Leaf nutrient resorption, leaf lifespan and the retention of nutrients in seagrass systems

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Abstract

Efficient nutrient resorption from senescing leaves, and extended leaf life spans are important strategies in order to conserve nutrients for plants in general. Despite the fact that seagrasses often grow in oligotrophic waters, these conservation strategies are not strongly developed in seagrasses. A compilation of literature data on nutrient resorption from seagrass leaves shows that the mean resorption of nitrogen is 20.4%, and that of phosphorus 21.9%, which is lower than comparable values for various groups of perennial terrestrial plants. The actual realised resorption in seagrasses may be even less as a result of premature losses of leaf fragments due to herbivory and hydrodynamic stresses, and due to leaching losses.

The leaf lifespan in seagrasses on average is 88.4 days, but is highly variable, ranging from 345 days in Posidonia oceanica to only a few days in Halophila ovalis. Leaf lifespan increases with increasing leaf weight, and decreases with increasing leaf formation rate. Furthermore, leaf longevity increases going from tropical to temperate latitudes. We compared seagrass leaf lifespan with those of freshwater angiosperms, terrestrial herbaceous plants, shrubs and trees. Considerable variability in leaf lifespan was also found in these plant groups, but comparison among data sets shows that seagrass leaf lifespan is significantly lower than the leaf lifespan of terrestrial herbaceous plants, shrubs and trees. No significant difference was found between the leaf lifespan of seagrasses and freshwater angiosperms.

Leaves are usually the major sink for nutrients in seagrasses. The combination of low nutrient resorption from the leaves and a short leaf lifespan is, therefore, expected to result in a low nutrient residence time in the plants. Indeed, field experiments with ¹⁵N labelled Thalassia hemprichii showed that less than 5% of the initial ¹⁵N amount was still within the living plant biomass 240 days after labelling.

Limited nutrient retention in the plant biomass necessitates the capture of new nutrients for persistent growth. We speculate that effective nutrient uptake by seagrass leaves is an important
strategy to maintain an adequate nutrient balance in seagrasses, particularly in thin vegetation or in small patches. The constraints imposed by the marine environment may have favoured the development of this strategy over the development of efficient nutrient conservation strategies.

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Keywords: Seagrasses; Nutrient resorption; Leaf lifespan; Nutrient retention; Nitrogen; Phosphorus

1. Introduction

Seagrasses abound in oligotrophic and mesotrophic waters, where they may develop extensive meadows. The capacity to exploit the nutrient reservoir of the sediment besides that of the water column (e.g. McRoy and Barsdate, 1970; Iizumi and Hattori, 1982; Thursby and Harlin, 1982), does not imply that nutrients are available to seagrasses in excess. On the contrary, nutrient-limited growth appears to be quite a common phenomenon (Orth, 1977; Bulthuis and Woelkering, 1981; Powell et al., 1989; Short et al., 1985, 1990; Perez et al., 1991; Bulthuis et al., 1992; Fourqurean et al., 1992; Murray et al., 1992; Agawin et al., 1996). Yet, a comparison among different plant communities shows that the primary production of seagrass meadows (calculated on the basis of the large number of productivity estimates published world-wide) ranks among the highest established, being in the range of tropical forests and swamps and marshes (Duarte and Chiscano, in press). The generally high productivity of seagrasses, which is logically paralleled by a high nutrient demand, in often nutrient-poor environments, has attracted attention since the expansion of seagrass research in the early seventies. In seagrass ecosystems, a number of plant-external processes such as hydrodynamic particle transport, nitrogen-fixation and denitrification, are directly relevant to the availability of nutrients for plant productivity (Hemminga et al., 1991). The efficient use of the available nutrients depends on specific plant properties. Seagrasses, as all plants, will be functionally adapted to their environment, tuning nutrient expenditure to nutrient availability. In this paper we focus on two plant characteristics that are potentially very important for the conservation of nutrients within the plant structure, i.e., nutrient resorption from senescing leaves, and leaf longevity. The resorption of nutrients from senescing leaves is a common phenomenon in plants. Resorption 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 environments (Grime, 1979; Chapin, 1980; Aerts, 1990). Low nutrient loss rates in habitats where nutrients are limiting, are expected to lead to a higher equilibrium biomass (Aerts and van der Peijl, 1993) and to competitive replacement of species with higher nutrient loss rates (Berendse, 1994). There is also empirical evidence that the extent of nutrient resorption and fitness are linked (May and Killingbeck, 1992). A second plant characteristic that is relevant to the conservation of plant nutrients is leaf lifespan (Monk, 1966; Chabot and Hicks, 1982). An extended leaf lifespan is known as an important mechanism to conserve nutrients in evergreen species, surpassing nutrient resorption in effectivity (Escudero et al., 1992; Reich et al., 1995).

