

Dugong grazing and turtle cropping: grazing optimization in tropical seagrass systems?

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Abstract Grazing by dugongs and cropping by green turtles have the capacity to alter the subsequent nutritional quality of seagrass regrowth. We examined the effects of simulated light and intensive grazing by dugongs and cropping by turtles on eight nutritionally relevant measures of seagrass chemical composition over two regrowth periods (short-term, 1–4 months; long-term, 11–13 months) at two seagrass communities (a mixed species community with *Zostera capricorni*, *Halophila ovalis*, *Halodule uninervis*, *Cymodocea rotundata* and *C. serrulate*; and a monospecific bed of *Halodule uninervis*) in tropical Queensland, Australia. The concentrations of organic matter, total nitrogen, total water-soluble carbohydrates, total starch, neutral detergent fiber, acid detergent fiber, acid lignin, as well as the in vitro dry matter digestibility (IVDMD) were

measured in the leaves and below-ground parts of each species using near-infrared reflectance spectroscopy (NIRS). Regrowth of preferred species such as *H. ovalis* and *H. uninervis* from simulated intensive dugong grazing after a year exhibited increased (by 35 and 25%, respectively, relative to controls) whole-plant N concentrations. Similarly, regrowth of *H. ovalis* from simulated turtle cropping showed an increase in the leaf N concentration of 30% after a year. However, these gains are tempered by reductions in starch concentrations and increases in fiber. In the short-term, the N concentrations increased while the fiber concentrations decreased. These data provide experimental support for a grazing optimization view of herbivory in the tropical seagrass system, but with feedback in a different manner. Furthermore, we suggest that in areas where grazing is the only major source of natural disturbance, it is likely that there are potential ecosystem level effects if and when numbers of dugongs and turtles are reduced.

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Introduction

Grazing by large mammalian herbivores can have many effects on terrestrial landscapes. Although the notion that herbivory invariably has a negative impact on plant communities has been challenged at multiple scales over the past two decades, a widespread review (Milchunas and Lauenroth 1993) of grazing in terrestrial ecosystems concluded that the most frequent effect was for primary productivity to be reduced or to

remain unaffected. However, grazers may have significant positive effects on grazed areas via their role in enhancing nutrient recycling or availability (McNaughton et al. 1997; Augustine et al. 2003). Even if net productivity does not increase, the nutritional value of the herbage to animal consumers may increase through changes in the nutrient concentration of regrowth. For example, moderate clipping of a mixed grass prairie led to significant increases in N concentration in regrowth and a significant increase in the potential N yield to grazers (Green and Detling 2000). These effects have been observed in many other ecosystems (Hik et al. 1991; Hamilton et al. 1998; Bryant 2003).

In marine environments, grazing by large mammalian and reptilian herbivores has the potential to affect plant communities in similar ways. Seagrasses constitute the main food of green turtles and dugongs (Marsh et al. 1982; Lanyon et al. 1989). Although seagrasses are not true grasses, the growth form is analogous, with plants tending to spread across the substrate via rhizomatous growth, with few resources invested in structural material. Thus we may expect the response of seagrass communities to grazing by large herbivores to reflect the patterns seen in terrestrial grass-grazer systems, as described above.

There have been a number of studies of feeding by dugongs and green turtles on seagrass communities (Heinsohn and Birch 1972; Anderson and Birtles 1978; Marsh et al. 1982; Lanyon 1991; Anderson 1994; de Iongh et al. 1995; Preen 1995; Anderson 1998; Aragones and Marsh 2000; Masini et al. 2001; André et al. 2005; Yamamuro and Chirapart 2005). These have most often addressed the effects of grazing on species composition of seagrass meadows, and in particular the abundance of preferred food species. In low-biomass seagrass communities, feeding by dugongs involves removal of the entire plant (i.e., including roots and rhizomes). This tends to prevent the development of a climax community and instead maintains an early seral stage which favors those species preferred by dugongs as food. This has been observed in both temperate (Preen 1995) and tropical (Aragones and Marsh 2000) regions. In contrast, feeding by green turtles, in which only the above-ground part of the plant is removed (referred to hereafter as “cropping”) has not been shown to affect species composition (Aragones and Marsh 2000). As in terrestrial systems (Augustine and McNaughton 1998), the community-level effect is likely to vary depending on the intensity and frequency of grazing and the recovery rates of the seagrass species present.

However, the feedback effects of grazing on the nutritional quality of the seagrass for herbivores might

be reduced in marine environments compared to those observed in terrestrial systems. The local scale fertilization effect seen in terrestrial systems via the input of fecal and urinary materials (Hobbs 1996; Augustine et al. 2003) is likely to be reduced or eliminated due to the role of the water column in transport (Nolet 2004). Similarly, water movement is likely to remove plant material dislodged by the grazers' activity so that it may not contribute to local detritus (Zieman et al. 1984). However, dugong grazing may lead to an increase in microbial activity in the sediment, increasing N fixation which increases sediment N and thus foliar N of seagrass (Perry and Dennison 1996, 1999). In fact, the effects seen in terrestrial systems, where proportions of regrowth tissue and nutrient concentrations within that tissue are increased (Bryant 2003), have been observed in seagrass communities. Repeated cropping by turtles has been found to result in increased nitrogen concentrations in *Thalassia testudinum* in the Caribbean, which was interpreted as improving the nutritional quality of those areas (Bjorndal 1980; Zieman et al. 1984). In this study we report on the effects of simulated grazing by dugongs and cropping by green turtles on the nutritional quality of a suite of seagrasses in intertidal seagrass meadows in North Queensland, Australia.

