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Nitrogen (^{15}N) retention in small *Thalassia hemprichii* seagrass plots in an offshore meadow in South Sulawesi, Indonesia

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Abstract

Nitrogen retention was investigated during 240 d in 1 × 1 m field plots of the tropical seagrass *Thalassia hemprichii*. Shoots were enriched with ^{15}N by brief exposure of the leaves to an elevated concentration of ^{15}N ammonium in the water column. Hereafter, the ^{15}N absorbed in the seagrass system declined rapidly. The decline was initially dominated by the loss of ^{15}N in detached leaf fragments. Of the lost leaf fragments, 19% were recovered within the boundaries of the experimental plots, and 25% were deposited outside these boundaries but inside the seagrass meadow. Of the remaining 56%, the fate could not be resolved, but export from the meadow is probably limited to ~10%. During the course of time, the ^{15}N half-life increased from 1 to ~2 months because of ^{15}N accumulation in compartments from which it was not easily exported (roots, rhizomes, and sedimentary detritus). The limited nitrogen retention in the seagrass plots is ascribed to the combined effects of a major allocation of nitrogen to leaf production, restricted nitrogen resorption from senescent leaves (28% of the gross N demand), and a dynamic environment facilitating detachment and export of leaf fragments from the experimental plots. At the scale of the whole meadow, however, nitrogen conservation via the detrital pathway could be of considerable significance. We found indications for a rather efficient reabsorption by the plant of nitrogen regenerated from seagrass leaf litter, with a meaningful role for the leaves, and postulate that increasing patch size may coincide with increasing nitrogen conservation in the system as a whole.

Seagrasses are the only descendants of terrestrial angiosperms that have been able to invade the marine environment. The plants form extensive submarine meadows that can be found in oligotrophic and mesotrophic shallow marine waters all over the world (Den Hartog 1970). A comparison among different plant communities shows that the primary production of seagrass meadows ranks among the highest established, being in the range of tropical forest and swamps and marshes (Duarte and Chiscano 1999). The generally high productivity of seagrasses, which is logically paralleled by a high nutrient demand, often in nutrient-poor environments, has attracted attention since the expansion of seagrass research in the early 1970s. Nutrient-limited growth appears to be a quite common phenomenon in seagrass ecology, despite the capacity of seagrasses to exploit the nutrient reservoirs of both the sediment and the water column (Iizumi and Hattori 1982; Thursby and Harlin 1982; Short et al. 1990; Bulthuis et al. 1992; Fourqurean et al. 1992; Hemminga et al. 1994; Agawin et al. 1996; Terrados and Williams 1997; Lee and Dunton 1999; Udy et al. 1999).

Seagrasses, like all plants, will be functionally adapted to their environment, tuning nutrient expenditure to nutrient availability. It seems likely, therefore, that seagrasses, especially in nutrient-poor environments such as those usually found in tropical areas, have developed specific properties to conserve nutrients. So far, research into nutrient conservation strategies in seagrasses is conspicuously limited. Studies of tropical southeast Asian seagrasses show that decomposition and production processes are well balanced in these systems and that accumulation of detritus does not occur (Brouns and Heijs 1986; Lindeboom and Sandee 1989; Erftemeijer et al. 1993*a*). These findings, combined with the very clear water column and low ambient nutrient concentrations, have led to the hypothesis that tropical seagrass meadows are self-sustaining systems in which most nutrients are captured in the large seagrass biomass and are efficiently recycled within the system (Nienhuis et al. 1989). Resorption of nutrients from senescing leaves is a common phenomenon in plants: it reduces the need for uptake of nutrients from the environment and, hence, is a strategy that can be of particular importance to plants growing in nutrient-poor habitats (Chapin 1980; Aerts 1990). An extended leaf lifespan is another important mechanism known to conserve nutrients in evergreen species, surpassing nutrient resorption in effectivity (Escudero et al. 1992). Recently, Stapel and Hemminga (1997) and Hemminga et al. (1999) presented evidence that these strategies are not strongly developed in seagrasses. Another possible nutrient conservation strategy for seagrasses is the efficient uptake of regenerated nutrients that have been released by decomposition of seagrass litter inside the meadow (Nienhuis et al. 1989; Hemminga et al. 1991; Pedersen and Borum 1993). This method of nutrient retention, external to the living plant, would be remarkable, however, in view of the dynamic environment of seagrass systems (shallow, mostly tidal coastal waters; Den Hartog 1970). Detached leaves and leaf fragments and dissolved (in)organic

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nutrients released from seagrass litter decomposing at the sediment surface are easily carried away from the seagrass bed by currents and tides. The particle-trapping capacity of the seagrass canopy (Bulthuis et al. 1984; Ward et al. 1984; Fonseca and Fischer 1986), however, may play a role in keeping detached leaf material inside the seagrass bed. Leaves, furthermore, have a clear capacity to absorb nutrients from the water column, even under nutrient-poor conditions (Iizumi and Hattori 1982; Short and McRoy 1984; Hemminga et al. 1994; Pedersen and Borum 1992, 1993; Stapel et al. 1996*a*; Pedersen et al. 1997; Lee and Dunton 1999). This capacity is often presumed to be important to counterbalance nutrient losses with nutrients from external sources, but it could also be very effective in recapturing the regenerated nutrients, contributing to nutrient conservation for the seagrass meadow as a whole.

Clark (1977) and White and Howes (1994), using pulse-labeling with ^{15}N in small (3 and 6 dm^2) field plots, estimated the residence time of nitrogen in a shortgrass prairie (*Bouteloua gracilis*) and in a salt marsh (*Spartina alterniflora*) system to be in the order of years to decades. The pathways available for nitrogen retention in prairies and salt marshes are, in principle, the same as those in seagrass beds. Storage of nitrogen in below-ground organic matter resulted in long-term retention, whereas internal translocation was primarily conductive to short-term retention. Following the method used by Clark (1977) and White and Howes (1994), the present study was undertaken to examine the mechanisms for nitrogen retention existing within a 1-m^2 field plot in an offshore *Thalassia hemprichii*–dominated coral island seagrass bed. We pulse-labeled the shoots of *T. hemprichii* in situ with ^{15}N, making use of the plants' capacity to take up ammonium with the leaves from the ambient water column (Stapel et al. 1996*a*). Hereafter, the course of ^{15}N in the plant and in detritus was modeled as a function of time.

Materials and methods

Study area—For the present study on nitrogen retention in *T. hemprichii*, we searched for a largely monospecific seagrass bed with rather constant biomass, productivity, and tissue nitrogen concentrations that could be considered to be in equilibrium (steady state). We found a seagrass bed matching these criteria in the Spermonde Archipelago, along the west coast of South Sulawesi, Indonesia. The archipelago consists of a large group of coral islands and submerged reefs, distributed on the continental shelf (Fig. 1). This area in the Indo-Pacific is characterized by rather constant climatic conditions. Winds prevail from the northwest and the east to southeast (depending on the monsoon), that rarely blow faster than 11 m s^{-1} but sometimes reach 20 m s^{-1} (average 2 m s^{-1}) (long-term data series of the Indonesian Meteorological Institute; Hoeksema 1990). The research was executed in a seagrass bed at the reef flat of Barang Lompo (5°03′S, 119°20′E), a coral island surrounded by a large carbonate reef flat with an extensive multispecies seagrass vegetation (50 ha). The annual average nitrogen concentration was 2.2 μM in the water column and 60 μM in the pore water and was rather stable throughout the year (Erftemeijer and Herman 1994; Stapel et al. 1996*a*). Because of its situation in the archipelago, ~14 km off the coast and 30 km from the shelf edge, the island lacks both the seasonal terrestrial influence of river discharge and the influence of upwelling from the deep Makassar Strait (Verheij 1993). The comparatively uniform temperature and day length in tropical shallow areas allow rather constant seagrass biomass and growth throughout the year, in comparison with temperate regions (Brouns 1985*a*, 1987; Duarte 1989). Erftemeijer and Herman (1994), who studied seasonal variability in the Spermonde Archipelago, concluded that seagrasses, even those occurring close to river outlets, are a relatively stable and constant factor in the system, except for seagrass communities occurring intertidally at the reef flats of coral islands. In periods during which the seagrasses are exposed to air during daylight—which is a seasonally occurring phenomenon in the study area—growth rate, biomass, and tissue nutrient contents of above- and below-ground organs are significantly affected (Erftemeijer and Herman 1994; Stapel et al. 1997). For this study, we therefore selected a subtidal area of the reef flat at the sheltered southwestern site of the island, 20–30 cm below extreme low water. The seagrass vegetation here consists of *T. hemprichii* (Ehrenb.) Aschers with patches of *Enhalus acoroides* (L.f.), the dominant constant species of stable environments in this part of the world