In this paper we present evidence that leaf nutrient resorption and extended leaf lifespans are not strongly developed nutrient conservation strategies in seagrasses. The evidence is based on a compilation of literature data allowing comparisons of these plant characteristics.
Table 1
Nitrogen and phosphorus resorption efficiency ($\%R_N$ and $\%R_P$, respectively) in seagrasses. Data from Stapel and Hemminga (1997) are based on measurements of nutrient concentrations and modelled leaf weights. BL: Barang Lompo; GT: Gusung Tallang; B: Bira; Z: Zandkreek; V: Veerse Meer

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>$%R_N$</th>
<th>$%R_P$</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thalassia hemprichii</td>
<td>Indonesia (BL)</td>
<td>18</td>
<td>–</td>
<td>Stapel and Hemminga (1997)</td>
</tr>
<tr>
<td>Thalassia hemprichii</td>
<td>Indonesia (GT)</td>
<td>28</td>
<td>31</td>
<td>idem</td>
</tr>
<tr>
<td>Enhalus acoroides</td>
<td>Indonesia (BL)</td>
<td>14</td>
<td>12</td>
<td>idem</td>
</tr>
<tr>
<td>Enhalus acoroides</td>
<td>Indonesia (GT)</td>
<td>17</td>
<td>29</td>
<td>idem</td>
</tr>
<tr>
<td>Cymodocea rotundata</td>
<td>Indonesia (BL)</td>
<td>20</td>
<td>51</td>
<td>idem</td>
</tr>
<tr>
<td>Thalassodendron ciliatum</td>
<td>Indonesia (B)</td>
<td>9.8</td>
<td>30</td>
<td>idem</td>
</tr>
<tr>
<td>Thalassodendron ciliatum</td>
<td>Kenya (Gazi)</td>
<td>4.1</td>
<td>2.3</td>
<td>idem</td>
</tr>
<tr>
<td>Thalassodendron ciliatum</td>
<td>Kenya (Gazi)</td>
<td>4.1</td>
<td>5.7</td>
<td>idem</td>
</tr>
<tr>
<td>Thalassodendron ciliatum</td>
<td>Kenya (Gazi)</td>
<td>29</td>
<td>33</td>
<td>idem</td>
</tr>
<tr>
<td>Posidonia oceanica</td>
<td>Spain</td>
<td>24</td>
<td>35</td>
<td>idem</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>Netherlands (Z)</td>
<td>3.8</td>
<td>0</td>
<td>idem</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>Netherlands (V)</td>
<td>3.8</td>
<td>0</td>
<td>idem</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>Canada</td>
<td>28$^a$</td>
<td>–</td>
<td>Harrison and Mann (1975)</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>USA</td>
<td>36$^a$</td>
<td>–</td>
<td>Thayer et al. (1977)</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>USA</td>
<td>39$^a$</td>
<td>–</td>
<td>Borum et al. (1989)</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>Denmark</td>
<td>12$^a$</td>
<td>–</td>
<td>Pedersen and Borum (1992)</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>Denmark</td>
<td>23$^a$</td>
<td>–</td>
<td>Pedersen and Borum (1993)</td>
</tr>
<tr>
<td>Posidonia oceanica</td>
<td>Spain</td>
<td>40$^b$</td>
<td>34$^b$</td>
<td>Alcoverro (1995)</td>
</tr>
<tr>
<td>Amphibolis antarctica</td>
<td>Australia</td>
<td>34$^b$</td>
<td>–</td>
<td>Pedersen et al. (1997)</td>
</tr>
</tbody>
</table>

Data extracted from other papers are based

- $^a$ on the change in leaf nutrient concentration assuming no change in leaf weight during senescence, or
- $^b$ on the change in absolute leaf nutrient content. Data derived from Pedersen and Borum (1992, 1993) are seasonal averages; for calculations, differences in nutrient levels between the 4th and 6th leaves were used. Data derived from Borum et al. (1989) are based on comparisons between the 3rd and 5th leaves. Data derived from Harrison and Mann (1975) are seasonal averages, based on comparisons between mature green and old (senesced) leaves. Data derived from Alcoverro (1995) are seasonal averages, based on comparisons between leaves 25–50 days old and leaves 100–150 days old.

in seagrasses and in other plant groups, complemented with data on the retention of labelled nitrogen in a seagrass system and in other ecosystems.

