 cm of the sediment of a *Zostera novaezelandica* bed varied between 1.2 and 6.0  $\text{mg N m}^{-2} \text{d}^{-1}$  (Kaspar 1983). The denitrification rates reported for seagrass beds thus are on the low end of the range of activities measured in coastal bays and estuarine sediments (0 to 130  $\text{mg N m}^{-2} \text{d}^{-1}$ ; see review by Koike & Sørensen 1988). However, the potential denitrification rates in the sediment of seagrass meadows (measured in nitrate-saturated soil slurries), are much higher (Kaspar 1983, Caffrey & Kemp 1990). It is possible, therefore, that under favourable conditions of high nitrate availability higher in situ denitrification rates do occur, but this remains to be investigated. On the basis of the scarce data presently available, the losses due to denitrification would be somewhere in the range 0.1 to 2  $\text{g N m}^{-2} \text{yr}^{-1}$ .

## Diffusion

Mineralization processes in the sediment of marine systems result in the formation of ammonium, which subsequently (or after oxidation to nitrate) may diffuse into the overlying water. Ammonium in the sediment of the seagrass bed will result primarily from the decomposition of particulate organic material, which contains the major part of the nitrogen pool in the sediment (Boon 1986b), but deamination of amino acids exuded by seagrasses (Jørgensen et al. 1981) may be another source (Boon et al. 1986b). Although several studies report on ammonium regeneration in seagrass beds (Iizumi et al. 1982, Short 1983a, Short et al. 1985, Boon et al. 1986a, b, Dennison et al. 1987), an estimation of diffusion losses of ammonium from the sediment of a seagrass bed has been obtained only by Short (1983a). This author found in field perturbation experiments that removing eelgrass leaves and sealing the sediment surface resulted in a rapid increase of the sediment interstitial ammonium concentration. In sealed plots net ammonium production, calculated from the soil profiles of accumulated ammonium, was 47  $\text{mg N m}^{-2} \text{d}^{-1}$ . Ammonium diffusion was calculated as the difference between the production in the sealed plots and the estimated ammonium uptake by the root system of the local seagrass vegetation, resulting in a diffusion rate of 30  $\text{mg N m}^{-2} \text{d}^{-1}$ . This rate is within the range reported in non-vegetated sediments (Hale 1976, Nixon et al. 1976, Blackburn & Henriksen 1983). Such a diffusion rate would represent a substantial loss (64 %) of the net ammonium production in the sediment, but the moderate interstitial ammonium concentrations and the rather low production rate of this nutrient in the seagrass beds studied by Short, as compared to other data on interstitial concentrations and production (e.g. Dennison et al. 1987), may imply that it is not a particularly high rate for seagrass sediments. It should be added here that diffusion of nutrients from the sediment does not necessarily equal a loss of nutrients from the seagrass meadow: although diffused nutrients evade root uptake, the seagrass leaves (and also benthic algae and leaf epiphytes present in the system) may capture a part of the released nutrients (cf. Prieto & Corredor 1984); however, the effectiveness of this mechanism in the seagrass biotope is unknown.

## INPUTS OF NUTRIENTS TO SEAGRASS BEDS

As counterparts for the processes which result in nutrient losses from the seagrass beds, there are several processes potentially able to enrich the pools of nutrients. First, nitrogen-fixation specifically results in

enrichment with nitrogen nutrients. Second, sedimentation of particles from the watercolumn may resupply the soil both with micro- and macronutrients. Finally, nutrient uptake by the leaves of the plants offers a third mechanism by which nutrient pools of the seagrass bed may be resupplied. These 3 processes will be discussed successively in the next section.

### Nitrogen fixation

The observation of Patriquin & Knowles (1972) that nitrogen fixation occurred in the rhizosphere of several tropical and temperate seagrass species was followed by a number of studies, which were no doubt elicited by the suggestion of the authors that the nitrogen requirements of the seagrasses could be completely covered by this process. Some of the nitrogen-fixing bacteria in the sediment of seagrass beds are present in close association with roots and rhizomes. Davidson et al. (1984) showed with the aid of a fluorescent antibody technique that nitrogen-fixing bacteria were located in the intercellular spaces between root cortical cells in *Halodule wrightii*. This type of association may be of direct benefit to the growing plants; however, to what extent the relation between seagrasses and nitrogen-fixers resembles the symbiotic association between diazotrophs and higher plants (Schubert 1986) is unknown. Capone & Taylor (1980) reported that nitrogen-fixation rates were related to weight of below-ground biomass in beds of *Thalassia testudinum*. Seagrasses transport gases and organic compounds, synthesized during photosynthesis, to their root zones (Oremland & Taylor 1977, Wetzel & Penhale 1979, Iizumi et al. 1980, Moriarty et al. 1986), and nitrogen-fixers are probably stimulated by these processes. It may be for this reason that, on a wet weight basis, the