Before undertaking a study of the nutritional aspects of seagrass chemistry, it is important to consider which features are the likely determinants of food quality for these herbivores. There is currently no definitive answer to this issue, due in part to the problems in defining diet quality for any herbivore and, for these particular species, the difficulties inherent in conducting manipulative experiments with captive animals. Within these limitations, studies conducted thus far generally agree that preferences shown by both dugongs and green turtles relate to plants higher in nitrogen (\approx protein) and soluble carbohydrates and lower in fiber (Bjorndal 1980; Lanyon 1991; Preen 1993; de Iongh et al. 1995; Yamamuro and Chirapart 2005). For this reason, we have measured a suite of attributes relating to these factors. In an attempt to integrate different chemical components, we have also quantified *in vitro* dry matter digestibility, a functional measure likely to be appropriate to the herbivores.

Materials and methods

Study sites

The experiments were conducted in the intertidal regions of two seagrass meadows in tropical North

Queensland, Australia. The meadow at Ellie Point (16°53'S, 145°46'E) was dominated by *Zostera capricorni* (wide variety) with patches of *Halophila ovalis*, *Cymodocea rotundata* and *C. serrulata*. *Halodule uninervis* was present but only in low abundance. At Cardwell (18°15'S, 146°01'E) the experiment was conducted in a monospecific meadow of *Halodule uninervis*. Some *Halophila ovalis* occurred subtidally in this meadow.

Grazing experiments

We present here a summary of the experimental design and protocol. A full description is provided in Aragones and Marsh (2000). In all experiments we simulated grazing by dugongs or cropping by green turtles by manual removal of plants or plant parts to resemble that made by the animals. Below we refer to simulated feeding by dugongs, in which plants are uprooted and both leaves and roots/rhizomes (to 0.08 m depth) are removed, as “grazing.” “Cropping” refers to our removal of only the above-ground parts, as done by green turtles.

Long-term experiments

Long-term experiments commenced in May–June and were conducted at both Ellie Point (11 months) and Cardwell (13 months). The four grazing treatments were arranged in a 4 × 4 Latin square at each of four sites approximately 30 m apart, 200 m from, and parallel to, the shoreline. The treatments of the first row and column of each Latin square were assigned by lottery. Manipulations were made in replicated 1 m² quadrats. Seagrass samples for chemical analysis were taken at the end of the experimental period.

The four treatments used were: (1) intensive grazing—all above-ground material removed from plot; some below-ground left; (2) light grazing: plants removed from three evenly-spaced 15 cm-wide feeding strips. This represented an average of 69, 79 and 84% of the above-ground biomass of *H. ovalis*, *Zostera/Cymodocea* and *H. uninervis*; (3) leaf cropping: leaves cut 1–2 cm above-ground (except for *H. ovalis* for which the entire above-ground biomass was removed), and; (4) controls.

Short-term experiments

A short-term experiment at Cardwell was monitored for four months. This experiment was similar to the long-term experiment but used four 6 × 6 Latin squares with the following treatments: (1) light grazing

harvested after four months; (2) control for Treatment 1; (3) cropping 1 harvested after one month; (4) control for Treatment 3; (5) cropping 2 harvested after two months, and; (6) control for Treatment 5. Each plot was 0.4356 m² (0.66 × 0.66 m). Intensive grazing was not included because the monitoring period was insufficient for significant recovery from this treatment.

Chemical analyses

Chemical assays were performed on each species separately, with the exception of *Zostera capricorni* and the *Cymodocea* species. These were combined due to difficulty in distinguishing these species in the video monitoring system described in the complementary paper on species composition and abundance (Aragones and Marsh 2000). *Cymodocea* made only a minor contribution to the biomass in any *Zostera/Cymodocea* sample.

All determinations conducted in these experiments were made using near-infrared reflectance spectroscopy (NIRS), a technique that is now widely accepted as a method for the determination of chemical attributes of organic materials (Shenk and Westerhaus 1994; ASTM 1995; Foley et al. 1998; André and Lawler 2003; Lawler et al. 2006). We used an NIRSystems (Silver Spring, MD, USA) 6500 laboratory instrument equipped with a spinning cup sample holder. Calibrations for each of the chemical constituents were developed using reference laboratory values from standard techniques for subsets of the data. Calibrations were developed using partial least squares regression to relate spectral variation to reference laboratory values (Shenk and Westerhaus 1991). Full details of calibration development procedures and further background on the use of NIRS are provided elsewhere (Lawler et al. 2006).

Samples in the calibration set were analyzed for eight constituents. We assayed organic matter (OM) by burning a sample in a muffle furnace at 550 °C for 4 h. Total N was assayed using a semi-micro Kjeldahl method (Foley 1992). We measured several components of fiber: neutral detergent fiber, acid detergent fiber and acid lignin (Van Soest et al. 1991) using an ANKOM plant fiber analyzer (Komarek 1994). Total water soluble carbohydrates were extracted using 80% aqueous ethanol and water (Radojevic et al. 1994) and quantified as fructose equivalents using the anthrone reaction (Jermyn 1975). The insoluble material remaining from this extraction was analyzed for starch enzymatically using a commercial total starch assay kit (Megazyme total starch kit: Megazyme International, Bray, Ireland). We solubilized any resistant starch with dimethyl sulfoxide prior to the enzymatic treatments.