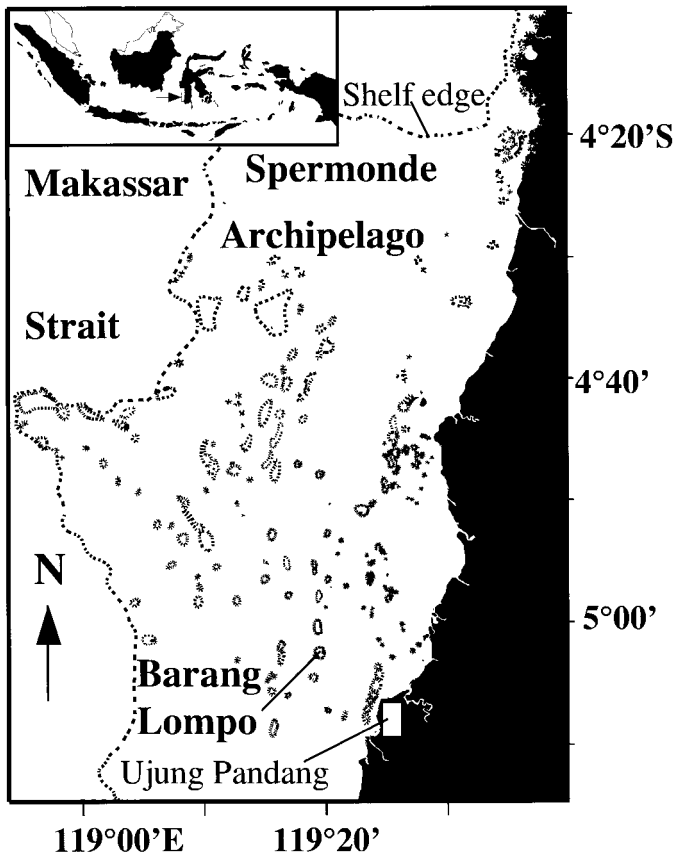

Fig. 1. Study area, showing islands and submerged reefs (dashed spots) of the Spermonde Archipelago along the west coast of South Sulawesi. Dashed line: shelf edge (200 m). Inset: Indonesian Archipelago.

and permanently present in climax vegetations (Verheij and Erftemeijer 1993). The vegetation (biomass, productivity, and nitrogen content) has not significantly changed over the past decade (Erftemeijer 1993; Verheij 1993; Stapel 1997). Community production and respiration are in balance (Erftemeijer et al. 1993*b*). Grazing by herbivores, potentially capable of removing a considerable amount of nutrients from the seagrass bed (Zieman et al. 1984), plays no role of any significance in this system. Sea turtles and dugongs are practically extinct because of severe hunting pressure by the indigenous people (De Iongh 1996). Occasionally, clusters of parrotfish (Scaridae) and rabbitfish (Siganidae) are observed inside the seagrass meadow, but no bite scars were recorded on the leaves of *T. hemprichii* in the area selected for the research (P. Van Avesaath unpubl. data).

Leaf biomass production, leaf biomass loss, and gross and net nitrogen demand—The youngest leaves of 9 replicate sets of 10 shoots were marked by punching a hole in the tip ~1 cm above the basal meristem. A bamboo stick was inserted into the sediment next to the shoot as a reference that indicated the level of this mark. After $t = 16$ days, all newly emerged leaves that had reached the reference level were counted. These measurements allowed calculation of the leaf plastochrone interval (PI; the time interval between the onset of two consecutive leaves; Erickson and Michelini 1957) as an estimation of leaf production. The PI was calculated according to

$$\mathrm{PI} = \frac{St}{L} \tag{1}$$

in which PI is the plastochrone interval of the leaves (days), S is the number of shoots of which the youngest leaves were marked, t is the time interval between marking and harvesting (days), and L is the number of new leaves reaching the reference level. This method has been successfully used on *T. hemprichii* before—in Papua New Guinea, by Brouns (1985*b*); in Indonesia, by Erftemeijer et al. (1993*b*, 1994); and in The Philippines, by Vermaat et al. (1995)—and agrees with leaf growth based on oxygen evolution (Erftemeijer et al. 1993*b*). If the nitrogen concentration and the biomass of leaves of a given age remain constant, and if biomass production and loss are in equilibrium in the seagrass bed, the gross leaf nitrogen demand of a seagrass shoot is equivalent to the total amount of nitrogen in the one leaf with the highest nitrogen content, over a period of 1 PI. Similarly, the leaf biomass production of a shoot is equal to the biomass of the heaviest leaf on that shoot PI^{-1}. To calculate the average gross leaf N demand, we averaged the N contents of the leaves with the highest value in each of 21 samples that were taken during this experiment (see the ''Labeling and recovery of ^{15}N'' section for sampling details). In a similar way, we calculated the average leaf biomass production (the average of the maximum leaf weights of each individual shoot). We assumed that the seagrass bed under investigation was in steady state (no increase or decline in biomass or N content), and therefore biomass production equals biomass loss. As leaves become older, fragmentation processes, e.g., caused by mechanical stress (wave action), reduce their biomass. During leaf development, the nitrogen concentration declines (Stapel and Hemminga 1997). The nitrogen that is lost from a shoot along with detached leaf fragments is therefore not proportional to the biomass loss. Part of the nitrogen may be resorbed from aging leaves before they detach and may be used in young growing tissue. To estimate how much nitrogen is resorbed, we calculated the amount of nitrogen lost because of leaf fragmentation. The leaf samples were divided into subsamples containing leaves from the same age category, numbered from 1 (youngest leaves, L_1) to 5 (oldest leaves, L_5). Because we do not know when a leaf fragment was lost from a shoot during a PI, we cannot be sure of the nitrogen content of this fragment. We therefore calculated an average amount of nitrogen loss by multiplying the averaged nitrogen concentration of the ith leaf (L_i) and the ith + 1 leaf ($L_i + 1$) with the biomass difference of $L_i - L_i + 1$ (i.e., the biomass of the lost leaf fragment[s]). We did this for all leaves L_i declining in biomass from L_i to $L_i + 1$. Hereafter, we calculated for each of the 21 samples the total amount of nitrogen loss. These figures represent the amount of nitrogen that is lost from the leaves during 1 PI that needs to be replenished by uptake from the environment: the net leaf N demand. From the difference between the net leaf N demand and the gross leaf N demand, we calculated for each sample a leaf nitrogen resorption percentage. Finally, these resorption figures were averaged.

Labeling and recovery of ^{15}N—To trace the dynamics of nitrogen in the different compartments of the seagrass system, the leaves of *T. hemprichii* were pulse labeled with ^{15}N. On 10 August 1993, three replicate 1 × 1 m field plots (located ~10 m from each other) were enclosed with wooden boxes that were open at the top. The shoots of *T. hemprichii* in the three enclosed field plots were subsequently incubated with ^{15}N–NH_4Cl (99% ^{15}N) at low tide, the height of the water column above the sediment being ~20 cm. The ammonium concentration in the water column at the start of the incubation was ~45 μM. This concentration is about twice the value of the half-saturation constant (K_M) for ammonium uptake by leaves of *T. hemprichii* (Stapel et al. 1996*a*). The incubations lasted 3–4 h. After this period, the wooden boxes were removed. We harvested one cylindrical core (28.3 cm^2) from the inner 0.5 × 0.5 m of each plot at $t = 0$, 19, 33, 60, 121, 183, and 240 d. The cores were divided into above- and below-ground compartments. The above-ground compartments were subsequently divided into samples containing leaves of the same age category and a sample of dead sheaths. The latter remain attached to the shoot after leaf abscission. The below-ground compartments were divided into 2-cm sections, to a depth of 12 cm (the depth range of the roots of *T. hemprichii* at this research site). Living roots and horizontal and vertical rhizomes of each core were collected from the different sediment sections, yielding one root and one rhizome sample per core. The particulate organic matter (POM) >50 μm in each sediment section was obtained by use of the difference in the specific weight of sediment particles and POM. Each sediment section was flushed with tap water in a plastic container. The overflowing water was sieved over screens with 1-mm and 50-μm mesh until the sediment in the container was free of POM. The fractions collected on both sieves

contained POM and smaller sediment particles. These fractions were cleaned again according to the method described above, now flushing the water with lesser force. This procedure was repeated until the POM fractions were free of sediment. The origin of the recognizable POM (leaves or other tissue of *T. hemprichii* and organic matter from other sources) was identified by use of a binocular microscope. We assumed that the origin of the not-recognizable amorphous POM fraction was proportional to that of the identified POM. The remaining sediment fractions were kept for analysis of N and ^{15}N in the adsorbed organic matter or in POM that had not been separated from the sediment despite the flushing procedure described above. We assumed that the origin of this organic matter was also proportional to that of the identified POM.

All samples (leaves, roots, rhizomes, sheaths, POM, and sediment) were dried to constant dry weight (DW) at 80°C and weighed. Analysis of the samples for total N and ^{15}N was carried out using a Carlo Erba NA 1500 CN analyzer and a Finnigan Mat delta S isotopic ratio mass spectrometer coupled to a Fisons NA 1500 CN analyzer via a coflow interface, respectively. After subtraction of the natural abundance of ^{15}N (being 0.37% of total N), the ^{15}N enrichment (percentage of DW) of each sample was multiplied by the corresponding average DW that was calculated by use of the samples taken from the three plots at all seven harvesting occasions ($n = 21$). Herewith, we obtained for each plot and at each sampling occasion average values for the ^{15}N enrichment (g m^{-2}) in the various leaf classes, in the roots, rhizomes, and POM, and in the various sediment sections. The ^{15}N enrichments of each plot were expressed as a proportion of the total amount of ^{15}N enrichment of the corresponding plot at $t = 0$, and the figures of corresponding sample type and time were considered to be replicates.