numbers of nitrogen-fixing bacteria associated with roots are several orders of magnitude higher than in the sediment between the roots (Shieh et al. 1989). The diurnal and seasonal variation in nitrogen fixation rates in the root zone of seagrass beds (Capone & Taylor 1977, 1980, Smith & Hayasaka 1982) also points to the importance of metabolic activities of the seagrass plants to the nitrogen-fixing community. However, active populations of nitrogen-fixing bacteria are also associated with rhizome detritus in the sediment, which suggests that degradation of this detrital material can also support the process of nitrogen-fixation (Kenworthy et al. 1987). It is somewhat remarkable that seagrass detritus does not show an accumulation of nitrogen during decay (see review by Harrison 1989). This may either be due to a rapid release of fixed nitrogen from the seagrass detritus or to the relatively minor contribution of diazotrophs to the nitrogen pool of the detritus. As Kenworthy et al. (1987) calculated that  $0.565 \text{ g N m}^{-2} \text{ yr}^{-1}$ , which is equivalent to only 1 to  $2 \text{ mg N m}^{-2} \text{ d}^{-1}$ , was supplied by nitrogen-fixation associated with the detritus, the latter alternative is more probable.

Nutrient enrichment of the seagrass biotope by nitrogen-fixing organisms may also be found in the phyllosphere, but the consistency of the process is less than in the rhizosphere (Goering & Parker 1972, Capone & Taylor 1977). The direct association of diazotrophs with the living plant leaves again offers the possibility of a close coupling between nitrogen fixation and uptake of nitrogen by the leaves. Nutrient transfer from seagrass leaves to epiphytes has been found (Harlin 1973, McRoy & Goering 1974, Penhale & Thayer 1980), and the reverse process also has been demonstrated (Harlin 1973).

The nitrogen input by nitrogen-fixation in meadows of a subtropical (*Thalassia testudinum*) and a temper-

Table 2. Estimates of daily nitrogen input by nitrogen fixation in seagrass meadows

Vegetation	Compartment	N <sub>2</sub> -fixation (mg m <sup>-2</sup> d <sup>-1</sup> )	Source
<i>Thalassia testudinum</i>	Various	± 0	McRoy et al. (1973)
<i>Thalassia testudinum</i>	Rhizosphere	5.1–5.3	Capone et al. (1979)
<i>Thalassia testudinum</i>	Rhizosphere	5–24	Capone & Taylor (1980)
<i>Thalassia testudinum</i>	Phyllosphere	0–5	Capone & Taylor (1977)
<i>Thalassia testudinum</i>	Phyllosphere	150	Goering & Parker (1972)
<i>Thalassia testudinum</i>	Phyllosphere	1.1–3.2	Capone et al. (1979)
<i>Thalassia testudinum</i>	Detritus	0.6–0.8	Capone et al. (1979)
<i>Zostera marina</i>	Various	0	McRoy et al. (1973)
<i>Zostera marina</i>	Rhizosphere	3.9–6.5	Capone (1982)
<i>Zostera marina</i>	Rhizosphere	0.2	Smith & Hayasaka (1982)
<i>Zostera marina</i>	Phyllosphere	0.2	Smith & Hayasaka (1982)
<i>Zostera marina</i>	Detritus	1.3	Kenworthy et al. (1987)



ate species (*Zostera marina*) as measured in various studies is summarized in Table 2. Additional data on nitrogen-fixation in seagrass beds can be found in reviews of Capone (1983, 1988). Except for the early studies of Goering & Parker (1972) and McRoy et al. (1973), the values indicate that nitrogen-fixation leads to a daily input of several to several tens of milligrams  $N\ m^{-2}$ . The seasonal fluctuations of nitrogen-fixation rates makes it difficult to estimate inputs on an annual basis, but this figure may amount to 1 to 6  $g\ m^{-2}$  if we combine the estimated annual inputs in both rhizosphere and phyllosphere of *T. testudinum* given by Capone & Taylor (1977, 1980).