Finally, we measured the in vitro dry matter digestibility (IVDMD) of each sample (Choo et al. 1981). The in vitro digestibility method attempts to simulate digestive processes in herbivorous mammals using the enzymes pepsin and cellulase and is potentially useful as a way to integrate all of the individual assays for each sample.

Chemical determinations were made on leaves and roots/rhizomes separately, with whole plant values estimated from these based on the biomass ratios of leaves to below-ground parts. However, for brevity, and because the focus of this paper is on herbivore nutrition, we present only the leaf values and the whole plant values, as these reflect the likely intake of green turtles and dugongs, respectively, were they to feed on these plants.

Statistical analysis

Analysis of variance was used to test the effects of treatments on *Halodule uninervis* in both the long- and short-term experiments at Cardwell. Data for ADF were log-transformed to normalize the variances. For all other variables, untransformed data were used. For all other experiments, restricted maximum likelihood (REML) analysis was used because of the lack of balance in some treatment combinations.

Results

Long-term experiments

Halodule uninervis, Cardwell

Only the simulated grazing treatments had significant effects on the nutritional chemistry of *H. uninervis* leaves, whereas all treatments altered some chemical characteristics of whole plants (Table 1; Fig. 1a). The effect of simulated grazing tended to be greater for the intensive treatment. While some of the effects may be considered to improve putative nutritional quality for the herbivores (such as increases in nitrogen), others may act to decrease quality (increased lignin, decreased starch).

Zostera

Only two effects of cropping were recorded for *Zostera*, these being reductions in the whole plant concentrations of nitrogen and organic matter (Table 1; Fig. 1b). Both would likely reduce the nutritional quality of the plant for large herbivores.

Halophila ovalis

Simulated grazing had several significant effects on both leaf and whole-plant nutritional values, while no significant effects of simulated cropping were recorded (Table 1; Fig. 1c). Nutritional quality was likely to be improved via substantial ($\geq 30\%$) increases in leaf and whole plant nitrogen concentrations under intensive grazing ($\geq 15\%$ for intermediate grazing) but may be countered by increases in leaf fiber and hemicellulose in leaves and whole plants under simulated intensive grazing.

Short-term experiments: *Halodule uninervis*

A range of parameters were affected by the treatments over the shorter term of this experiment (Table 2; Fig. 2). However, while statistically significant, many of them were relatively small changes. The ones that might be expected to be of greatest nutritional significance were a reduction in starch concentration of nearly 60% one month after cropping and increases in nitrogen of approximately 10% four months after grazing and two months after cropping. Thus, it appears that nutritional quality may decrease in the short term after simulated cropping, but may then increase in the medium term.

Discussion

Our results show that simulated grazing by dugongs and cropping by green turtles both have the capacity to alter the subsequent nutritional quality of seagrass regrowth. While the changes in nutritionally relevant chemical composition may be small in absolute terms, relative to controls they can be substantial (Table 1). Dugongs returning to beds of *Halophila ovalis* or *Halodule uninervis* that have been subjected to simulated intensive grazing in the previous year may benefit from increases in whole plant nitrogen concentrations of 35 and 25%, respectively. Turtles grazing those same areas may also benefit from a 30% increase in the leaf N concentration of *Halophila ovalis*. However, these gains are tempered by reductions in starch concentrations and increases in fiber.

It is difficult then to conclude decisively that the nutritional quality for these large herbivores has either increased or decreased, because all chemical measures of food are only proxies for animal performance. In particular, it is difficult to measure the refractory fiber component of the plants. To this end, IVDMD is perhaps the most informative of the measures we have described, because it uses the mammalian enzymes

Table 1 Summary of statistically significant effects of simulated grazing or cropping on the chemical compositions of seagrass species from long-term experiment

	<i>Halodule uninervis</i>			<i>Halophila ovalis</i>			<i>Zostera capricorni</i>		
	Treatment	% Change relative to control (<i>P</i> value)		Treatment	% Change relative to control (<i>P</i> value)		Treatment	% Change relative to control (<i>P</i> value)	
Leaf									
IVDMD	Intermediate grazing	0.5 (0.003)		Hemicellulose	Intensive grazing	21.1 (0.035)			No significant effects
Nitrogen	Intensive grazing	4.5 (0.0012)		Nitrogen	Intensive grazing	29.4 (<0.0001)			
Starch	Intermediate grazing	3.1 (0.0012)		NDF	Intermediate grazing	15.6 (<0.0001)			
	Intensive grazing	-24.6 (0.0034)		Organic matter	Intensive grazing	10.3 (0.047)			
	Intermediate grazing	-21.8 (0.0034)			Intensive grazing	5.9 (0.02)			
Whole plant									
ADF	Intensive grazing	18.5 (0.0001)		Hemicellulose	Intensive grazing	33.6 (0.002)			
IVDMD	Intensive grazing	1.2 (0.02)		Nitrogen	Intensive grazing	35.5 (<0.0001)			
NDF	Intermediate grazing	0.8 (0.02)		Organic matter	Intermediate grazing	17.6 (<0.0001)			
	Intensive grazing	12.8 (0.0001)			Intensive grazing	6.8(0.0127)			
Organic matter	Intensive grazing	2.5 (0.006)							
Lignin	Intensive grazing	40.1 (0.0001)							
	Intermediate grazing	11.5 (0.0001)							
	Cropping	11.6 (0.0001)							
Nitrogen	Intensive grazing	24.6 (0.0001)							
	Intermediate grazing	9.4 (0.0001)							
	Cropping	6.6 (0.0001)							
Starch	Intensive grazing	-14.3 (0.029)							
	Cropping	-17.7 (0.029)							