2. Nutrient resorption from seagrass leaves

The nutrient resorption efficiency is defined as the amount of nutrients resorbed during senescence and is expressed as the percentage reduction of nutrients between green and senesced leaves. The nutrient resorption efficiency has been determined in all kinds of terrestrial plants, but only few data are available for seagrasses (Table 1). Calculations based solely on the difference in the concentration of nutrients between mature green and senescent leaves ignore possible changes in specific leaf mass during senescence which may occur e.g. due to resorption of carbon compounds. Data on the individual weight of the leaf classes are, therefore, also needed. In seagrasses, however, the oldest leaves are usually incomplete due to losses caused by hydrodynamical stress and herbivory, which obviously prevents a proper calculation of the exact resorption efficiency. Stapel and Hemminga (1997) tried to solve this problem by combining data on the nitrogen and phosphorus concentrations...
Table 2
Nitrogen and phosphorus resorption efficiency ($%R_N$ and $%R_P$, respectively) in terrestrial perennial plants and in seagrasses. Means $\pm$ SD. The number of observations are shown in parentheses. Data on terrestrial plants are derived from Aerts (1996). The figures on seagrasses are based on the data of Table 1.

<table>
<thead>
<tr>
<th>Plant group</th>
<th>$%R_N$</th>
<th>$%R_P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Evergreen shrubs and trees</td>
<td>46.7 $\pm$ 16.4 (108)</td>
<td>51.4 $\pm$ 21.7 (88)</td>
</tr>
<tr>
<td>Deciduous shrubs and trees</td>
<td>54.0 $\pm$ 15.9 (115)</td>
<td>50.4 $\pm$ 19.7 (98)</td>
</tr>
<tr>
<td>Forbs</td>
<td>41.4 $\pm$ 21.4 (33)</td>
<td>42.4 $\pm$ 30.3 (18)</td>
</tr>
<tr>
<td>Graminoids</td>
<td>58.5 $\pm$ 14.2 (31)</td>
<td>71.5 $\pm$ 16.0 (22)</td>
</tr>
<tr>
<td>Seagrasses</td>
<td>20.4 $\pm$ 12.2 (19)</td>
<td>21.9 $\pm$ 17.0 (12)</td>
</tr>
</tbody>
</table>

in the leaf tissue with models of leaf mass development, thus allowing the estimation of complete leaf weights. This data set is, however, limited, and in order to obtain a wider view on nutrient resorption in seagrasses, published data on nutrient resorption based solely on N and P concentrations in mature green and senescent leaves are added in Table 1. Some of the data included in Table 1 are mean values of seasonal data. It can be gathered from the original seasonal data (not shown in the table) that the resorption efficiency may vary conspicuously over the seasons (Harrison and Mann, 1975; Pedersen and Borum, 1992, 1993; Alcoverro, 1995). Hence, the nutrient resorption efficiency is not a fixed characteristic, but one that may change, probably depending on both plant status and environmental factors.

Seagrasses, on average, resorb 20.4% of the leaf nitrogen, and 21.9% of the phosphorus. The realised nutrient resorption from seagrass leaves may, however, be lower than these values. The hydrodynamic stresses imposed upon seagrass leaves may lead to losses of more or less substantial fragments from the leaves. In addition, herbivores may consume a variable fraction of the leaves during leaf growth and senescence. This activity will at the same time reduce the mechanical strength of the leaves, enhancing the chances of further losses of leaf fragments by hydrodynamic forces. The physiological resorption potential of the leaves will, therefore, often not be fully realised. It was found that, when premature losses of leaves and leaf fragments were taken into account, in Indonesian seagrasses only between 56 and 77% of the physiological resorption potential actually was realised (Stapel and Hemminga, 1997).