### Sedimentation

Quantitative observations of sediment texture in beds of seagrass vegetations frequently have shown that mean particle size of sediment grains is low compared to unvegetated sediments. This phenomenon generally has been ascribed to a decrease in current velocity by the resistance of the seagrass canopy, which causes a reduction in the sediment-carrying capacity of the water. Reduction of current velocities inside seagrass vegetations repeatedly has been reported (Scoffin 1970, Fonseca et al. 1982, Harlin et al. 1982, Almasi et al. 1987). Sedimentation in seagrass beds is influenced by several factors: Short & Short (1984) added various types of sediment particles to culture systems with and without seagrasses. Turbidity consistently decreased more rapidly in the systems with seagrasses. A clear species difference, however, was noticed, the flat-bladed species *Halodule wrightii* being more efficient at trapping particles than *Syringodium filiforme*, which has cylindrical leaves. Both differences in the morphology of the leaves and in shoot density were held responsible for this phenomenon. Other factors such as flow velocity and relative water depth are also expected to affect sedimentation (Scoffin 1970, Fonseca & Fisher 1986).

It is obvious that the trapping effect of seagrass canopies is not restricted to sediment particles suspended in the water, but also will include organic particles such as phytoplankton and detritus. The observations carried out in a tributary of Chesapeake Bay are illustrative in this respect. In submersed vascular plant beds dominated by the macrophytes *Ruppia maritima* and *Potamogeton perfoliatus*, a decreased level of planktonic chlorophyll *a* was demonstrated in the water column (Kemp et al. 1984, Ward et al. 1984). Moreover, sediments in the plant beds were significantly enriched in organic carbon and chlorophyll *a* compared to unvegetated beds. Applying measure-

ments of stable carbon isotope ratios in sediments and phytoplankton, Kemp et al. (1984) concluded that ca 40 % of the vegetated sediment carbon probably was of planktonic origin. Sediment organic  $\delta^{13}C$  values in a *Zostera marina* meadow were intermediate between eelgrass and phytoplankton (Cooper 1989), which may also indicate the contribution of phytoplankton to sediment organic carbon in seagrass beds, but the unknown effect of benthic algae on the values hampers a simple interpretation.

The quantitative importance of sedimentation for the input of nutrients to seagrass beds can only be assessed in a very preliminary way with the limited data available. Harlin et al. (1982) found a sediment accretion of 2.5 cm in field plots of *Zostera marina* in a low energy area in Rhode Island (current velocity  $3\ cm\ s^{-1}$  at 20 cm above the sediment) between August and October, i.e. from the period of highest shoot density through the period of population decline in autumn. Assuming a specific gravity of  $2.4\ g\ cm^{-3}$ , and a nitrogen content of 0.1 % on a wet weight basis, this would represent an input of  $60\ g\ N\ m^{-2}$ . In comparison, the organic input from phytoplankton to an eelgrass sediment has been estimated as 50 to  $300\ g\ C\ m^{-2}\ yr^{-1}$  (Kenworthy & Thayer 1984) which is equivalent to ca 7 to  $45\ g\ N\ m^{-2}\ yr^{-1}$ . Thus sedimentation may provide the vegetation with more nitrogen than we estimated is demanded annually for biomass production ( $5\ to\ 35\ g\ m^{-2}$ ). Sedimentation rates, however, may differ strongly between sites: in a dynamic area (current velocity  $17.5\ cm\ s^{-1}$ ), Harlin et al. (1982) found little sediment fluctuation; at higher current velocities in sparse vegetations, erosion between shoots can be observed (Scoffin 1970). A limited sedimentation rate,  $4.96\ g\ dry\ wt\ m^{-2}\ wk^{-1}$  in summer and  $1.60\ g\ dry\ wt\ m^{-2}\ wk^{-1}$  in winter (equivalent to ca  $0.3\ g\ N\ m^{-2}\ yr^{-1}$ ), was also found by Almasi et al. (1987) in plots of *Thalassia*. Apart from the large variations in sedimentation rates between various growth locations, an assessment of the importance of sedimentation processes for nutrient budgets in seagrass beds is complicated by the fact that accretion may only be a seasonal phenomenon, coinciding with the production of above-ground biomass. After senescence and die-back of the canopy, the bed surface is no longer protected and scouring will result in the gradual disappearance of the sediment depositions. Such a chain of events can be derived from the experiments of Harlin et al. (1982), who denuded plots of eelgrass and found that rapid sediment erosion followed. Presumably, this process will nullify the nutrient input coincident with the preceding sediment deposition. Theoretically, seasonal erosion may even outreach seasonal deposition, resulting in a net loss of nutrients from the system, but there appear to be no quantitative data to substantiate this possibility.

