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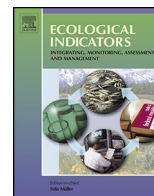
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What lies beneath: Why knowledge of belowground biomass dynamics is crucial to effective seagrass management



J. Arie Vonk^{a,*}, Marjolijn J.A. Christianen^b, Johan Stapel^c, Katherine R. O'Brien^d

^a Department of Aquatic Environmental Ecology, Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, PO Box 94248, 1090 GE Amsterdam, The Netherlands

^b Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

^c Caribbean Netherlands Science Institute (CNSI), PO Box 65, St Eustatius, Caribbean, The Netherlands

^d School of Chemical Engineering, The University of Queensland, St Lucia 4072, Australia

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ABSTRACT

Conservation of seagrasses meadows is important, because these habitats are ecologically important and under threat. Monitoring and modelling are essential tools for assessing seagrass condition and potential threats, however there are many seagrass indicators to choose from, and differentiating between natural variability and declining conditions poses a serious challenge. Tropical seagrass meadows in the Indo-Pacific, in contrast to most temperate meadows, are characterized by a multi-species composition and a year-round growth. Differences in characteristics between species growing within one meadow could induce uncertainty in the assessment of the dynamics of these meadows if variation in productivity and related biomass turnover timescales are not taken into consideration. We present data on biomass distribution, production and turnover timescales of above- and belowground tissues for three key tropical seagrass species (*Thalassia hemprichii*, *Cymodocea rotundata* and *Halodule uninervis*) in two mixed-species meadows in the Spermonde Archipelago, Indonesia. Seagrass leaf turnover time scales were comparable for the three studied seagrass species and varied between 25 and 30 days. Variation in leaf and rhizome turnover timescales were small (or insignificant) between the two meadows. In contrast, rhizome turnover time scales were around ten times longer than leaf turnover timescales, and large differences in rhizome turnover time scales (200–500 days) were observed between the species. The late-successional species *T. hemprichii* had much slower rhizome turnover compared to the two early successional species. Furthermore, since rhizome biomass has a much longer turnover time compared to leaf biomass, changes in rhizome biomass reflect effects on seagrass meadows on a much longer timescale compared to changes in leaf biomass for these tropical meadows. We conclude that belowground biomass dynamics are an important proxy to assess long-term effects of environmental stressors on seagrass ecosystems and should be included in tropical seagrass management programmes.

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1. Introduction

Seagrasses meadows are ecologically important and provide many ecosystem services, including food provisioning and sediment stabilization (Koch et al., 2012; Christianen et al., 2013), and feeding habitats for many fauna species (Heck et al., 2003; Van Tussenbroek et al., 2006; Christianen et al., 2014). As vegetated coastal habitat, seagrass systems also play a role in CO₂ sequestration (blue carbon; Mcleod et al., 2011). Yet, the rate of seagrass loss worldwide exceeds the rate of expansion, resulting in a global

crisis for seagrass systems (cf. Orth et al., 2006; Waycott et al., 2009). Threats to seagrass occur at a wide spatial scale (Grech et al., 2012), ranging from local (e.g. dredging, anchoring, trampling; Di Carlo and Kenworthy, 2008) to regional (e.g. land-use change, coastal development; Roca et al., 2014) and global scale (e.g. climate change; Koch et al., 2013). Overall, this results in increased adverse environmental conditions for seagrass meadows and challenges for seagrass management and restoration.

Assessing current seagrass condition and predicting future changes is essential for successful seagrass management. Since seagrasses can be modelled easily due to their modular growth form (Duarte et al., 2005), models are useful tools to estimate ecological functions like carbon storage rates and to determine thresholds of seagrass meadow loss and recovery (Sintes et al., 2005; Van der

* Corresponding author. Tel.: +31 20 525 7352; fax: +31 20 525 7832.
E-mail address: j.a.vonk@uva.nl (J.A. Vonk).

Heide et al., 2007; Carr et al., 2010; Grech and Coles, 2010). Seagrass models typically consider either a single species (e.g. Van der Heide et al., 2007, 2010), or model seagrass assemblages as a single functional group (e.g. Carr et al., 2010, 2012). This is reasonable in temperate systems, where species diversity is typically low (Short et al., 2007). However, tropical seagrass systems in the Indo-Pacific are often characterized by diverse mixed species meadows consisting of early- and late-successional species (Brouns, 1987; Vermaat et al., 1995). The differences in above- and belowground turnover rates between these species (Duarte, 1991; Rollon et al., 1998; Kiswara et al., 2009) will result in strong variations of biomass turnover timescales for tropical meadows and thus variations in the ability of meadows to withstand adverse conditions.