Another process that may lead to an overestimation of the proportion of leaf nutrients that is resorbed during senescence is leaching. It has been demonstrated that part of the phosphorus that is taken up by the roots, may be subsequently lost via the leaf surface (Penhale and Thayer, 1980; Pérez-Lloréns et al., 1993), although the consistency of this process is uncertain (Kirkman et al., 1979; Brix and Lyngby, 1985). If nutrient leaching continues during senescence, the resultant reduction in tissue nutrient levels will be incorrectly attributed to nutrient resorption if this process is estimated from the reduction in nutrient levels during leaf ageing. As data both on premature leaf losses and on leaching are presently too scarce to allow general quantitative statements, we will ignore these aspects in further discussions.

When comparing the resorption efficiency of seagrasses to perennial terrestrial plants (reviewed by Aerts, 1996), it is clear that the extent of nutrient resorption in seagrasses is low (Table 2). Average nitrogen and phosphorus resorption in different groups of terrestrial plants varies between 41–58% (nitrogen) and 42–71% (phosphorus), respectively. The average values for nitrogen and phosphorus resorption in seagrasses are well below these values.
Table 3
Concentrations (%DW) of nitrogen and phosphorus in senesced seagrass leaves. The values given are measured in the oldest leaf class that was found on the shoots

<table>
<thead>
<tr>
<th>Species</th>
<th>Locationa</th>
<th>%N</th>
<th>%P</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Thalassia hemprichii</em></td>
<td>Indonesia (BL)</td>
<td>1.34</td>
<td>–</td>
<td>Stapel and Hemminga (1997)</td>
</tr>
<tr>
<td><em>Thalassia hemprichii</em></td>
<td>Indonesia (GT)</td>
<td>1.54</td>
<td>0.13</td>
<td>idem</td>
</tr>
<tr>
<td><em>Enhalus acoroides</em></td>
<td>Indonesia (BL)</td>
<td>1.47</td>
<td>0.13</td>
<td>idem</td>
</tr>
<tr>
<td><em>Cymodocea rotundata</em></td>
<td>Indonesia (BL)</td>
<td>2.21</td>
<td>0.22</td>
<td>idem</td>
</tr>
<tr>
<td><em>Thalassodendron ciliatum</em></td>
<td>Indonesia (B)</td>
<td>1.63</td>
<td>0.09</td>
<td>idem</td>
</tr>
<tr>
<td><em>Thalassodendron ciliatum</em></td>
<td>Kenya (Gazi)</td>
<td>1.10</td>
<td>0.13</td>
<td>idem</td>
</tr>
<tr>
<td><em>Thalassodendron ciliatum</em></td>
<td>Kenya (Gazi)</td>
<td>1.40</td>
<td>0.11</td>
<td>idem</td>
</tr>
<tr>
<td><em>Thalassodendron ciliatum</em></td>
<td>Kenya (Gazi)</td>
<td>1.51</td>
<td>0.10</td>
<td>idem</td>
</tr>
<tr>
<td><em>Posidonia oceanica</em></td>
<td>Spain</td>
<td>1.11</td>
<td>0.07</td>
<td>idem</td>
</tr>
<tr>
<td><em>Zostera marina</em></td>
<td>Netherlands (Z)</td>
<td>2.61</td>
<td>0.25</td>
<td>idem</td>
</tr>
<tr>
<td><em>Zostera marina</em></td>
<td>Netherlands (V)</td>
<td>1.80</td>
<td>0.23</td>
<td>idem</td>
</tr>
<tr>
<td><em>Zostera marina</em></td>
<td>Canada</td>
<td>1.0b</td>
<td>–</td>
<td>Harrison and Mann (1975)</td>
</tr>
<tr>
<td><em>Zostera marina</em></td>
<td>USA</td>
<td>1.18</td>
<td>–</td>
<td>Thayer et al. (1977)</td>
</tr>
<tr>
<td><em>Zostera marina</em></td>
<td>USA</td>
<td>0.96b</td>
<td>–</td>
<td>Borum et al. (1989)</td>
</tr>
<tr>
<td><em>Zostera marina</em></td>
<td>Denmark</td>
<td>0.96b</td>
<td>–</td>
<td>Pedersen and Borum (1992)</td>
</tr>
<tr>
<td><em>Zostera marina</em></td>
<td>Denmark</td>
<td>1.33b</td>
<td>–</td>
<td>Pedersen and Borum (1993)</td>
</tr>
<tr>
<td><em>Zostera marina</em></td>
<td>Denmark</td>
<td>1.12b</td>
<td>0.07b</td>
<td>Pedersen and Borum (1994)</td>
</tr>
<tr>
<td><em>Posidonia oceanica</em></td>
<td>Spain</td>
<td>1.7b</td>
<td>0.09b</td>
<td>Alcoverro (1995)</td>
</tr>
<tr>
<td><em>Amphibolis antarctica</em></td>
<td>Australia</td>
<td>1.06</td>
<td>–</td>
<td>Pedersen et al. (1997)</td>
</tr>
<tr>
<td><em>Halodule uninervis</em></td>
<td>Tanzania</td>
<td>1.64</td>
<td>0.05</td>
<td>Hemminga (unpublished data)</td>
</tr>
<tr>
<td>Average (± SD)</td>
<td></td>
<td>1.42 ± 0.42</td>
<td>0.13 ± 0.06</td>
<td></td>
</tr>
</tbody>
</table>