Modeling of ^{15}N dynamics—The ^{15}N contents in the living seagrass leaves and the detritus compartments of the labeled plots as a function of time are described by two differential equations:

$$\frac{dL}{dt} = -aL \tag{2}$$

$$\frac{dD}{dt} = \beta aL - bD. \tag{3}$$

In these equations, L is the fraction of the initial ^{15}N enrichment present in the seagrass leaves (sum of ^{15}N in all leaf classes), and D is the fraction of ^{15}N enrichment present in detritus, i.e., the summed quantities of ^{15}N in POM in the upper 12 cm of the sediment, ^{15}N adsorbed to the remaining sediment, and ^{15}N in the dead sheaths of detached leaves. The parameters a and b describe first-order rate constants at which ^{15}N declines in L and D, respectively. The parameter β describes a constant portion of the disappearance of ^{15}N from L that is translocated to D. Roots and rhizomes were not included in the modeling. The role of these tissues in the net ^{15}N cycling was considered unimportant, since the ^{15}N concentration remained low throughout the experiment and did not significantly change in time. Epiphytes colonizing especially the older leaves of *T. hemprichii* at Barang Lompo (Erftemeijer 1994) most likely absorbed a considerable portion of the added ^{15}N as well. Although epiphytes are an important part of the seagrass ecosystem too, one of the foci of this study is on internal reuse processes in seagrass plants. Obviously, ^{15}N contained in epiphytes does not take part in this process. To reduce the potential erroneous contribution of epiphytic ^{15}N to the total ^{15}N in the seagrass plant as much as possible, the first 19 d of the experiment were not included in the mathematical modeling. After these 19 d, most ^{15}N-containing epiphytes are lost from the plant because of the detachment of the leaves they colonize. Another important aspect is that during this period of 19 d after pulse labeling, the absorbed ^{15}N has readily been cycling and distributed through the various plant components and assimilated into cell structures, resulting in a more homogeneous ^{15}N pattern in the different plant parts. Because the ^{15}N figures were expressed as percentage of total initial enrichment (i.e., total ^{15}N excess) and not as a ^{15}N : ^{14}N ratio, the ^{14}N in (new) epiphytes on the seagrass leaves after day 19 has no effect on the modeling of the ^{15}N dynamics. Now, solving Eqs. 2 and 3, these expressions become

$$L_t = L_{19}e^{[-a(t-19)]}, \tag{4}$$

$$D_t = \left(D_{19} + \beta aL_{19}\frac{e^{(b-a)(t-19)} - 1}{b - a}\right)e^{[-b(t-19)]}, \tag{5}$$

where L_t, D_t, L_{19}, and D_{19} are the measured ^{15}N contents (percentage of initial enrichment) of L and D at time t and at $t = 19$ d, respectively. Equation 4 was fitted first, by use of nonlinear least-squares regression. Hereafter, the resulting value for a (9 decimals) was substituted in Eq. 5, which was then also fitted by use of nonlinear least-squares regression.

Verification of model parameters—The value for a as it is obtained from the model above describes the *total* loss of ^{15}N from leaves—that is, loss due to leaf detachment, to above- to below-ground translocation, and to possible leaching. On the basis of the data of the measured leaf nitrogen contents and the PI, we are also able to calculate a rate constant for leaf nitrogen decline due to loss of leaves and leaf fragments only. For this calculation, we used the following differential equation:

$$\frac{d\mathrm{N}_t}{dt} = I - a'\mathrm{N}_I, \tag{6}$$

in which N_I is ''new'' nitrogen input to the leaves (g m^{-2}), I is the nitrogen input constant (g m^{-2} d^{-1}), and a' is the first-order rate constant of nitrogen decline due to leaf detachment only (d^{-1}). Solving this equation gives

$$\mathrm{N}_I = \frac{I(1 - e^{-a't})}{a'}. \tag{7}$$

For $t \to \infty$, the leaf nitrogen of a seagrass shoot ($\mathrm{N}_{\mathrm{tot}}$) consists of newly absorbed nitrogen (N_I) only. Equation 7 then becomes

$$N_{tot} = \frac{I}{a'}. \quad (8)$$

Thus, from the total leaf nitrogen content of a seagrass shoot (the nitrogen contents of all leaves summed; N_{tot}; g m^{-2}), the nitrogen input (net nitrogen demand; g m^{-2} PI^{-1}) as calculated from the nitrogen loss due to leaf fragmentation (see earlier, in the ''Material and Methods'' section) and the PI as time constant, we can calculate the value for a' (d^{-1}). The value for a' approaches the value for a when above- to below-ground translocation and leaching are quantitatively unimportant processes.

The value for b as it is obtained from the model describes the decline of total ^{15}N in deposited leaf fragments caused by decomposition processes and the (bed load) export of deposited leaf particles. The decomposition rate of *T. hemprichii* leaves was established in litterbag experiments. Detached, floating leaves were collected at the research site in May and transported to the laboratory in buckets filled with seawater. The material was dried on filter paper at room temperature (28°C–30°C), for exactly 1 h. Litterbags (10 × 10 cm; 1-mm mesh) were then filled with a known mass (~7 g wet weight) of this material. The filled litterbags (132 in total) were retransported in seawater to the research site and deployed in the sediment–water interface inside the seagrass vegetation. Twelve litterbags were harvested from the deployment site at each sampling occasion (t = 0, 2, 4, 6, 10, 12, 16, 24, 36, 44, and 52 d). The contents were recovered on a 1-mm sieve and rinsed with seawater to remove sediment. The samples were then dried on filter paper at room temperature for exactly 1 h, weighed, and dried at 80°C until constant DW. From six litterbags, samples of 0.4 g were taken. Three samples were pooled together, resulting in two replicate samples in which the nitrogen content was measured. From the remaining material and the contents of the other six litterbags, the ash-free dry weight (AFDW) was established by combustion at 540°C for 1 h. Wet to DW and AFDW conversion factors were established by using the litterbags of t = 0 (DW = 0.14 ± 0.005 × wet weight [WW], n = 21; AFDW = 0.081 ± 0.005 × WW, n = 13). The remaining AFDW or nitrogen content at time t were expressed as a fraction of the initial value (t = 0). The data were fitted according to a single first-order exponential decay function, by use of nonlinear least-squares regression:

$$G_t = G_0 e^{-kt} \quad (9)$$

In this equation, G_t is the remaining AFDW or N content of the material in the litterbags at time t, G_0 is the initial AFDW or N content, t is the time (days of field exposure), and k is the first-order decomposition rate (d^{-1}). The value for k approaches the value for b when export of deposited ^{15}N containing leaf detritus out of the experimental plots is a quantitatively unimportant process.

The ^{15}N modeling described above does not take into account the possibility of reabsorption of ^{15}N regenerated by decomposition of enriched leaf detritus within the experimental plots. To check whether this process could be of significance in describing the ^{15}N dynamics, we included this possibility in the model. The differential Eqs. 2 and 3 now become

$$\frac{dL}{dt} = -aL + \alpha bD, \quad (10)$$

$$\frac{dD}{dt} = \beta aL - bD, \quad (11)$$

in which α describes a constant portion of ^{15}N regenerated from D that is reused again in the seagrass leaves (absorbed directly from the water column or via the roots). The other parameters are as described before. The solutions of these equations are, because of their complexity, not given here. The values possible for α are between 0 and 1 (i.e., between 0 and 100% reabsorption).

^{15}N dilution—A disproportional decline of ^{15}N, compared with the total N decline in aging leaves, points to dilution of the nitrogen pool with ^{14}N. ''New'' (^{14}N) nitrogen is mixed with the existing $^{14+15}N$ pool and, because the total N content of these senescent leaves declines (Stapel and Hemminga 1997), is subsequently allocated to other plant parts (young growing tissue) or leached into the environment. Dilution of ^{15}N in the leaves allows calculation of the amount of ^{14}N input to these leaves. Heretofore, two simple differential equations were used:

$$\frac{d^{15}N}{dt} = -f_l {}^{15}N_l, \quad (12)$$

$$\frac{d^{14}N}{dt} = I_l - f_l {}^{14}N_l, \quad (13)$$

in which $^{15}N_l$ and $^{14}N_l$ are the concentrations of the two nitrogen species in Leaf l, f_l is the first-order rate constant of ''old'' nitrogen decline in l (d^{-1}), I_l is the daily ^{14}N nitrogen input in l (g N g^{-1} DW d^{-1}), and t is the time in days. Solving these equations gives

$$^{15}N_{l,t} = {}^{15}N_l e^{-f_l t}, \quad (14)$$

$$^{14}N_{l,t} = {}^{14}N_l e^{-ft} + \frac{I_l(1 - e^{-f_l t})}{f_l}, \quad (15)$$

in which $^{15}N_{l,t}$ and $^{14}N_{l,t}$ are the ^{15}N and ^{14}N concentrations of a particular leaf l after time t. By use of the decline in ^{15}N concentration in a particular leaf l, f_l was estimated and subsequently substituted in Eq. l5 to estimate I_l.