### Nutrient uptake by leaves

As is the case for other submerged aquatic macrophytes, seagrasses are capable of removing N-nutrients from both the water column and the sediment. In the current literature on seagrass ecology, however, it is usually assumed that nutrient absorption by the roots is of major importance. This assumption is based on several pieces of evidence. Several studies have shown that intensive ammonium regeneration occurs in the sediment of seagrass meadows; comparisons of ammonium regeneration rates with estimates of plant nitrogen requirements indicate that in most cases the ammonium produced equals or even exceeds plant nitrogen demands (Iizumi et al. 1982, Short 1983a, Dennison et al. 1987, Caffrey & Kemp 1990); only in one case, regeneration (in an organic-poor sediment) seemed inadequate to match plant demands (Short 1983a). Ammonium regeneration in the water column is limited compared to regeneration in the sediment (Iizumi et al. 1982). Obviously, the relatively high ammonium regeneration rate in the sediment a priori advocates the role of the roots in plant nitrogen uptake. Furthermore, the relationship between sediment type and plant morphology was noted decades ago (e.g. Ostensfeld 1908), and in recent times this relationship has been shown to involve sediment nutrient conditions (Short 1983b, 1987). Experimental enrichment of the sediment resulted in increased leaf growth rate (Bulthuis & Woelkerling 1981), leaf length, biomass and number of shoots (Orth 1977). Finally, the potential of the root-rhizome system as measured by in vitro incubation experiments is such that, in relation to concentrations of interstitial ammonium and nitrate, the major part of the plant nitrogen uptake may occur via these organs (Iizumi & Hattori 1982, Short & McRoy 1984). A recent study of glutamine synthetase activity in *Zostera marina* roots points to a similar conclusion. After ammonia uptake, this enzyme performs the initial assimilatory step by combining ammonia with glutamate to form glutamine. The potential capacity of this enzyme in the roots appeared to be more than sufficient to meet the plant nitrogen requirements (Pregnall et al. 1987).

Caution, however, should be observed in allotting the root system the dominant role in nutrient uptake in the existing variety of field situations. It should be realized that much of the evidence mentioned above, such as the high ammonium regeneration rate in the sediment, is no direct proof for the presumed importance of root uptake. Furthermore, the data given in several studies indicate that translocation of both N- and P-tracers from roots to leaves is less intensive than the reverse process (Penhale & Thayer 1980, Borum et al. 1989, Iizumi & Hattori 1982). The latter authors, for

instance, found that after a 24 h incubation of the leaves of *Zostera marina* with  $^{15}\text{N}$ -ammonium, tracer enrichment in the root-rhizome tissue was similar to that in the leaf tissue, indicating rapid translocation from leaves to below-ground tissues. However, when the roots had been exposed to the tracer, the  $^{15}\text{N}$  enrichment of the leaves remained behind that of the root system by at least an order of magnitude. In another investigation with  $^{32}\text{P}$ -tracer hardly any translocation was found: transport between above- and below-ground tissues was only about 3 to 4 % of the tracer taken up during a 120 h incubation period (Brix & Lyngby 1985). These findings are remarkable in view of the fact that the larger part of biomass production generally occurs above-ground, and transport of nutrients would be expected to be mainly in the acropetal direction if nutrient uptake was dominated by the root system.