a Location codes (between brackets) as in Table 1.
b Value read from graph.

A new concept relevant to nutrient resorption is that of the nutrient resorption proficiency, put forward by Killingbeck (1996). The nutrient resorption proficiency is defined as the minimum level to which a plant can reduce an element in senescing leaves. According to Killingbeck, nutrient resorption efficiency and proficiency give different insights in the resorption process. While the nutrient resorption efficiency gives insight in the relative degree to which plants can conserve nutrients invested in leaves in order to minimize nutrient uptake, the proficiency value may be a better measure of the degree to which selection has acted to minimize nutrient losses. Killingbeck (1996) compiled a data base on nutrient levels in senesced leaves from more than 70 species of deciduous and evergreen woody perennials. Mean N and P concentrations in senesced leaves of these species were 0.87 and 0.06%, respectively. The author considered resorption to be highly proficient in species that were able to reduce the N and P concentrations in their senescing leaves to levels below 0.7 and 0.05%, respectively. The available data on nutrient levels in the oldest leaf classes in seagrasses are presented in Table 3, which shows that the average levels, i.e., 1.4 and 0.13% for nitrogen and phosphorus, respectively, are considerably higher than the critical levels suggested by Killingbeck.

The comparisons between seagrasses and terrestrial plants presented in Tables 2 and 3 must be considered with caution. The data set on seagrasses is rather limited, the nutrient resorption efficiency in seagrasses has been established in various ways (as is the case for the
data on terrestrial plants as well), and in the case of the new nutrient proficiency concept, to the best of our knowledge, only a substantial published database on woody perennial species is available for comparison with seagrasses. Obviously, we are a long way from the ultimate comparison and definite statements should not be made yet. We can, however, safely conclude that the data available so far do not present any evidence for a pronounced role of nutrient resorption in the conservation of nutrients in seagrasses.

3. Leaf lifespan in seagrasses

The limited nutrient resorption efficiency (~20%) in seagrasses makes it pertinent to scrutinize the available data on leaf lifespan in seagrasses. We, therefore, compiled 71 published, and nine unpublished, data on leaf lifespan in seagrasses, and, for comparison, also collected data on leaf lifespan of freshwater plants (25), terrestrial herbs (83), shrubs (70) and trees (158). Most of the estimates of leaf lifespan have been obtained as the average or median leaf lifespan of the plant populations. Leaf lifespan was measured following leaf cohorts in time, or from the leaf age structure of the population. Alternatively, leaf lifespan was calculated as the number of standing leaves divided by the number of leaves produced per shoot during 1 year.

Seagrass leaf lifespan is highly variable (Fig. 1). The highest values (between 202 and 345 days) are found in the Mediterranean species *Posidonia oceanica*. On the low end of the scale is *Halophila ovalis*, with leaf longevities down to 4.4 days. Mean seagrass leaf lifespan is 88.4 days. Plotting the observations on leaf lifespan versus the geographical latitude of the observation site shows that leaf lifespan significantly; \( p = 0.0012 \) increases going from tropical to temperate latitudes (Fig. 2). Leaf turnover on average thus appears faster in tropical than in temperate regions.

For part of the 80 observations, data on leaf dry weight and leaf formation rate per shoot per year were also available. Seagrass leaf lifespan scales to leaf mass and leaf formation rate (Table 4). Thus, leaf longevity increases with increasing leaf weight, and decreases with increasing leaf formation rate.