Results

Study site—The biomass and N concentration of each of the leaf classes, sheaths, rhizomes, and roots of *T. hemprichii* and detritus at Barang Lompo remained constant during the experiment ($P > 0.05$; one-way ANOVA). We therefore calculated the average biomasses, N concentrations, and contents of the different compartments on the basis of all samples. The living compartment consists of 126 g DW m^{-2} leaves, 229 g DW m^{-2} rhizomes, and 109 g DW m^{-2} roots. Altogether, leaves, rhizomes, and roots contain 4.94 g N m^{-2} (Table 1). POM accounted for a total of 889 g DW m^{-2} in the top 12 cm of the sediment and in dead sheaths that are still attached to the seagrass shoots. POM and these sheaths contained 6.20 g N m^{-2}. A total of 38 g N m^{-2} is adsorbed

Table 1. Mass (g DW m^{-2}), nitrogen concentration (% of dry weight) and nitrogen content (g N m^{-2}), ± SD, of *T. hemprichii* leaves, rhizomes, roots, and dead sheaths of detached leaves (Sheaths), of the POM in successive 2-cm sediment sections, and of the sediment fractions excluding POM. For POM in the sediment, the percentage (dry weight [DW]) originating from leaf material is indicated. $n = 21$ unless indicated otherwise.

Sample	Mass (g DW m^{-2})	Nitrogen concentration (% of DW)	Nitrogen content (g N m^{-2})
Leaf 1	19.3 ± 5.9	3.27 ± 0.70	0.625 ± 0.151
Leaf 2	31.9 ± 9.9	2.60 ± 0.44	0.825 ± 0.223
Leaf 3	38.3 ± 11.5	2.02 ± 0.37	0.793 ± 0.275
Leaf 4	29.0 ± 14.4	1.66 ± 0.46	0.506 ± 0.298
Leaf 5	7.5 ± 13.6	1.42 ± 0.27 (n = 6)	0.106 ± 0.194
Total leaves	126 ± 30		2.85 ± 0.73
Rhizomes	229 ± 130	0.64 ± 0.19	1.47 ± 0.44
Roots	109 ± 69	0.57 ± 0.19	0.62 ± 0.21
Sheaths	82 ± 44	0.58 ± 0.16	0.48 ± 0.13
POM 0–2 ($n = 15$)	188 ± 66 (81% leaf)	0.71 ± 0.19	1.34 ± 0.32
POM 2–4 ($n = 15$)	193 ± 54 (54% leaf)	0.66 ± 0.19	1.41 ± 0.30
POM 4–6 ($n = 15$)	153 ± 57 (25% leaf)	0.59 ± 0.16	1.03 ± 0.17
POM 6–8 ($n = 14$)	113 ± 43 (25% leaf)	0.62 ± 0.19	0.83 ± 0.17
POM 8–10 ($n = 11$)	80 ± 30 (21% leaf)	0.57 ± 0.13	0.55 ± 0.08
POM 10–12 ($n = 1$)	74 (21% leaf)	0.63 ± 0.20	0.55
Total POM	807 ± 215	0.65	5.72 ± 1.19
Sediment 0–2 ($n = 18$)	(23 ± 4) × 10^3	0.026 ± 0.015	5.9 ± 3.4
Sediment 2–4 ($n = 18$)	(28 ± 2) × 10^3	0.023 ± 0.012	6.4 ± 3.5
Sediment 4–6 ($n = 18$)	(29 ± 4) × 10^3	0.024 ± 0.012	7.1 ± 3.3
Sediment 6–8 ($n = 17$)	(29 ± 5) × 10^3	0.022 ± 0.010	6.3 ± 3.0
Sediment 8–10 ($n = 13$)	(31 ± 6) × 10^3	0.017 ± 0.011	5.2 ± 3.4
Sediment 10–12 ($n = 1$)	25 × 10^3	0.03	7.6
Total sediment	(165 ± 10) × 10^3	0.024	38 ± 7.4

to the sediment grains (top 12 cm). Identification showed that 81% of the POM DW originated from *T. hemprichii* leaves in the top 2 cm of the sediment. This figure was reduced to 54% between 2 and 4 cm, to 25% between 4 and 8 cm, and to 21% from 8 to 12 cm depth in the sediment. Hence, there is a POM N pool, originating from leaves, of 3.02 g m^{-2} in the top 12 cm of the sediment and in dead sheaths. The remaining part (3.18 g POM N m^{-2}) was primarily composed by dead *T. hemprichii* roots and rhizomes. Only ~4% of the total POM N pool originated from sources other than *T. hemprichii*.

Leaf production and nitrogen demand—The PI of *T. hemprichii* leaves was 9.9 ± 1.3 d ($n = 9$). This value is within the relatively narrow range of PI values reported previously for *T. hemprichii* leaves from Papua New Guinea, Indonesia, and the Philippines (9.3–10.9 d: Brouns 1985*b*; Erftemeijer et al. 1993*b*, 1994; Vermaat et al. 1995), which makes it likely that fluctuations in the PI during the experiment were negligible. The maximum leaf biomass of *T. hemprichii* was 41.0 ± 11.2 g DW m^{-2} ($n = 21$) and was reached at a leaf age of 3.1 PI. This figure represents the average of the heaviest leaves of all sampled shoots. These leaves were not all of the same age. Sometimes leaf 2 had the highest biomass, sometimes leaf 3 or 4. Because of this, the maximum leaf biomass does not correspond with the heaviest leaf class in Table 1, which is the average biomass of all leaves 3. We used the maximum average leaf biomass to calculate leaf production. During one PI, *T. hemprichii* thus produces 41.0 g DW of new leaf biomass per m^2. This is equivalent to 0.033 ± 0.008 g g^{-1} leaf DW d^{-1}, which is also well within the annual range previously reported for *T. hemprichii* from the same research site by Erftemeijer et al. (1993*b*) and Erftemeijer and Herman (1994) (0.022–0.056 g g^{-1} leaf DW d^{-1}). The gross leaf nitrogen demand was 34.3 ± 9.6 g N m^{-2} yr^{-1} ($n = 21$), equivalent to the average maximum leaf N content PI^{-1} (0.930 ± 0.229 g m^{-2} PI^{-1}) that was reached at a leaf age of 2.5 PI. Total nitrogen loss due to leaf fragmentation and detachment was 24.8 ± 8.7 g m^{-2} yr^{-1} ($n = 21$). From the difference between the net N demand (=total N loss) and the gross N demand, we calculated a leaf nitrogen resorption of 28 ± 16% ($n = 21$). The nitrogen loss rate due to leaf detachment (a') was 0.024 ± 0.008 d^{-1} ($n = 21$).

^{15}N nitrogen dynamics—Addition of ^{15}N–NH_4Cl to the water column above the *T. hemprichii* plots resulted in enrichment of the leaf tissue ^{15}N concentration from the natural background level of 0.37% of total N to an average of ~2%. The ^{15}N enrichment at t_0 as a proportion of the total initial ^{15}N enrichment per gram leaf DW was lowest in L_1, whereas $L_2 - L_5$ had equal concentrations of label (Table 2). After the first 19 d (~2 PI), the newly produced classes L_1 and L_2 contained substantial levels of ^{15}N: 0.42% and 0.33% of the total initial enrichment g^{-1} DW, respectively. The leaf trajectory $L_{1,t=0} \rightarrow L_{3,t=19}$ showed no significant change in ^{15}N concentration during the first 19 d, but, considering the difference in biomass between $L_{1,t=0}$ (19.3 g DW m^{-2}) and $L_{3,t=19}$ (31.9 g DW m^{-2}), it is obvious that considerable input of ^{15}N had occurred. The ^{15}N concentrations in $L_{4,t=19}$ and

Table 2. Time course of ^{15}N content (% of initial enrichment g^{-1} DW ± SD where possible) in the five different leaf classes, sheaths, rhizomes (Rh), and roots (Ro) of *T. hemprichii* after short-term exposure (3–4 h) of the shoots to ^{15}N–NH_4Cl, $n = 3$; *, $n = 2$.