Only those treatments shown to be different from the controls in pairwise comparison are shown

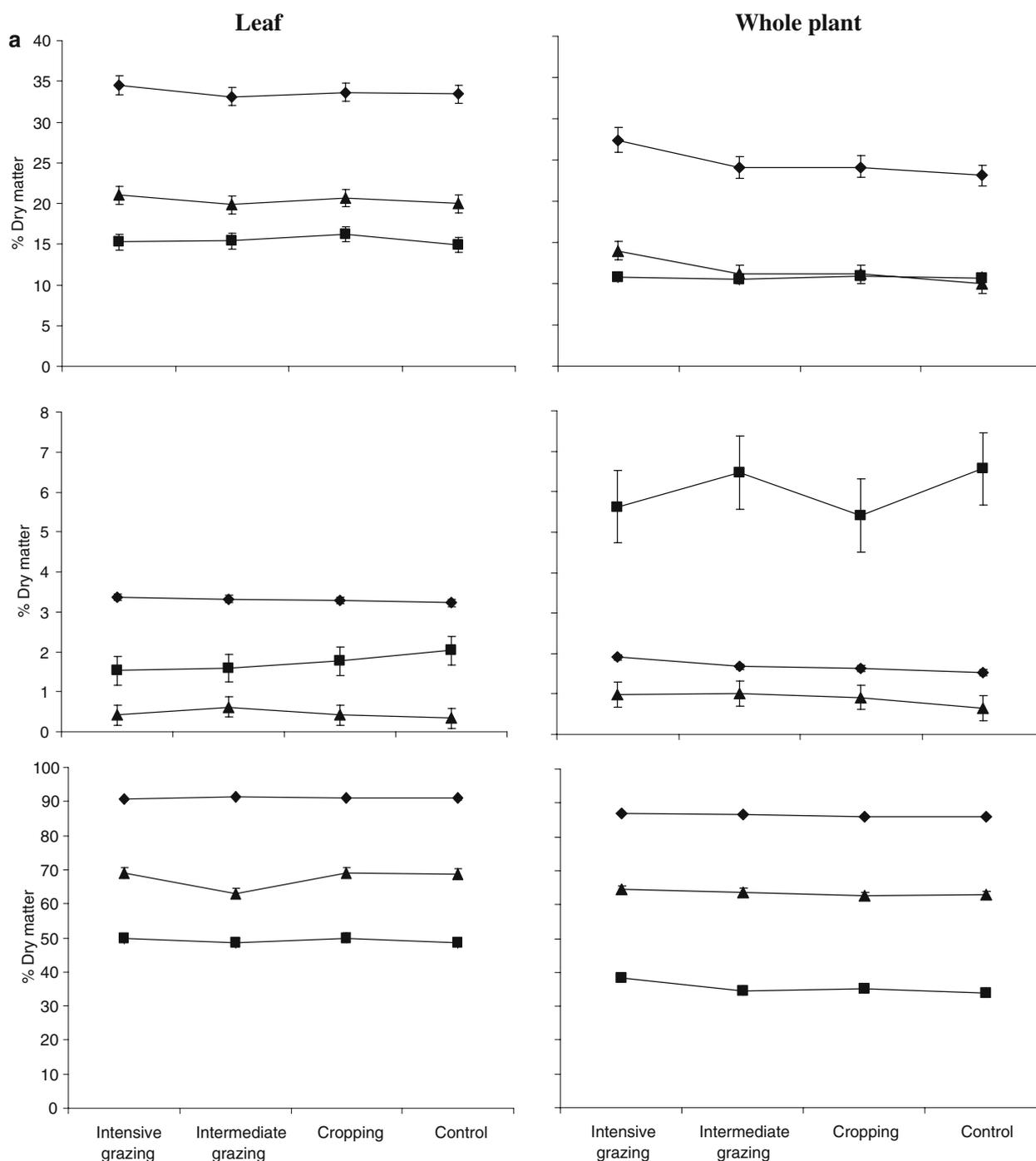


Fig. 1 a Effect of simulated feeding by dugongs and turtles after 13 months of recovery at Cardwell (*Halodule uninervis*). All values are means with 95% confidence limits. Note that in some cases the confidence limit bars are not apparent due to low variability in the data. Row 1: squares hemicellulose, diamonds acid detergent fiber, triangles lignin. Row 2: squares starch, diamonds nitrogen, triangles water-soluble carbohydrates. Row 3: squares neutral detergent fiber, diamonds in vitro dry matter digestibility, triangles organic matter. **b** Effects of simulated feeding by dugongs and turtles after 11 months of recovery at Ellie Point (*Zostera capricorni*). All values are means with 95% confidence limits. Note that in some cases the confidence limit bars are not apparent due to low variability in the data. Row 1: squares hemicellulose,

diamonds acid detergent fiber, triangles lignin. Row 2: squares starch, diamonds nitrogen, triangles water-soluble carbohydrates. Row 3: squares neutral detergent fiber, diamonds in vitro dry matter digestibility, triangles organic matter