The capacity of the leaves for nutrient uptake is suggested by observations showing that seagrass communities are able to reduce ammonium concentrations in the water column drastically (e.g. Short & Short 1984, Short & McRoy 1984). As far as N-nutrients are concerned, both ammonium and nitrate are taken up by the leaves, to an extent dependent on the ambient concentration (Iizumi & Hattori 1982, Short & McRoy 1984). In contrast to the results obtained by the former authors, the data given by Short & McRoy indicated a preference for ammonium over nitrate uptake. In line with these results are the observations of Doddema & Howari (1983) on nitrate reductase activity in *Halophila stipulacea*. This enzyme catalyzes the first step in the reduction of nitrate, which is necessary for incorporation of the nitrogen moiety of the nitrate molecule into cellular compounds. Only very low activities were found, both in above-ground and below-ground plant parts, suggesting that nitrate was only a marginal source of nitrogen to the plant. More substantial activities of the enzyme were established in *Zostera marina* (Roth & Pregnall 1988); leaf activity was found to be conspicuously higher than root activity; moreover, 6 d exposure of the seagrass plants to high nitrate concentrations induced increased nitrate reductase activity in certain plants. The physiological capacity of seagrasses for nitrate uptake and assimilation therefore appears to be variable, possibly depending on ambient nitrate concentrations and the presence of an alternative nitrogen source.

The observation that leaves of *Zostera marina*, on a dry weight basis, have a greater affinity for ammonium than roots (Thursby & Harlin 1982) can be interpreted as an adaptation to the relatively low nutrient conditions of the water column. Indeed, the nutrient uptake capacities measured for *Zostera marina* leaves indicate that these plant parts can be very important in captur-

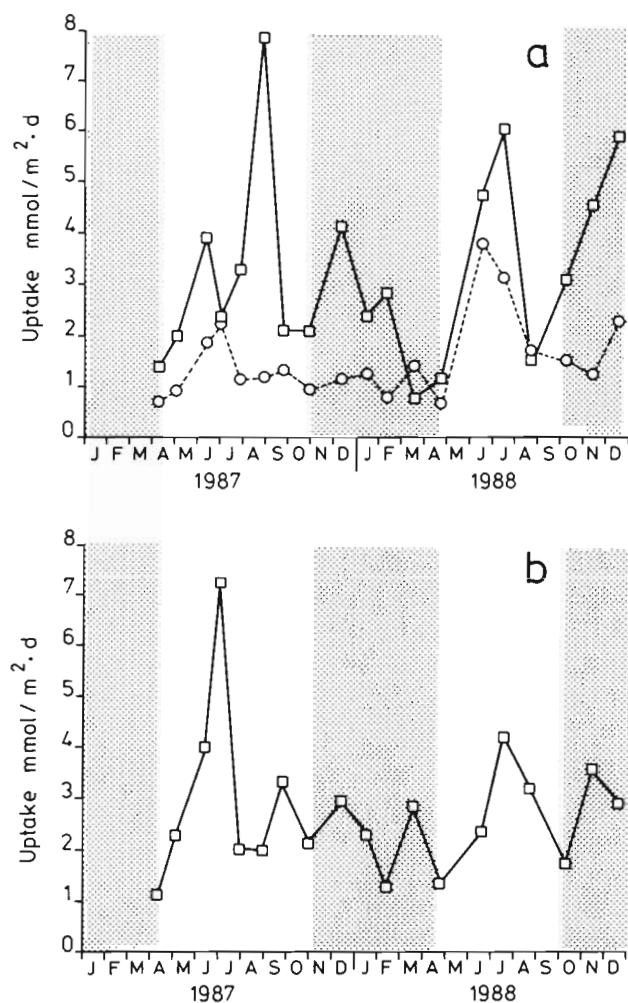


Fig. 1. Time course of calculated ammonium ( $\square$ ) and nitrate ( $\circ$ ) uptake by a *Zostera marina* population in Lake Grevelingen (The Netherlands). (a) Leaf uptake; (b) root uptake. The population is located on a permanently submersed, low current site. Data on sediment interstitial ammonium (depth 0 to 10 cm), ammonium and nitrate in the watercolumn, and determinations of above- and below-ground biomass, carried out periodically in the seagrass bed, were combined with the following regressions derived from data of Short & McRoy (1984):  $y = 0.8x + 0.89$  and  $y = 0.47x + 0.84$ , describing leaf uptake ( $y$ ) by *Z. marina* as a function of ammonium and nitrate concentration ( $x$ ) in the water column, respectively; and  $y = 0.008x + 0.93$ , describing root uptake as a function of ambient ammonium concentration in the root compartment. The part of the curves in the non-shaded periods was used for calculation of cumulative annual nutrient uptake.