Variability in leaf lifespan is not restricted to seagrasses, but was also found in the data pertaining to freshwater angiosperms, terrestrial herbaceous plants, shrubs and trees. Despite the observed variation, significant differences are detectable between groups (Fig. 3).

| Table 4 |
| Relationships between leaf longevity and leaf dry weight (upper part) and between leaf longevity and leaf formation rate (lower part), in tropical and temperate seagrasses. Regressions were carried out with logarithmically transformed data |

<table>
<thead>
<tr>
<th>Log leaf longevity (days) = ( A + B ) log leaf weight (g DW)</th>
<th>( A )</th>
<th>( B )</th>
<th>( R^2 )</th>
<th>( N )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical seagrasses</td>
<td>2.25 (±0.13)</td>
<td>0.82 (±0.15)</td>
<td>0.65</td>
<td>17</td>
<td>&lt;0.0005</td>
</tr>
<tr>
<td>Temperate seagrasses</td>
<td>2.34 (±0.1)</td>
<td>0.55 (±0.14)</td>
<td>0.29</td>
<td>35</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Log leaf longevity (days) = ( A + B ) log leaf formation rate (leaves year(^{-1}))</th>
<th>( A )</th>
<th>( B )</th>
<th>( R^2 )</th>
<th>( N )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical seagrasses</td>
<td>2.83 (±0.2)</td>
<td>-0.85 (±0.13)</td>
<td>0.70</td>
<td>18</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td>Temperate seagrasses</td>
<td>2.69 (±0.12)</td>
<td>-0.80 (±0.12)</td>
<td>0.62</td>
<td>22</td>
<td>&lt;0.00001</td>
</tr>
</tbody>
</table>
Aquatic plants (both seagrasses and freshwater plants) have a relatively short leaf lifespan compared to terrestrial herbs, shrubs and trees. Terrestrial herbs rank in the middle, whereas shrubs and trees have comparatively long-lived leaves. This picture is statistically supported by analysis of variance carried out on the logarithmically transformed leaf lifespan data, followed by multiple comparisons using the Tukey HSD test (Table 5). The latter test shows that seagrass leaf lifespan differs significantly from those of terrestrial herbs, shrubs and trees,
but not from freshwater angiosperms \((p = 0.57)\). Our data set on freshwater angiosperms, however, contains only 25 observations and should, therefore, be considered with caution.

4. Nutrient retention in seagrass systems

Seagrass leaf production usually accounts for the major part of total plant production (Duarte and Chiscano, in press). Moreover, nutrient levels in the leaves are higher than in the roots/rhizomes (e.g. Pérez-Lloréns and Niell, 1993; Erftemeyer et al., 1994; Pérez and Romero, 1994; Agawin et al., 1996), making the leaves the dominant sink for nutrients. This feature, in combination with low nutrient resorption from the leaves and a short leaf lifespan, is expected to result in a relatively low residence time of nutrients within the plants. This is indeed what has been observed in a pulse-labelling experiment in which the stable nitrogen isotope \(^{15}\text{N}\) was used as tracer to follow nitrogen cycling in a \(T. hemprichii\) meadow. The details of this experiment will be described in a separate paper (Stapel et al., in prep.). In brief, 1 m\(^2\) plots within the meadow were temporarily enclosed at low tide, and, subsequently, the overlying water was enriched with ammonium chloride in which the nitrogen moiety for 99% consisted of \(^{15}\text{N}\). The ammonium concentration in the water column directly after enrichment was approximately 45 \(\mu\text{M}\). The incubation period lasted ca. 3.5 h. After the labelling event, the amount of \(^{15}\text{N}\)-tracer was measured in different compartments of the meadow (leaves, living roots/rhizomes, detritus and sediment). It was found that the \(^{15}\text{N}\)-content of the total leaf biomass declined with a half-life of 15 days only. Small amounts of \(^{15}\text{N}\) were retrieved in the detritus and root/rhizome fractions, but most of the \(^{15}\text{N}\) disappearing from the living leaf compartment was lost from the plots. 240 days

After labelling, the amount of $^{15}$N still present within the plots was only 6.6% of the amount initially incorporated in the plant biomass; leaves accounted for 1.1%, roots/rhizomes and detritus for 2.3 and 3.2%, respectively.