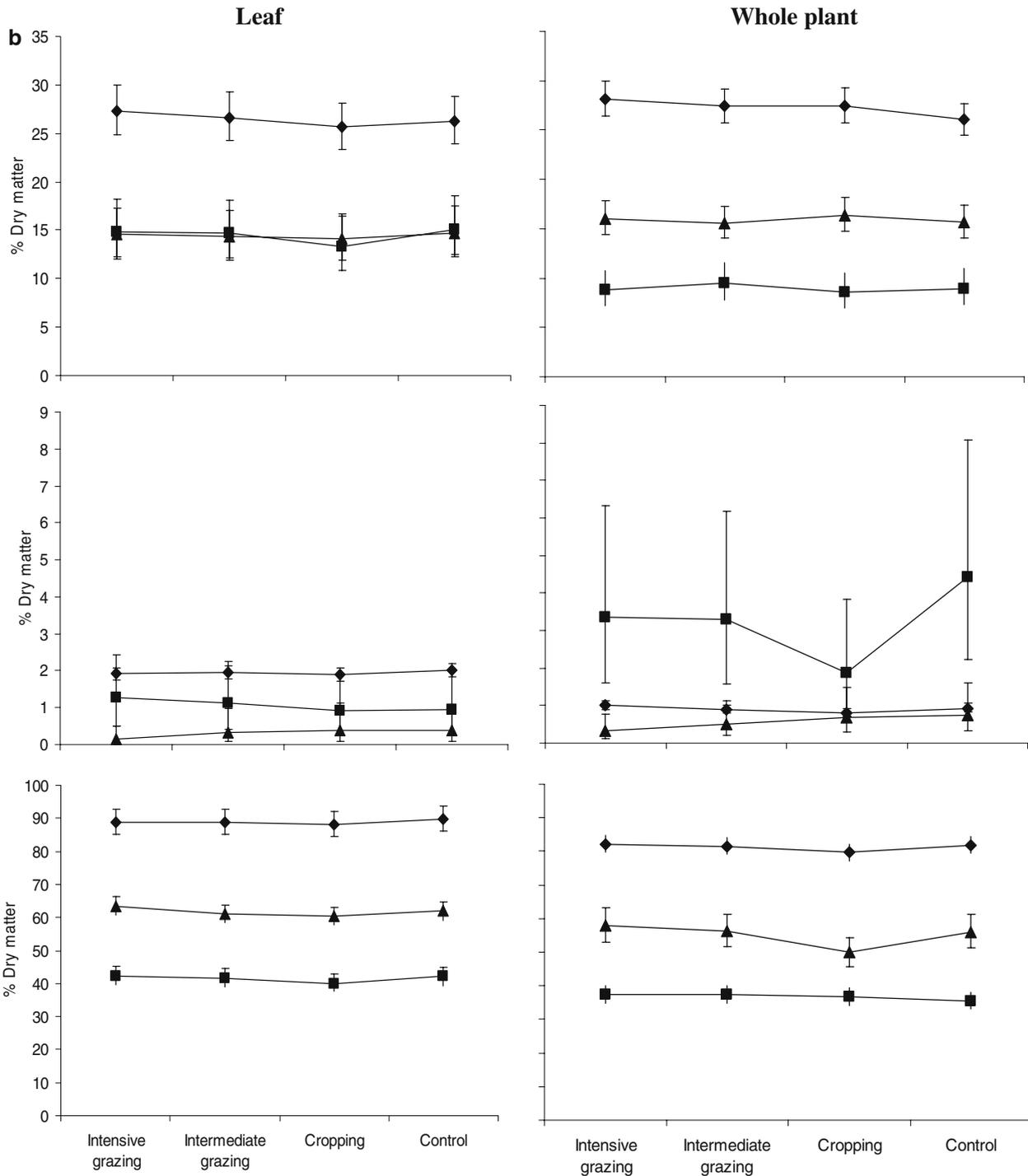


Fig. 1 continued

pepsin and cellulase to digest the plants and is thus most analogous to the capacity of dugongs to digest the seagrasses. IVDMD was uniformly high across all seagrass species and experimental treatments. While there were some statistically significant effects, the greatest of these varied by only 1.2% from the control (Table 1). Interestingly, the values for IVDMD were

similar to the high values estimated for dugongs *in vivo*, which range between 80 and 90% (Murray et al. 1977; Aketa et al. 2001; Aketa and Kawamura 2001), perhaps indicating that these high digestibilities are a function of seagrass composition, rather than dugong digestive adaptations. Overall, we conclude that the changes observed here are most likely to result in