Large scale monitoring of seagrass systems is often based on leaf biomass estimations of meadows (Knudby and Nordlund, 2011), especially with the increasing availability of satellite images allowing fast assessment of seagrass extent and canopy density (Lyons et al., 2013). For many tropical seagrass species the largest part of their biomass is belowground (Nienhuis et al., 1989; Duarte and Chiscano, 1999) and their rhizome structure provides essential functions for the plants (e.g. storage of carbohydrates, spatial extension; Hemminga, 1998) and the seagrass system (e.g. stabilization of sediment; Christianen et al., 2013). Insight into of the relationship between above- and belowground seagrass parts is needed to predict the productivity and stability of seagrass systems (Di Carlo and Kenworthy, 2008). Although accumulation of belowground materials can form large storages of carbon (e.g. Romero et al., 1994), sampling of belowground parts is less common, due to its destructive nature, labour intensity, and the need to actually visit all meadows.

However there are a myriad of different indicators of seagrass condition related to biomass or growth for seagrass health (e.g. shoot density, leaf biomass, meadow extension rate). Key challenges to both monitoring and modelling of seagrass meadows are knowing which indicators to use and discerning between natural variability and declining conditions. This study addresses these two important questions by quantifying biomass distribution, production and turnover timescales of above- and belowground tissues as indicators of seagrass condition, and investigates how these indicators vary between three key tropical seagrass species (*Thalassia hemprichii*, *Cymodocea rotundata* and *Halodule uninervis*) in mixed-species meadows with different canopies (leaf biomass). It further indicates the relative importance of seagrass species characteristics (e.g. growth form or successional type) and meadow density on these turnover timescales and discusses the importance of belowground biomass dynamics to estimate the ability of tropical mixed-species meadows to withstand adverse environmental conditions.

2. Methods

2.1. Study area

The Spermonde Archipelago (200 km long, 40 km wide) consists of a large group of coral islands and submerged reefs on the continental shelf along the west coast of South Sulawesi (Fig. 1). This area is characterized by rather constant seagrass growth over the year (Stapel et al., 2001). The measurements on seagrasses were executed at Bone Batang (5°01'00" S, 119°19'30" E) an uninhabited island located approximately 15 km off the coast and 30 km from the shelf edge consisting of a reef platform with a (moving) sandbank on top (Vonk et al., 2008; Kneer, 2013). The reef flat was covered by macrophyte vegetation (cover density up to 80%), with the seagrass species *T. hemprichii*, *C. rotundata* and *H. uninervis* forming the main cover of the meadows. These species are the most

common Indo-pacific seagrass species (Mukai, 1993) that often grow together in multispecies meadows (Verheij and Erfteimeijer, 1993; Vonk et al., 2008; Kiswara et al., 2009) and represent a range from late-successional to early-successional species, respectively (Birch and Birch, 1984). *Halophila ovalis* and *Enhalus acoroides* were also observed in the meadows. These species occurred in low densities or small patches and were therefore excluded from our study. We selected two adjacent seagrass meadows differing in total seagrass density and leaf biomass (Vonk et al., 2010) and were therefore qualified as closed canopy (high seagrass leaf biomass) and open canopy (low seagrass leaf biomass) meadows, respectively. No differences in sediment conditions (detritus content and pore-water nutrients) or grazing intensity (sea urchins) were observed between the meadows (Vonk, 2008). Both meadows were sub-tidal to exclude the (seasonal) influence of day-time dry fall (e.g. Erfteimeijer and Herman, 1994; Stapel et al., 1997).

In each meadow, three permanent transects of 15 m × 1 m were marked. Each transect was perpendicular to the edge of the meadow, with the first of 15 quadrants of 1 m² starting 2 m inside the edge of the meadow (Vonk et al., 2010). All seagrass measurements were performed in or near the permanent transects between October 2004 and November 2005. An overview of the seagrass parameters measured in the field is provided in Fig. 2. These measurements were performed for each of the three seagrass species (*T. hemprichii*, *C. rotundata* and *H. uninervis*) in both meadows.

2.2. Seagrass mass, growth, and plastochrone

Seagrass leaf, rhizome and root mass was estimated from cores (diameter 16 cm, depth 20 cm,) taken in between transects in November 2004 and May/June 2005 ($n = 10$ per meadow). The cores were washed out over a 1 mm screen, after which shoots were counted, sorted by species, and divided into different plant parts (Fig. 2). The material was briefly rinsed with demineralised water and weighed after at least 48 h at 70 °C (all reported mass values are based on dry weight).

Seagrass leaf growth was measured using a needle marking method (Short and Duarte, 2001). At 11 occasions during one year, we marked approximately 15 shoot meristems of each species in both meadows. Three weeks later, we harvested the shoots, counted the number of new leaves, and determined the amount of new leaf material. Horizontal rhizome growth was measured once (October 2005) using the rhizome marking technique according to Dennison (1990). Horizontal rhizome meristems were carefully uncovered, marked with cable ties, and covered again with sediment. After 4 weeks, 40–50 rhizomes per species were recovered and the length, number of new nodes and new shoots were measured. The material of 10 meristems (shoot or rhizome) was pooled together and weighed (i.e., $n = 4–5$ per meadow). Growth of vertical (shoot) and horizontal (rhizome) meristems was determined together with the plastochrone, i.e. the time interval between the onsets of two consecutive plant parts in days for leaves (PI_L), vertical rhizome nodes (PI_{VR}), horizontal rhizome nodes (PI_{HR}), and shoot (PI_S) (cf. Short and Duarte, 2001). Vertical rhizome node mass was determined by counting nodes and weighing five pooled rhizome samples.