Leaf class	Time (days after pulse labeling)						
	0	19	33	60	121	183	240
L_1	0.27 ± 0.21	0.42 ± 0.09	0.23 ± 0.05	0.095 ± 0.021	0.047 ± 0.014	0.021 ± 0.010	0.013 ± 0.006
L_2	0.97 ± 0.24	0.33 ± 0.05	0.22 ± 0.08	0.075 ± 0.017	0.035 ± 0.010	0.016 ± 0.006	0.010 ± 0.004
L_3	0.92 ± 0.08	0.32 ± 0.09	0.19 ± 0.05	0.062 ± 0.019	0.027 ± 0.0010	0.011 ± 0.005	0.008 ± 0.003
L_4	0.82 ± 0.48	0.22 ± 0.07*	0.18 ± 0.04	0.047 ± 0.021	0.021 ± 0.005	0.008 ± 0.007*	0.007 ± 0.003
L_5	0.97	0.13	0.12 ± 0.03*		0.011	0.007	
Sheath	0.012 ± 0.007	0.019 ± 0.016	0.012 ± 0.006	0.023 ± 0.024	0.013 ± 0.005	0.005 ± 0.002	0.005 ± 0.002
Rh	0.006 ± 0.004	0.009 ± 0.001	0.016 ± 0.010	0.011 ± 0.007	0.011 ± 0.004	0.007 ± 0.003	0.007 ± 0.002
Ro	0.003 ± 0.001	0.005 ± 0.004	0.007 ± 0.002	0.004 ± 0.001	0.009 ± 0.005	0.006 ± 0.003	0.006 ± 0.003

$L_{5,t=19}$ were significantly less than those of the leaf classes from which they had emerged (leaf classes $L_{2,t=0}$ and $L_{3,t=0}$). During the next period of 14 d, the ^{15}N concentration declined in all leaf classes. Part of this decline coincided with N allocation to new leaves, as is illustrated by the occurrence of ^{15}N in (newly emerged) L_1. The same picture appeared in the rest of the experiment: the total leaf ^{15}N content declined, but some of the ^{15}N was allocated to newly emerging leaves. Following the ^{15}N concentration of particular leaves over time and comparing this with the N concentrations of different leaf ages given in Table 1, it appears that the ^{15}N-concentration decline is much faster. Under the assumption that that there is no preference for ^{15}N translocation over ^{14}N translocation, this observation points to dilution of the ^{15}N pool in these leaves with ^{14}N. Using Eqs. 14 and 15, we estimated the ^{14}N input to leaves over the period $t_{19\rightarrow33}$ (Table 3). The period $t_{0\rightarrow19}$ was not considered because a large fraction of the ^{15}N decline could have been caused by the loss of ^{15}N absorbed by the epiphytes on the older leaves during the ^{15}N incubation. Other periods (i.e., $t_{33\rightarrow60}$, and so on) were not considered because of the time gap between sampling dates, which makes it impossible to follow a particular leaf in time. Furthermore, over longer periods of time, leaves change from sink to source tissue. During the period $t_{19\rightarrow33}$, the ''new'' nitrogen input to the leaves L_2 and L_3 was 0.47 mg N g^{-1} DW d^{-1}. Extrapolating this figure to all source leaves ($l \geq L_2$), the ^{14}N input totals 49 mg N m^{-2} d^{-1}. This amount of nitrogen, however, is not incorporated in the source leaf tissue (the N content does not increase) but most likely is transported to other plant parts. On top of that, there is an additional 26 mg m^{-2} d^{-1} (9.5 g N m^{-2} yr^{-1}) N resorption from these leaves for use elsewhere in the plant. Source leaves thus supplied a total of 75 mg N m^{-2} d^{-1}. The ^{15}N loss due to leaf fragmentation over the period $t_{19\rightarrow33}$ was 11% of the initial enrichment (Table 4). The total plant ^{15}N decline over this period was 12% of the initial enrichment (Fig. 2). Of the potential available ^{15}N for translocation from $l \geq L_2$ at t_{19}, being 9% of initial enrichment (30% in leaves at t_{19} minus 10% remaining in those leaves at t_{33} minus 11% loss by leaf fragmentation), 7% was retrieved in young leaves and 1% in roots and rhizomes, leaving 1% unaccounted loss.

Part of the ^{15}N that was lost from the leaves in the period after the initial ^{15}N addition was recovered in roots and rhizomes and in detritus (Table 2; Fig. 3). The dynamics of ^{15}N in the seagrass leaves and in detritus were analyzed using Eqs. 4 and 5. The rate at which ^{15}N disappeared from the leaves starting at 19 d after labeling was 0.031 d^{-1} (rate constant a; 95% confidence interval [CI] 0.025–0.037). Within the experimental plots, there was deposition of 19% (β; 95% CI −13–51) of the ^{15}N lost from the leaves by fragmentation and detachment. ^{15}N declined in detritus at a rate of 0.010 d^{-1} (b; 95% CI 0.004–0.017). The overall R^2 of this model was 0.900. A small amount of the ^{15}N was

Table 3. Computation of the daily ^{14}N-nitrogen input (I) to leaves, using Eqs. (14) and (15). For calculations, $L_{2,t=19}$ and $L_{3,t=19}$ were followed in time. Because the time interval $t_{19} \rightarrow t_{33}$ is 14 d (~1.5 PI), $L_{i,t=19}$ may either have become $L_{i+1,t=33}$ or $L_{i+2,t=33}$. Therefore, two values for f_l and I_l were calculated for each leaf, L_i ($L_i \rightarrow L_{i+1}$ and $L_i \rightarrow L_{i+2}$) and subsequently averaged. $^{15}N_{l,t=19}$ and $^{15}N_{l,t=33}$ (Table 2) were substituted for $^{15}N_l$ and $^{15}N_{l,t}$, respectively, and $t = 14$ d. $^{14}N_{l,t=19}$ is taken from Table 1, and $^{14}N_{l,t=33}$ is the average N content of either L_3 and L_4 or L_4 and L_5. SD not given because of the propagation of errors. % IE = % of initial enrichment.

Leaf ($t = 19$)	$^{15}N_{l,t=19}$ (% IE)	$^{15}N_{l,t=33}$ (% IE)	f_l (d^{-1})	$^{14}N_{l,t=19}$ (gN g^{-1} DW)	$^{14}N_{l,t=33}$ (gN g^{-1} DW)	I_l (mgN g^{-1} DW d^{-1})
L_2	0.33	0.19 (L_3)	0.039	0.026	0.0181	0.29
		0.18 (L_4)	0.043	0.026	0.0181	0.37
	Average		0.041			0.33
L_3	0.32	0.18 (L_4)	0.041	0.0202	0.0151	0.35
		0.12 (L_5)	0.070	0.0202	0.0151	0.84
	Average		0.056			0.60
Grand average			$f = 0.048$			$l = 0.47$

Table 4. Computation of ^{15}N loss due to loss of leaf fragments. $^{15}N_{l,t=29}$ and $^{15}N_{l,t=33}$ were estimated using Eq. (14), substituting $f = 0.048$ (Table 3) and $^{15}N_l = {}^{15}N_{l,t=19}$. DW of the lost leaf fragment was the biomass difference between two consecutive leaf classes taken from Table 1 over the time interval $t_{19} \rightarrow t_{29}$ (1 PI) and half of this difference over the interval $t_{29} \rightarrow t_{33}$ (0.5 PI), and the ^{15}N concentration of the lost leaf fragment was the average of $^{15}N_{l,t}$ and $^{15}N_{l,t+\Delta t}$. SD not given because of the propagation of errors. % IE = % of initial enrichment.

Leaf l, $t = 19$	$^{15}N_{l,t=19}$ (% IE)	Leaf l, $t = 29$	$^{15}N_{l,t=29}$ (t_{19} + 1 PI) (% IE)	$^{15}N_{\text{loss, } t=19\rightarrow29}$ (% IE) $(DW_{Li} - DW_{Li+1}) \times (^{15}N_{Li} + {}^{15}N_{Li+1})/2$	Leaf l, $t = 33$	$^{15}N_{l,t=33}$ (% IE)	$^{15}N_{\text{loss, } t=29\rightarrow33}$ (% IE) $(DW_{Li} - DW_{Li+1})/2 \times (^{15}N_{Li} + {}^{15}N_{Li+1})/2$
L_2	0.33	L_3	0.20	—	$L_{3.5}$	0.17	0.9
L_3	0.32	L_4	0.20	2.4	$L_{4.5}$	0.16	1.9
L_4	0.22	L_5	0.14	3.8	Lost	0.14	1.0
L_5	0.13	Lost	0.13	1.0			
Total loss due to leaf fragmentation				$\overline{7.2}$	+		$\overline{3.8} = 11$

retrieved in the roots and rhizomes. The remaining part of the ^{15}N lost from the leaves was not recovered within the boundaries of the experimental plots. The half-life of ^{15}N in leaves only was ~22 d. The half-life of the total initial ^{15}N enrichment within the plots (*L, D,* and roots and rhizomes summed) was initially dominated by the loss of ^{15}N from leaves, but in the course of time, the ^{15}N remaining in the system tended to concentrate in compartments from where it was not easily exported (roots, rhizomes, and sedimentary detritus) or in more decay-resistant fractions. The half-life increased from 1 month in the first 60 d of the experiment to ~2 months (Fig. 3). After 240 d, only 6.64% of the initial ^{15}N enrichment remained. Leaves accounted for 1.12% and roots/rhizomes and detritus for 2.29% and 3.23%, respectively.