ing nutrients from the water column. Iizumi & Hattori (1982) estimated that at ambient ammonium and nitrate concentrations of 4 and 378 nM, respectively, 45 % of the nitrogen required for eelgrass growth can be supplied by leaf uptake. Short & McRoy (1984) calculated that at a water ammonium concentration of 3.7  $\mu\text{M}$  one-third of the eelgrass nitrogen requirement

could be obtained by leaf uptake at average production rates of  $0.003 \text{ g C g}^{-1} \text{ h}^{-1}$ ; at ammonium concentrations of 2  $\mu\text{M}$  and low production rates, potential leaf uptake would even exceed nitrogen demand.

Evidently, the total amount of nutrients obtained by the canopy will be strongly dependent on the fluctuating concentrations of ammonium and nitrate in the watercolumn and the seasonally changing shoot biomass. So far no attempt has been made to calculate nutrient uptake on an annual basis, taking into account the varying conditions throughout the year. To obtain such an estimate, we used the regressions of uptake by leaves and roots of *Zostera marina* vs ambient nutrient concentrations (ammonium, nitrate) determined by Short & McRoy (1984), and combined these results with our data for nutrient concentrations and biomass of a perennial population of *Z. marina* in Lake Grevelingen (The Netherlands), measured during a monitoring program in 1987 and 1988. Fig. 1 shows the calculated time course of the uptake of ammonium and nitrate by the above-ground biomass, and the uptake of ammonium by the roots. The characteristics of nitrate uptake by the roots were not measured by Short & McRoy, so the uptake of this compound by the roots could not be calculated; however, the interstitial concentrations of nitrate are low compared to ammonium (Boon 1986a, b, van Lent unpubl.), and therefore its relative importance for below-ground nitrogen uptake presumably is small. The uptake curves fluctuate with time, reflecting the variable concentrations of ammonium and nitrate measured, and the changing biomass. Living roots and shoots of *Z. marina* in Lake Grevelingen are present throughout the year; however, in view of the low water temperatures during winter and the fact that growth is restricted to spring and summer, uptake processes presumably are of quantitative importance only from April to October. Therefore the potential uptake of the various N-nutrients during the winter months, shown by the curves in Fig. 1, was ignored in the calculations of cumulative annual uptake, which was determined by calculating the area under the curves in the period from April to October/November (non-shaded in Fig. 1). Results are given in Table 3. Calculated ammonium and nitrate uptake by

Table 3 *Zostera marina*. Uptake of N-nutrients by leaves and by roots in Lake Grevelingen (The Netherlands). Cumulative uptake was calculated from the part of the curves (Fig. 1) in the non-shaded periods

	1987		1988	
	Leaves	Roots	Leaves	Roots
Ammonium ( $\text{g N m}^{-2}$ )	11.2	10.2	9.8	7.6
Nitrate ( $\text{g N m}^{-2}$ )	4.3	—	6.0	—



the leaves in 1987 and 1988 is equivalent to 15.5 and 15.8 g N m<sup>-2</sup>, respectively. These data indicate that the leaves are responsible for 60 to 70 % of the total plant uptake. The dominance of the leaves not only holds when leaf uptake of ammonium and nitrate is contrasted with root uptake of ammonium, but also when ammonium uptake only is considered.

This calculation exercise of course has its limitations; for instance, fluctuating environmental factors such as light and temperature influence biomass production and undoubtedly also will affect nutrient uptake. The effects of these and other modifying factors are not included in the calculation, and the figures therefore give only an indication of potential uptake values. The relevant aspect of this calculation, however, is that it shows the relative importance of leaf uptake vs root uptake, on an annual basis.

By capturing ammonium and nitrate from the water column, seagrass meadows are potentially enriched with a substantial amount of nitrogen originating from outside the seagrass beds, a point which must be stressed in the context of this paper. Moreover, leaf uptake presumably will reduce the losses of nutrients from the seagrass bed as nutrients diffusing from the sediment to some extent will be intercepted by the canopy. In view of the capacity of the leaves for uptake of N-nutrients, as discussed above, we may even go one step further and hypothesize that the ammonium resources supplied by regeneration processes in the sediment of seagrass beds are not primarily tapped by the roots, but by the leaves.