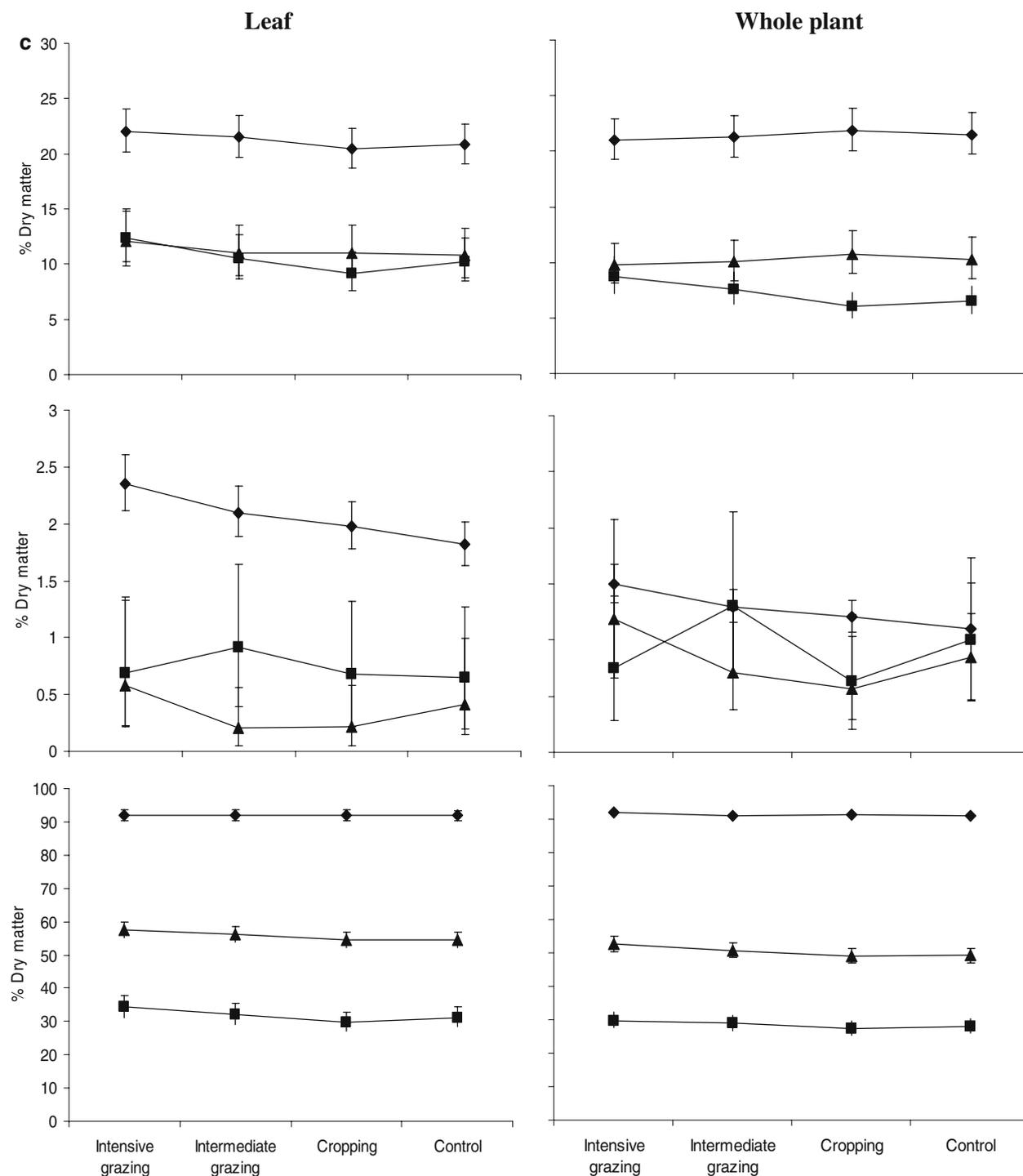


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improved nutritional quality of seagrasses for large herbivores. That both dugongs and turtles have clearly been shown to re-graze sites at stages of recovery similar to those we describe here supports the conclusion that the nutritional benefits are likely to outweigh perceived negative effects (Bjorndal 1980; Preen 1995; de Iongh 1996).

The changes in leaf N recorded here parallel those seen in many terrestrial systems, increasing in response to herbivory. These data provide experimental support for a grazing optimization view of dugong and turtle herbivory, with return visits yielding greater N returns, as suggested by previous authors (Bjorndal 1980; Preen 1995; de Iongh 1996). However, the mechanism by

Table 2 Summary of statistically significant effects on the chemical composition of *Halodule uninervis* in short-term experiment

	<i>P</i> value	Treatment	% Change (relative to control)
Leaf			
ADF	0.001	Cropping 1 month	-6.9
IVDMD	0.011	Cropping 1 month	1.4
Lignin	<0.0001	Cropping 1 month	-10.8
Nitrogen	<0.0001	Grazing	10.8
	<0.0001	Cropping 2 months	8.7
NDF	<0.0001	Cropping 1 month	-5.6
Organic matter	0.022	Cropping 1 month	-3.0
	0.041	Cropping 2 months	2.6
Starch	0.007	Cropping 1 month	-59.2
Whole plant			
ADF	0.005	Cropping 1 month	-7.3

which feedback operates in this system is likely to differ from the terrestrial environment. Discussion of grazing optimization in terrestrial systems often focuses on the replenishment of the soil N pool via defecation and urination by the herbivores, often via movement of nutrients into favored sites (De Mazancourt et al. 1998; Augustine et al. 2003).

As we noted earlier, in the marine environment, these feedback mechanisms may not exist because of solubility and physical transport via the water. This is compounded by two factors: (1) both dugongs and turtles often feed intertidally, and (2) both species also have very long gut retention times, 146–166 h and 156–325 h for dugongs and turtles, respectively (Lanyon and Marsh 1995; Brand et al. 1999). Either animal feeding intertidally would have moved away from the feeding area at least ten times between ingesting a meal and defecating. Thus, even without the effect of transport of fecal or urinary material itself, the link between feeding area and return of material to that area is weak.