To investigate whether reabsorption of ^{15}N, regenerated by decomposition of enriched leaf detritus within the experimental plots could be of significance in describing the observed ^{15}N dynamics, we also fitted our data according to Eqs. 10 and 11. This resulted in values for a, b, and β of 0.037, 0.15, and 0.010, respectively, and in a value for α of 0.62, meaning that 62% of the ^{15}N, regenerated from leaf detritus inside the experimental plots, was reabsorbed (least-squares regression $R^2 = 0.903$; 95% CI not computed). The R^2 of this alternative, more-complex model, however, was not significantly larger than the model without reabsorption. Also, the values for a, b, and β computed by this model were not significantly different from those resulting from the model described above. It is therefore statistically not sound

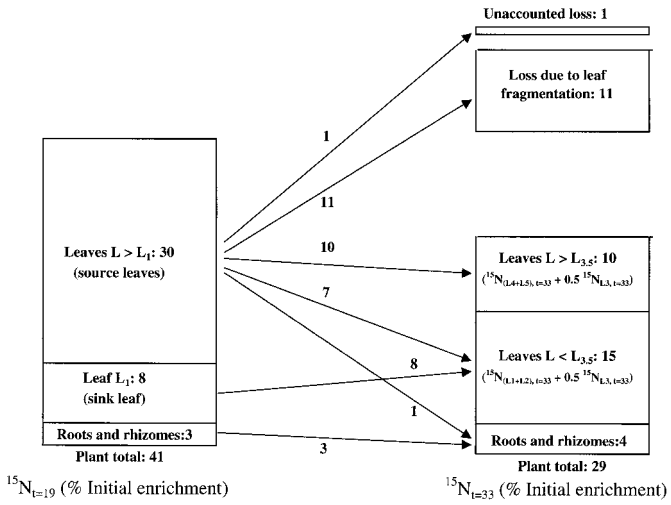

Fig. 2. ^{15}N redistribution in the plant and loss from the plant (^{15}N contents and flow in percentage of initial enrichment) in experimental plots of *T. hemprichii* between 19 and 33 d after absorption by leaves of ^{15}N–NH_4Cl, added to water column. SD not given because of propagation of errors.

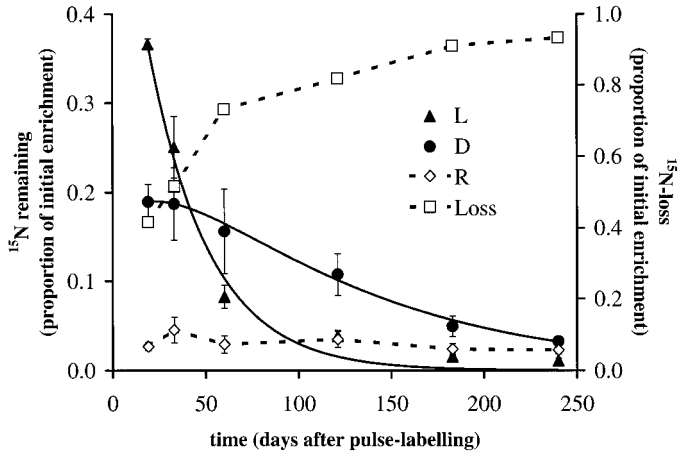

Fig. 3. Remaining ^{15}N enrichment in leaves (*L*), roots and rhizomes (*R*), and detritus (*D*) (proportion of initial enrichment), as a function of time in field plots of *T. hemprichii*, after absorption by leaves of ^{15}N–NH_4Cl, added to water column. Symbols represent the averages of three replicate figures. Solid lines represent the model fit for leaves and detritus (nonlinear least-squares regression) using Eqs. 4 and 5, respectively ($a = 0.031$ d^{-1}, 95% CI 0.025–0.037, $R^2 = 0.963$; $\beta = 0.19$, 95% CI −0.13–0.51; $b = 0.010$ d^{-1}, 95% CI 0.004–0.017, $R^2 = 0.742$; see Materials and Methods section for the description of parameters). R^2 of the complete model (*L* and *D*) is 0.900. Open squares (plotted on secondary *y* axis) represent the proportion of the ^{15}N enrichment that is not recovered within the dimensions of the experimental plots and are the resultant of $1 - (L + R + D)$. Error bars represent the standard deviation of the mean ($SD/\sqrt{n}$).

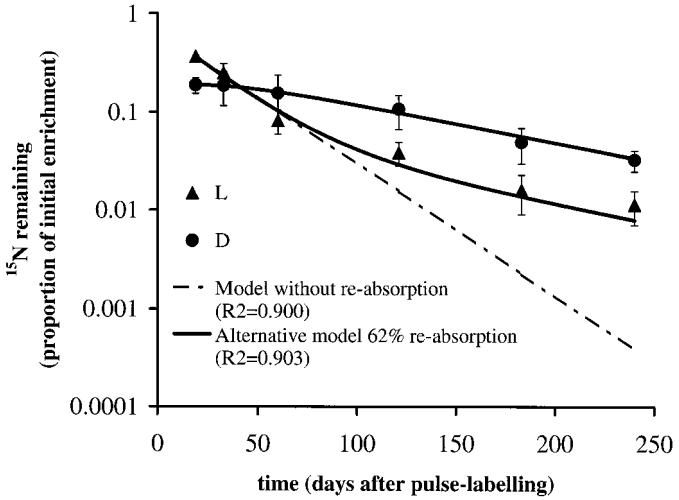

Fig. 4. Remaining ^{15}N enrichment in leaves (*L*) and detritus (*D*) (proportion of initial enrichment) on a logarithmic scale, as a function of time in field plots of *T. hemprichii*, after absorption by leaves of ^{15}N–NH_4Cl, added to water column. Symbols represent the averages of three replicate figures. Dashed line represents the model fit for leaves (nonlinear least-squares regression) using Eqs. 4 and 5 (see Fig. 2; fit for detritus not shown, since it overlaps entirely with the solid line of the alternative model); solid lines represent the model fit for leaves and detritus (nonlinear least-squares regression) using Eqs. 10 and 11. (a = 0.037 d^{-1}, β = 0.15, b = 0.010 d^{-1}, α = 0.62; see ''Materials and Methods'' section for the description of parameters). Error bars represent the standard deviation (1 SD).

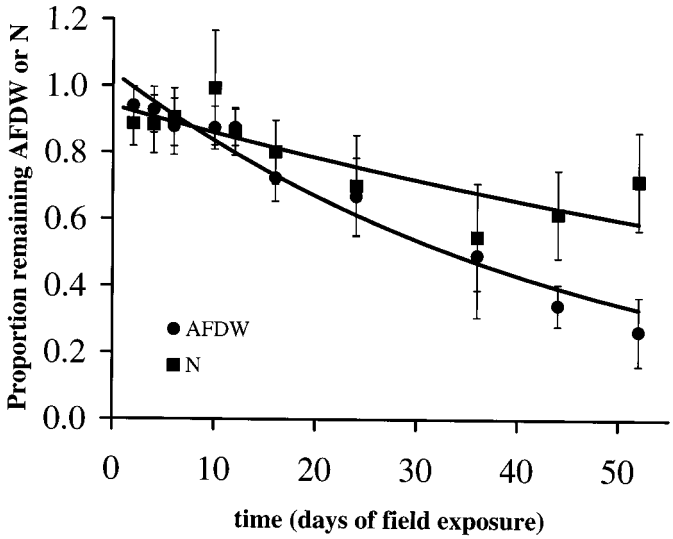

Fig. 5. Proportion of remaining AFDW or N content of *T. hemprichii* leaves in litterbags at the sediment–water interface as a function of time. Data were fitted (solid lines) according to Eq. 9 (nonlinear least-squares regression). G_0 and k describing decrease of AFDW were 1.04 (95% CI 1.00–1.07) and 0.022 d^{-1} (95% CI 0.020–0.024), respectively; R^2 = 0.836. G_0 and k describing decrease of N content were 0.94 (95% CI 0.88–1.00) and 0.009 d^{-1} (95% CI 0.006–0.012), respectively; R^2 = 0.401 (AFDW, n = 12, except at t = 36 and 52 where n = 10 and at t = 44 where n = 11. For N content n = 2). Error bars represent the standard deviation (1 SD) (see ''Materials and Methods'' section for explanation and parameter description).

to introduce the extra variable α (significance test for additional independent variables; Sokal and Rolf 1995). Despite this, the model is much better at describing the leaf ^{15}N values after 100 d, as is clearly shown when the data are plotted on a logarithmic scale (Fig. 4). It suggests that reabsorption of regenerated nitrogen, although not significant in describing the ^{15}N dynamics of the small experimental plots, could, in general, be an important process.

Decomposition of leaf detritus—Dead (detached) floating *T. hemprichii* leaves, deployed in the sediment–water interface in the seagrass vegetation, showed a decomposition rate of 0.022 d^{-1} AFDW (R^2 = 0.836; 95% CI 0.020–0.024; Fig. 5). Expressed as percentage of remaining nitrogen, the decomposition rate was 0.009 d^{-1} (R^2 = 0.401; 95% CI 0.006–0.012). During decomposition, the N concentration of the material increased from ~1.6% to >4% of AFDW.