These results can be compared with the retention of $^{15}$N in shortgrass prairie and salt marsh systems (Clark, 1977; White and Howes, 1994). In these studies small plots (20 and 27 cm diameter, respectively) were enriched with $^{15}$N. The label was added directly to the sediment, but the detailed study of White and Howes showed that 100 days after introduction only 1–7% of the $^{15}$N was present in the inorganic ammonium pool; the remainder occurred in living or dead plant material. Retention of $^{15}$N in the three different systems is shown in Fig. 4, which illustrates that the $^{15}$N retention in the T. hemprichii meadow is much less pronounced than in the semi-terrestrial salt marsh and the terrestrial shortgrass prairie system. Obviously, this difference is partly due to the dynamic and permanently submerged nature of the seagrass environment: detached leaves and detritus particles (and probably also dissolved inorganic nitrogen compounds generated by the mineralisation of leaf detritus on
Fig. 4. Time course of $^{15}$N retention in different ecosystems. Lines are drawn on the basis of data from Stapel et al. (In prep.; seagrass system), White and Howes (1994) (salt marsh system) and Clark (1977) (shortgrass prairie system). The $^{15}$N retention in the living (above- and belowground) plant biomass and in the sediment-associated detritus fraction after initial enrichment of field plots with either $^{15}$NH$_4^+$ or $^{15}$NO$_3^-$ is shown. In the case of the prairie shortgrass system, the detritus fraction also included dead aboveground biomass. The $^{15}$N retention is expressed as the percentage of total initial enrichment remaining in the specific fraction. Closed and open symbols indicate $^{15}$N in living plant biomass and in the detritus fraction, respectively.

The sediment surface), are easily carried away from the plots by currents and tides. This can only be part of the explanation, however, as the Spartina alterniflora vegetation studied by White and Howes (1994) also occurred in a dynamic tidal environment with considerable possibilities for hydrodynamic transport. $^{15}$N retention in salt marsh and shortgrass prairie systems is determined by the importance of the belowground compartment as a sink for nitrogen, internal recycling (resorption and translocation within the clonal plant structure), external recycling (mineralisation of detritus within the plot followed by re-uptake of nitrogen), and the gradual build-up of a refractory $^{15}$N-rich detritus pool in the soil compartment (Clark, 1977; White and Howes, 1994). The comparatively low $^{15}$N retention in the seagrass meadow may be determined by another combination of factors: the importance of the leaves as a sink for nitrogen, a limited resorption of nutrients from senescing leaves, a restricted leaf longevity, and hydrodynamic transport of leaf litter fragments.

The tracer study in the T. hemprichii meadow so far is the only one providing direct information on the time scale of nutrient retention in seagrass systems. It is conceivable that nutrient retention in other seagrass systems will show much the same pattern, in view of the shared plant features that were discussed above, but this remains to be investigated. It should be emphasized that high loss rates of nutrients from the plants do not give any indication on the nutrient status of the seagrass system as such. Several studies have shown that the total nutrient content of seagrass meadows (more particularly, that of the sediment compartment) on a per unit area basis may increase in time after establishment of the stands.
Whether this occurs, and to what extent, will depend on many factors such as the canopy characteristics relevant to the reduction of current flow, the particle load of the water column, the hydrodynamic environment of the meadow and species-dependent features of root mat development. The high loss rate of $^{15}$N from the Thalassia plots, on the one hand, and the regularly observed increase in total nutrient content of seagrass stands, on the other hand, clearly demonstrate the open character of seagrass meadows, which finds its expression in an extensive exchange of matter between the vegetation and its environment.

5. Concluding remarks

In the present paper, we compared seagrasses and other plants with respect to leaf nutrient resorption, leaf lifespan and nutrient retention. The limitations of this approach are obvious in view of the limited size of available data and the huge diversity of the plant world. Further comparisons with yet other plant groups may, therefore, lead to modifications of the picture emerging in this paper. It is clear that generalisations obscure existing variability, which also applies to the generalisations made in this paper. With respect to nutrient retention, for instance, it probably makes much difference that the leaf longevity of Posidonia oceanica can be as high as 345 days, whereas it may only be days in H. ovalis: the extended leaf lifespan in P. oceanica offers better possibilities for nutrient retention than the short leaf longevity of H. ovalis. The bottomline, nonetheless, is that the overall body of data does not point to pronounced roles of nutrient resorption and extended leaf lifespans in the conservation of nutrients in seagrasses, when compared to other, especially terrestrial, plant types.