## CONCLUDING COMMENTS

With regard to nutrient fluxes, the seagrass meadow must be considered as an open system. Fluxes of nutrients from and to these systems are associated with a series of commonly occurring processes. The persistence in time of most seagrass meadows obviously points to a balance between nutrient losses and nutrient gains. Such a balance in time need not imply a continuous, complete equilibrium. Many processes contribute to the final nutrient status of the seagrass system. Fluctuating biotic or abiotic factors in the dynamic marine environment may temporarily accentuate any of these processes, possibly resulting in year-to-year variations in net losses or net gains of nutrients. It is tempting to speculate that the consequences of such imbalances may find their reflection in fluctuations of the productivity of seagrass meadows.

We have discussed 3 processes which may dominate the replenishment of nutrients: nitrogen-fixation, sedimentation and leaf uptake. Nitrogen-fixation is a feature of nearly all seagrass beds investigated and

therefore is undoubtedly important for the nitrogen enrichment of these systems; however, for a continued biomass production other elements such as phosphorus and micronutrients are required as well. This means that crucial contributions must come from either leaf uptake or sedimentation, or – more likely – from a combination of both. Neither of these processes has received much attention in the seagrass literature, particularly not in the context of nutrient inputs to the seagrass systems. Sedimentation is a phenomenon which is not equally conspicuous in all habitats where seagrasses abound, for instance in water with low seston content or in high current areas, where sedimentation rates are low. Consequently, in these situations nutrient replenishment is expected to become more dependent on leaf uptake. It is interesting in this respect that decreased sedimentation rates resulting from higher current velocities may coincide with an enhanced potential for leaf nutrient uptake, due to the reduction of the leaf surface boundary layer (Fonseca & Kenworthy 1987). An intriguing situation presents itself where seagrasses show luxuriant growth in clear, i.e. seston-poor water, of oligotrophic character, such as may be found in tropical waters. In areas with nutrient-poor sediments (e.g. carbonate sediments derived from coral reefs) it is doubtful if the root system alone can ensure an adequate nutrient supply. It would be of great interest to measure uptake of nutrients by seagrass leaves in these systems, to determine how the plants have adapted to low ambient nutrient concentrations.

The potential importance of leaves for the input of N-nutrients into the seagrass meadow, which emerges from our discussion of leaf vs root uptake, is not surprising if the structure of the leaves and the implications of a submerged existence are considered. In terms of leaf structure 3 points are relevant. First, most seagrasses have leaves with a high ratio of absorptive surface area to volume of nutrient-requiring tissue, because of both their strap-like shape and the presence of gas-filled lacunae that occupy much of the interior. Second, the sites of high demand for nutrients, the photosynthetic cells, are concentrated in the epidermal layer, i.e. nearest the surrounding water. Third, an efficient apoplastic route (i.e. through cell walls) for the transfer of nutrients from seawater to the epidermal cells appears to exist (Barnabas 1988). Thus seagrass leaves are theoretically capable of acquiring nutrients without relying on root uptake. Considering that most seagrasses grow best when continually submerged, it is unlikely that acropetal transport of dissolved nutrients from roots to leaves will be efficient because the normal driving force, evapotranspiration from the leaves which pulls water up the xylem vessels, is missing. Other mechanisms such as root pressure could account for an

upward flow (Salisbury & Ross 1985) but for seagrasses the situation is unknown.

Direct absorption by seagrass leaves of large amounts of inorganic nutrients from the water column implies that seagrasses may compete with other organisms in their environment. Potential competitors include autotrophs such as phytoplankton and attached algae, but also heterotrophs associated with detritus. Comparative studies of the nutrient uptake characteristics of seagrass leaves and other components of shallow marine ecosystems are needed.

More study is required for all the processes covered in this review because data are scarce and not all the gains and losses have been measured in any one seagrass system. It is clear, however, that a better understanding of the nutrient balance of seagrass meadows can be obtained only if the plants are studied, not in isolation, but as integral parts of the complex ecosystem in which they function. Delta Institute communication no. 517.

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