Discussion

The values we obtained in this study for biomass production, nitrogen demand, and leaf turnover (PI) agree very well with existing literature on *T. hemprichii*, especially with previous data of the same research location (Brouns 1985*b*; Duarte 1991; Erftemeijer et al. 1993*b*, 1994; Vermaat et al. 1995). We used a simple model to describe the cycling of ^{15}N nitrogen in this seagrass system (Fig. 3). Two important model parameters, the leaf N-decline rate (a) and the detritus N-decline rate (b), were verified by conventional methods and agree well (see below). The half-life of ^{15}N in the enriched field plots of the *T. hemprichii* seagrass system (leaves, detritus + sediment-associated ^{15}N, and roots and rhizomes summed) initially was ~1 month but increased in time as leaves become less important as reservoirs of the remaining ^{15}N enrichment. Two pathways for nitrogen retention inside the seagrass bed have been described: retention via the detritus pathway, external to the living plant, and retention inside the living plant via nitrogen resorption from senescent leaves.

Processes external to the living plant—Only 19% of the ^{15}N in leaf litter deposited inside the experimental plots. What happened with the remaining 81% is not completely clear. It is not necessarily lost from the seagrass meadow. The actual total daily deposition of nitrogen in detached leaf fragments can be calculated, multiplying the N content of sediment POM originating from *T. hemprichii* leaves with the rate at which the total N content declines in this material as a result of mineralization of organic N, under the assumption that the N content of this material is the result of a steady state between leaf deposition and leaf decomposition. The decline rate of ^{15}N in detritus (b; 0.010 d^{-1}; Fig. 3) compares well with the N decline in leaf litter, as established with the litterbag experiments (k; 0.009 d^{-1}; Fig. 5). This makes it likely that decomposition only is responsible for the ^{15}N decline in deposited leaf litter and that (bed load) export of this material was not important. Hereafter, we con-

sider the rate of N decline in leaf litter during the experiment to be 0.010 d^{-1}. POM in the top 12 cm of the sediment and dead sheaths from detached leaves contained 3.02 g N m^{-2}, originating from *T. hemprichii* leaves. Multiplying this figure with the decomposition rate results in a leaf nitrogen input rate to the sediment of 0.030 g N m^{-2} d^{-1} (11 g N m^{-2} yr^{-1}). The total amount of nitrogen that is lost from the plants by leaf fragmentation and detachment was 25 g m^{-2} yr^{-1}. If we compare both figures, it follows that 44% of the nitrogen lost by leaf fragmentation is translocated to the sediment POM compartment of the seagrass bed. Our data showed that only 19% of the ^{15}N in detached leaf fragments deposited inside the experimental plots. This is much less than the 44% calculated above. There is no reason however, to assume that ^{15}N-enriched leaf fragments behave differently. It thus follows that an estimated 25% of the ^{15}N in leaf detritus was deposited outside the boundaries of the experimental plots but still inside the seagrass bed. What happened with the remaining 56%? Was this exported out of the system? Studies on leaf-export rates of seagrasses with a leaf morphology resembling that of *T. hemprichii* (*Thalassia testudinum, Enhalus acoroides, Cymodocea rotundata, Posidonia australis,* and *Zostera marina*; Kirkman and Reid 1979; Zieman et al. 1979; Josselyn et al. 1983; Bach et al. 1986) showed values of up to 30% of the produced leaf biomass. Stapel et al. (1996*b*) showed that only ~10% of the nitrogen incorporated in seagrass leaves was exported from a coral island seagrass meadow. This meadow (which is close to the present research location) is on a more exposed reef flat and experiences stronger, primarily unidirectional currents than Barang Lompo (unpubl. data). It seems unlikely, therefore, that, although at the small scale of the plots 56% of the nitrogen in detached leaf fragments may be exported, at the scale of the entire meadow >10% is exported. The estimation of 56% leaf nitrogen export follows from the visual examination of sediment organic material of the top 12 cm under a binocular microscope. The origin of the amorphous fraction was assumed to be proportionally the identified POM (*T. hemprichii* leaves, *T. hemprichii* roots and rhizomes, and other sources). By only examining the top 12 cm of the sediment and by not exactly knowing the composition of the amorphous POM, we could have underestimated the leaf-originated POM of the sediment. This would consequently have led to an overestimation of leaf export figures. Another variable used in estimating nitrogen export in leaf fragments is the decomposition rate. This rate was determined in two ways: modeling ^{15}N decline in leaf litter and litterbag experiments. Both methods may have overestimated the decomposition rate. By use of the ^{15}N method, leaf litter, once deposited onto the sediment, may subsequently have been exported from the experimental plots, whereas use of litterbags, leaf fragments smaller that the 1-mm mesh may have been lost from the bags. Underestimation of the decomposition rate by these methods seems unlikely. This means that the actual decomposition rate may have been smaller than that reported here. A smaller decomposition rate, however, would lead to larger leaf nitrogen export rates, which seems also unlikely. Besides, the decomposition rate reported here is not out of the range reported in literature on seagrass leaf litter decomposition (0.002–0.02; Rublee and Roman 1982; Peduzzi and Herndl 1991; Mateo and Romero 1996). Apart from leaf export, loss of ^{15}N from the plots may also have been caused by leaf-harvesting alpheid shrimps. At Barang Lompo, these shrimps harvested fresh leaf material and leaf litter, equivalent to ~53% of the daily produced leaf biomass of *T. hemprichii* and ~45% of the daily incorporated leaf nitrogen (Stapel and Erftemeijer 2000). The harvested leaf particles were pulled into the burrow systems of the shrimps, which extend as deep as 30 cm into the sediment (Gust and Harrison 1981; Erftemeijer et al. 1993*a*). A considerable amount of leaf litter may thus be translocated to layers deeper than 12 cm in the sediment—below sampling depth but not necessarily out of reach of seagrass roots (diffusion). Finally, the pore water, the only compartment in which we did not measure ^{15}N, may contain some of the missing ^{15}N. But since the N content of the pore water is <0.1% of the total N in the system, this amount is negligible (Erftemeijer and Middelburg 1995; Stapel et al. 1996*a*; this study). In conclusion, 19% of the ^{15}N in leaf litter deposits inside the experimental plot, 25% deposits outside these plots (but still inside the seagrass meadow), and alpheid shrimps harvested 45%, leaving 11% as a realistic rate for actual export and loss from the seagrass meadow. Altogether, the finding that only a limited amount of the ^{15}N-containing leaf litter actually deposits within the boundaries of the experimental plots does not change. We speculate that a large part of this ^{15}N may be reabsorbed by the seagrass plants after remineralization. Modeling the ^{15}N dynamics, including reabsorption of regenerated ^{15}N, suggests a 62% reuse. Considering that a substantial part of the remineralized nitrogen may be released in the (dynamic) water column and thus easily exported from the system, and lost because of denitrification (e.g., Blackburn et al. 1994), this reuse would be remarkably efficient.

Processes internal to the living plant—The results of the ^{15}N dynamics given in Table 2 show translocation of ^{15}N from old to young and newly grown leaves. Calculations of the net leaf N demand and the gross leaf N demand indicate that ~28% of the leaf nitrogen demand of *T. hemprichii* was met by internal reuse. The percentage recovery found here is consistent with values determined before for nitrogen resorption in seagrasses (3.8%–37%; Borum et al. 1989; Pedersen and Borum 1992; 1993; Alcoverro 1995; Pedersen et al. 1997; Stapel and Hemminga 1997). The rate of leaf nitrogen decline due to leaf loss only (a'; 0.024 d^{-1}) was not significantly different from the decline rate of ^{15}N (a; 0.031 d^{-1}). The value a' is expected to be lower than a because of above- to below-ground translocation and leaching. It is known that seagrasses leak organic carbon and nutrients through their leaves and that epiphytes and bacterioplankton probably grow on them (McRoy and Goering 1974; Blum and Mills 1991; Ziegler and Benner 1999). The significance of nitrogen leaching is for the seagrasses probably very small (Borum et al. 1989; Pedersen et al. 1997). The figures presented in Fig. 2 show that leaching could have occurred (unaccounted loss) but that it is of minor importance, compared with N loss due to leaf fragmentation processes. Cambridge and Hocking (1997) also found high nutrient loss

rates associated with export of *Posidonia sinuosa* and *P. australis* leaf litter.