We suggest instead that grazing optimization for dugongs may function via the effect of disturbance on bacterial N fixation. Feeding by dugongs usually produces serpentine feeding trails typically some 20 cm wide and 3–5 cm deep (Anderson and Birtles 1978). This feeding behavior introduces detritus into the sediment, aerating it and providing substrate for nitrogen fixation. Sediments from grazed areas show higher N

fixation rates than those from matching ungrazed areas, and these differences are explained largely in terms of aerobic N fixation rates (Perry and Dennison 1999). In fact, the N fixation rates reported from grazed sediments by Perry and Dennison (1999) were the highest recorded for a seagrass community.

In contrast, the effects seen in response to simulated cropping by turtles may not reflect optimization in the sense described above. In the short term, the same effect is seen, with N concentrations increasing and fiber concentrations decreasing. These effects are consistent simply with an increase in the proportion of new foliage with less structural material. We do not know of an identifiable feedback mechanism whereby the turtles may contribute N to the pool used by the seagrass. Consequently, where this phenomenon has been studied more closely, and where recropping rates may be more frequent, the sediment N pool is ultimately depleted as seagrasses continue to invest N in regrowth after each subsequent recropping. Thus, later iterations of regrowth have lower N concentration in foliage, to which turtles ultimately respond by abandoning the plot and moving to create another grazing plot elsewhere (Bjorndal 1980; Zieman et al. 1984).

The timing of the recropping or regrazing is also important. The optimal nutritional status of herbivores may be reached at a particular frequency of return (Green and Detling 2000), but this will vary depending on the recovery rate of the plant. While, for example, turtles recropping *H. uninervis* beds two months after initial cropping would receive a benefit in the form of increased leaf nitrogen, those returning after only a month would receive no significant gain in nitrogen, and substantially less energy gain in the form of carbohydrates. Experimental field trials of natural and simulated dugong feeding trails at various locations on the east coast of Queensland indicate that the recovery time of seagrasses from grazing disturbances by dugongs depends on the location of the seagrass bed, the timing and the intensity of the grazing, the species composition and the location within the beds (which are generally confounded), and the occurrence of additional disturbance from dugongs or other sources during recovery (Aragones and Marsh 2000; Marsh et al. 2005). Biomass recovery times are <30–200 days (exceptionally clear water in eastern Moreton Bay ~27°S; Preen 1995, Kathryn McMahon, personal communication, 2004) or several months to a year [turbid water more typical of the region at our study site (Aragones and Marsh 2000)]. Thus the appropriate timing for either dugongs or turtles to revisit sites is likely to vary greatly. Preen (1995) documents variable return times