Both the resorption of nutrients from senescing leaves and extended leaf lifespans can be important strategies for plants to diminish the need for uptake of nutrients from the environment. Apparently, these strategies are not strongly developed in seagrasses, and thus seagrasses appear to be rather ‘wasteful’ as far as the use of nutrients is concerned. Therefore, the abundant presence of seagrasses in nutrient-poor waters may seem paradoxical. The low nutrient use efficiency in seagrasses appears to be more characteristic of high-productivity species from nutrient-rich habitats than of low productivity species from nutrient-poor habitats (cf. Grime, 1979). Why this is the case is not clear. The relatively short leaf longevity in seagrasses (and possibly freshwater angiosperms as well) may be related to the high stresses imposed upon the leaves in an aquatic environment as compared to leaves growing in air, or to the gradual coverage of the leaf blades by silt and epiphytes in the aquatic environment. Both factors could be an increasing burden to the functioning of the leaf with increasing age, precluding the development of long-lived leaves. The physiological background of the low nutrient resorption efficiency in seagrasses, at present, can only be a matter of speculation.

Restricted nutrient resorption and a relatively short leaf lifespan result in considerable losses of nutrients from the plant structure per unit of time. If the nutrients in the leaf litter are not recycled within the the plant patch (and transport of these litter particles away from their origin is easy conceivable), then continued growth and survival of the plants ultimately depends on the capture of ‘new’ nutrients from outside sources. The particle-trapping character of seagrass stands, already referred to above, is undoubtedly an important feature in this respect, although the input of particles is not a very predictable or consistent phenomenon.
For example, deposition of particles is expected to be less conspicuous in thin vegetation or in small patches than in extensive, dense meadows, as flow reduction (and, hence, the particle carrying capacity of the water) is influenced by shoot density and the distance covered by the flowing water through the canopy (Eckman, 1987; Gambi et al., 1990; Worcester, 1995). Particularly in the afore-mentioned situations nutrient uptake by the leaves may be a crucial process for survival of the plants. Earlier studies have shown that seagrasses readily take up dissolved nutrients from the water column (Iizumi and Hattori, 1982; Thursby and Harlin, 1982; Short and McRoy, 1984; Brix and Lyngby, 1985; Hemminga et al., 1994; Stapel et al., 1996; Pedersen et al., 1997; Terrados and Williams, 1997). The capacity of the leaves to take up nutrients is considerable, and even in nutrient-poor waters typical for many tropical areas, seagrass leaves may acquire a substantial part of their total demand from the water column (Stapel et al., 1996). Leaf nutrient uptake may be thus an effective mechanism to counterbalance nutrient losses from the living plant structure, and indeed, from the patch as a whole. Hence, we speculate that effective nutrient uptake by seagrass leaves is an important strategy to maintain an adequate nutrient balance in seagrasses. The constraints imposed by the marine environment may have favoured the development of this strategy over the development of efficient nutrient conservation strategies.

In this paper we have confined ourselves to comparisons between seagrasses and other, mostly terrestrial, angiosperm plant groups or plant communities. A final remark concerns the performance of seagrasses with regard to the economic use of nutrients relative to other groups of primary producers in the marine aquatic environment (phytoplankton, macroalgae). An extensive comparison is outside the scope of this paper, but it can be safely assumed that, in such a comparison, seagrasses would come out rather well. In brief, the main arguments for this assumption are, firstly, that nitrogen and phosphorus tissue levels in seagrasses are lower than in phytoplankton, decreasing the nutrient requirements for growth (Duarte, 1992, 1995), and, secondly, that nutrient resorption is non-existent or unimportant in phytoplankton and ephemeral macroalgae (but it may be more important in the larger and morphologically more complex macroalgae; Schmitz and Lobban, 1976; Pedersen and Borum, 1996). As a result, seagrasses and large, long-living macroalgae are superior competitors in nutrient-poor environments (Duarte, 1995). Hence, the conclusion that, among angiosperm plant groups, seagrasses have comparatively poorly developed nutrient conservation strategies, must not obscure the ecologically relevant point that their use of nutrients is efficient relative to non-angiosperm competitors in the marine coastal environment.

References