The dilution of ^{15}N in source leaves of *T. hemprichii* ($l \geq L_2$) is illustrative for the continued ^{14}N input to these leaves, although their total N content is declining and may thus be regarded as nursing organs (Pedersen and Borum 1992). The ^{14}N input to these leaves may come from either the sediment (uptake by roots) or the water column (uptake by leaves). Under the assumption that all leaves are involved in absorbing the 0.47 mg N g^{-1} DW d^{-1} calculated to comprehend the ^{15}N-concentration decline over the period $t_{19\rightarrow33}$, the seagrass canopy may take up as much as 22 g N m^{-2} yr^{-1}. The net leaf N demand was 24.8 g m^{-2} yr^{-1}. Thus, from the dilution of ^{15}N in source leaves, it appears that leaves may have absorbed 88% of their net nitrogen demand. Previous studies on the nitrogen acquisition of roots and leaves have shown that leaves contributed up to 90% of the total N demand (Iizumi and Hattori 1982; Thursby and Harlin 1982; Short and McRoy 1984; Pedersen and Borum 1992, 1993; Hemminga et al. 1994; Pedersen et al. 1997; Terrados and Williams 1997; Lee and Dunton 1999). Borum et al. (1989), Pedersen and Borum (1992, 1993), and Pedersen et al. (1997), using ^{15}N, found that all leaves of *Z. marina* absorbed nitrogen from the water column and that nitrogen absorbed by older, fully grown leaves was subsequently translocated along with reclaimed N to growing plant parts. They assumed that the dilution of ^{15}N in leaves was caused by ammonium uptake from the water column but failed to discuss the possibility that roots absorbed the nitrogen that diluted the ^{15}N in leaves. Results of Borum et al. (1989), as well as ours, show an increasing ^{15}N concentration in roots and rhizomes over the examined period, most likely because of translocation from above- (where the ^{15}N concentration was higher) to below-ground tissue. Uptake of ^{14}N by roots would suggest a dilution of ^{15}N in the below-ground tissue. It is, however, not impossible that the nitrogen absorbed by roots is first allocated to the leaves, where it is mixed with the existing nitrogen ($^{14+15}N$) pool, synthesized into various (organic) compounds, and subsequently reallocated to roots and rhizomes. Such processes are commonly described in handbooks of (terrestrial) plant physiology (e.g., Marschner 1995). We cannot, however, completely rule out the possibility that roots absorbed ^{15}N regenerated from leaf detritus, being responsible for the observed ^{15}N increase in below-ground tissue. Although we are not able to distinguish between sites of nitrogen uptake, we cannot deny that leaves of *T. hemprichii* have a clear capability of absorbing ammonium. Laboratory experiments by Stapel et al. (1996*a*) already showed that at natural concentrations, where the N concentration in water column is much lower than in the pore water (2.2 vs. 60 μM), both leaves and roots of *T. hemprichii* at Barang Lompo were potentially capable of absorbing 100% of the plants' N demand. It is obvious that if such a capacity exists, it will also be used. This study shows that in a field situation leaves of *T. hemprichii* at maximum absorb 88% of their total net nitrogen demand.

Evaluation of nitrogen retention in an off-shore T. hemprichii *meadow*—As is the case in the small shortgrass prairie plots (3 dm^2; Clark 1977) and salt marsh plots (6 dm^2; White and Howes 1994), retention of ^{15}N in *T. hemprichii* occurs via burial of detritus and via internal resorption. The ^{15}N half-life in the 1 m^2 *T. hemprichii* plots, however, is much less (months, compared with years or decades). What can be the explanation for this relatively short ^{15}N retention in the seagrass system?

The average lifespan of a *T. hemprichii* leaf is ~50 d (the PI multiplied by the number of leaves per shoot). The production of these leaves accounts for ~90% of the plant's total nitrogen demand (Brouns 1985*b*; Erftemeijer et al. 1993*b*). The nutrient concentrations in seagrass leaves decrease at senescence (Stapel and Hemminga 1997; this study). Before leaves are lost from the shoots, therefore, a considerable amount of their nutrients may have been resorbed and used for growth of new tissue. It has been hypothesized that, in particular, seagrasses from highly productive meadows in nutrient-poor habitats such as the *T. hemprichii* bed under investigation (Erftemeijer et al. 1993*b*) have efficient nutrient resorption mechanisms to reduce the plant's dependence on an external nutrient supply (Pedersen and Borum 1992; Erftemeijer and Middelburg 1993). We found a nitrogen resorption efficiency of 28% from leaves of *T. hemprichii.* In comparison with different groups of terrestrial plants, of which the average nitrogen resorption efficiency values vary between 40% and 79% (Chapin and Kedrowski 1983; Aerts 1996), this is remarkably low. Seagrasses, furthermore, grow in the dynamic environment of shallow coastal tidal waters. Therefore, leaves and leaf fragments that are disconnected from the shoots (e.g., because of senescence or physical stress) may easily be carried away. The results of this study indicate that most of the ^{15}N decline in the experimental plots was indeed associated with the export of leaf fragments from the plots. Cambridge and Hocking (1997) also found considerable nutrient losses via seagrass leaf detritus, indicating a lower degree of nutrient conservation than might be expected in a low nutrient environment. The average lifespan of *B. gracilis* and *S. alterniflora* leaves is not much different from that of *T. hemprichii.* Also, the nitrogen resorption efficiency from leaves of *B. gracilis* and *S. alterniflora* is rather limited (33% and 6%, respectively; Clark 1977; White and Howes 1994). Furthermore, the salt marsh habitat is highly dynamic as well, and tidal export of nitrogen in *S. alterniflora* litter is equivalent to 8%–14% of the annual plant N demand (White and Howes 1994). However, the below-ground demand of *B. gracilis* is twice that of the canopy (Clark 1977), and, also in *S. alterniflora,* below-ground biomass production generally prevails over above-ground production and ranges between 27% and 90% of the total plant production (average, 58%; see Hemminga et al. 1996 and references therein). In these systems, most of the nitrogen, which initially is part of the living root and rhizome biomass and later of root and rhizome detritus, probably remains below ground and, hence, is not easily exported. The N dynamics of the marine system investigated in this study, a tropical off-shore coral island seagrass system, is thus essentially different from prairies and salt marshes (Clark 1977; White and Howes 1994). The primary cause of the short ^{15}N-retention time in *T. hemprichii* is the fact that the above-ground biomass, and not the below-ground biomass, is the major sink for nitrogen.

The limited nitrogen resorption from senescent leaves in combination with the dynamic environment subsequently allows a rapid loss of this nitrogen from the plots. Thus, within the scale of the experimental plots used in this study there is, in contrast to the small shortgrass prairie and salt marsh plots used by Clark (1977) and White and Howes (1994), no efficient long-term retention of nitrogen. However, on the scale of the entire meadow, another picture may arise. The particle-capturing capacity of the canopy (Bulthuis et al. 1984; Ward et al. 1984; Fonseca and Fischer 1986) may play a role in the deposition of nitrogen in detached leaf fragments outside the boundaries of the experimental plots but inside the *T. hemprichii* meadow. Seagrass systems are detritus-based ecosystems—that is, most of the produced biomass enters the detrital food chain, because the nutritional quality is too poor to be used directly by herbivores (Fenchel 1977; Klug 1980; Kenworthy et al. 1989). But also the bacterial carbon conversion efficiency of sedimentary seagrass litter into a form that is available to higher trophic levels seems very low, suggesting that a substantial portion of the primary production is mineralized in the seagrass bed (Blum and Mills 1991). Some of the regenerated nitrogen may be lost by denitrification, and some will be released into the water column and the pore water, where it becomes available for plant use (Blackburn et al. 1994). Studies on seagrass leaf decomposition indicate that, especially in the first few days of decay, substantial amounts of dissolved organic matter are released in the water column, where it is an important source for bacterioplankton metabolism (Blum and Mills 1991; Peduzzi and Herndl 1991; Ziegler and Benner 1999). Regeneration of plant nutrients may thus also take place for an important part in the water column. On the basis of the results of modeling the ^{15}N dynamics, including reabsorption, we speculate that efficient reuptake of regenerated nitrogen compounds by the roots and leaves is a highly effective conservation mechanism on the scale of the entire meadow. The high affinity of *T. hemprichii* leaves for ammonium uptake (Stapel et al. 1996*a*) allows efficient uptake from the water column, even at low concentrations. This speculation is in line with results of Lindeboom and Sandee (1989) and Nienhuis et al. (1989). They found that production and respiration processes in East Indonesian seagrass beds are approximately in balance, that input of allochtonous organic material and export of the produced organic matter is very limited, and that large accumulations of decomposing seagrass within the meadow and along the shore or on the outer reef flat does not occur. Combined with the low inorganic nutrient concentrations, they argued that East Indonesian seagrass meadows, as a whole, are to a large extent energetically self-sustaining as to which nutrients are quickly and efficiently recycled within the system. Trapping of leaf litter becomes more efficient with increasing size of the seagrass bed (Gambi et al. 1990; Worcester 1995) and so may the reabsorption by leaves of regenerated nutrients released in the water column. This adds a new aspect to the chances of survival of small seagrass patches. So far, improved anchoring, mutual physical protection, and physiological integration among shoots have been mentioned as factors explaining a reduced mortality with increasing patch age and size (Duarte and Sand-Jensen 1990; Olesen and Sand-Jensen 1994). We suggest that increasing patch size may also coincide with increasing nutrient retention in the system as a whole, which, especially in nutrient-poor environments, may increase chances of survival.

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