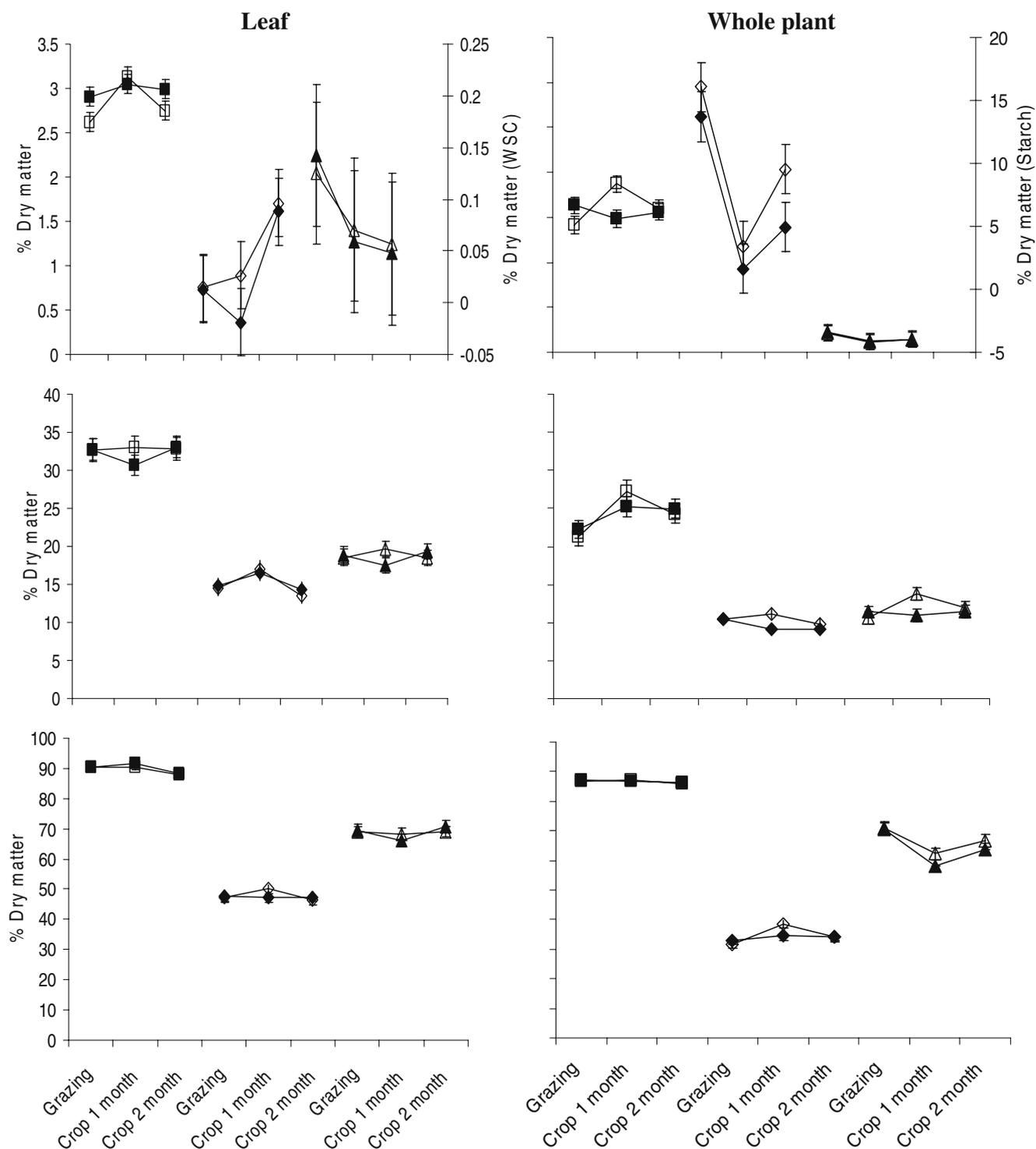


Fig 2 Effects of simulated feeding by dugongs and turtles in the short-term experiment at Cardwell (*Halodule uninervis*). The left hand column shows values for leaves, the right hand column values for whole plants. Treatment values given as solid symbols, control values as hollow symbols. All values are means with 95%

confidence limits. Row 1: squares nitrogen, diamonds starch, triangles water-soluble carbohydrates. Row 2: squares acid detergent fiber, diamonds hemicellulose, triangles lignin. Row 3: squares in vitro dry matter digestibility, diamonds neutral detergent fiber, triangles organic matter

ranging from <17 days to 5 months for dugongs grazing in Moreton Bay, but the data are insufficient to identify possible reasons for this variation. Similarly,

our data give us some insights into the processes, but do not allow us to make predictions about optimal return rates to grazing areas.

The changes to plant chemical composition following grazing were surprisingly long-lasting, with both *Halophila ovalis* and *H. uninervis* showing significantly elevated whole-plant N concentrations in response to all treatments after 11 and 13 months, respectively. These species are generally believed to recover quickly from such disturbances (Aragones 1994; Preen 1995; Supanwanid 1996). In fact, in the companion paper to this study (Aragones and Marsh 2000), we report recovery times (i.e., time for biomass in treatments to equal that in controls) from the intensive grazing treatment of between two and eight months for *H. ovalis* and *Z. capricorni*, respectively. Thus, even though the seagrasses had apparently recovered in terms of biomass, compositional changes potentially significant to herbivores remained. In the short-term experiment, biomass recovery was not complete at harvesting (Aragones and Marsh 2000), which likely explains the greater number of significant effects on chemical composition. In particular, the low starch concentrations of the cropping treatment after one month are probably due to mobilization of energy reserves when rebuilding the above-ground biomass (Dawes and Lawrence 1979; Chapman et al. 1992).

Elsewhere, we have shown (Aragones and Marsh 2000) that the ratio of below-ground to above-ground biomass was reduced by all treatments over the long term, with the effects greatest for simulated intensive grazing. Simulated cropping increased the ratio of below-ground to above-ground biomass only in the short term. These results are also consistent with the view that the seagrasses have mobilized below-ground energy reserves to enable rebuilding of above-ground structures. The change in this ratio must also at least partly explain the cases reported here, where the effects on nitrogen, for example, were greater in the whole-plant values than for leaves alone (e.g., *H. uninervis*, Table 1). This provides further support for, and helps to elucidate the mechanism for, the hypothesis that regrazing of sites by turtles and dugongs, even up to a year later, primarily provides benefits in terms of greater nitrogen availability.

Our demonstration of compositional changes following simulated grazing and cropping should be viewed in the light of concurrent changes in species composition and abundance. Aragones and Marsh (2000) report the effects of the experiments described here on seagrass community composition and abundance. In addition to the improved nutritional quality we report, the composition of the mixed species bed at Ellie Point changed to favor the pioneer species, *Halophila* and *Halodule*, both of which are preferred forage species by dugongs and turtles. Similar results were

found by Preen (1995) for subtropical Moreton Bay. After a year, the abundance of these species was higher (Aragones and Marsh 2000) and the forage was of higher quality (this study). Once again, similar effects of grazing on plant species composition have been seen in terrestrial systems (Augustine and McNaughton 1998; Adler et al. 2005).

Finally, some consideration is warranted here of the potential ecosystem-level effects of reduced numbers of dugongs and turtles. There have been a number of reports in recent years of greatly reduced populations of both dugongs and green turtles (Jackson 1997; Bjorndal et al. 2000; Jackson et al. 2001; Marsh et al. 2005). Intensive feeding by both these species tends to increase subsequent forage quality in terms of both species composition and nutritional quality within those species. Consequently, substantial reductions in the densities of the populations of these species have the potential to lead to degradation of the habitat in nutritional terms, as seagrass communities tend towards climax communities. Whether this process, if unimpeded by physical disturbance such as cyclones, can pass a threshold that prevents dugongs or turtles feeding and thus reinhabiting an area, thus preventing recovery of their populations, is a question that cannot be answered at the moment, but it may prove a valuable avenue for future research.

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