2.3. Density, biomass and production of meadows

At 5 occasions throughout the year, the number of seagrass shoots was counted in a random 10 cm × 10 cm plot within each quadrant. Since no statistical differences in densities were observed over the seasons, we pooled the five measurements per quadrant together, resulting in $n = 45$ observations per meadow. Horizontal rhizome meristem densities were counted from cores (diameter

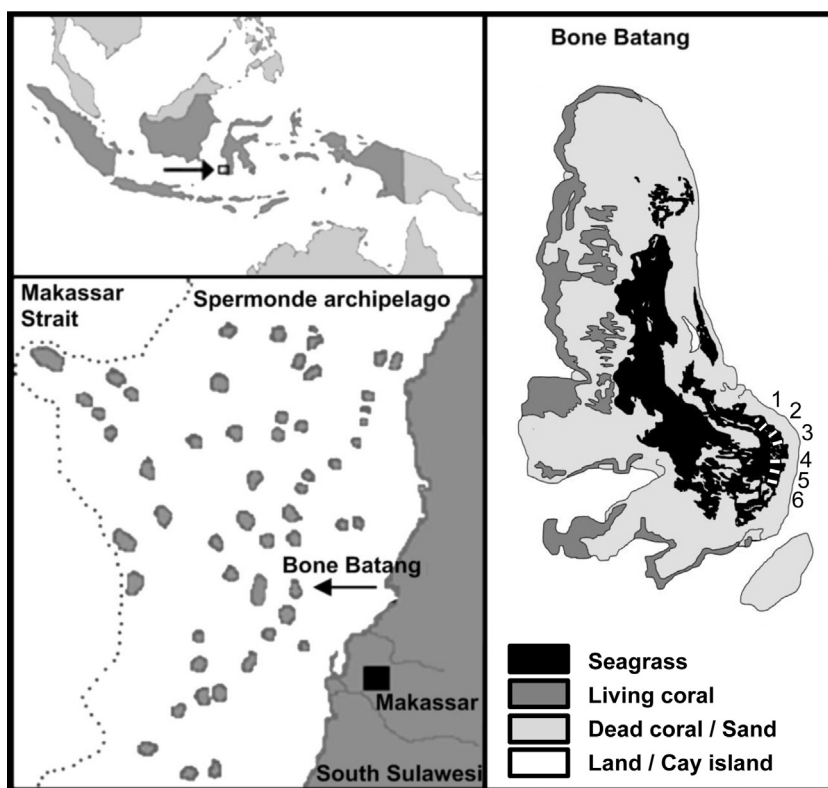


Fig. 1. Study area showing the location and the islands of the Spermonde Archipelago along the west coast of South Sulawesi (dotted line: shelf edge 200 m; Vonk et al., 2008) and overview of the island Bone Batang (5°01'00" S; 119°19'30" E), its seagrass meadows (Kneer, 2013), and the permanent transects (white dashes) in the closed (1–3) and open (4–6) canopy meadow.

16 cm, depth 20 cm, $n = 15$) in each meadow, collected in close vicinity alongside each transects (5 cores/transect) in November 2005.

Biomass (B ; $g\ m^{-2}$) for leaf, rhizome and root were determined from shoot density (N_S ; shoot m^{-2}) multiplied by average mass (M ; $g\ shoot^{-1}$) of leaf, rhizome, and root, respectively (i.e. $B = M \times N_S$) for each species separately and added together as the total biomass. Shoot density (N_S) times leaf growth (G_L ; $g\ shoot^{-1}\ d^{-1}$) resulted in leaf production ($N_S \times G_L = P_L$; $g\ m^{-2}\ d^{-1}$). Total rhizome

production (P_R ; $g\ m^{-2}\ d^{-1}$) was calculated as the sum of horizontal rhizome production (P_{HR} ; $g\ m^{-2}\ d^{-1}$), derived from the horizontal meristem growth (G_{HR} ; $g\ meristem^{-1}\ d^{-1}$) multiplied by horizontal rhizome meristem density (N_{HR} ; $meristem\ d\ m^{-2}$), and vertical rhizome production (P_{VR} ; $g\ m^{-2}\ d^{-1}$), derived from the vertical rhizome node mass (M_{VR} ; $g\ node^{-1}$) divided by vertical rhizome plastochrone (PI_{VR} ; $node\ d^{-1}$) and multiplied by shoot density (N_S), i.e. $P_R = P_{HR} + P_{VR} = (G_{HR} \times N_{HR}) + ((M_{VR}/PI_{VR}) \times N_S)$.

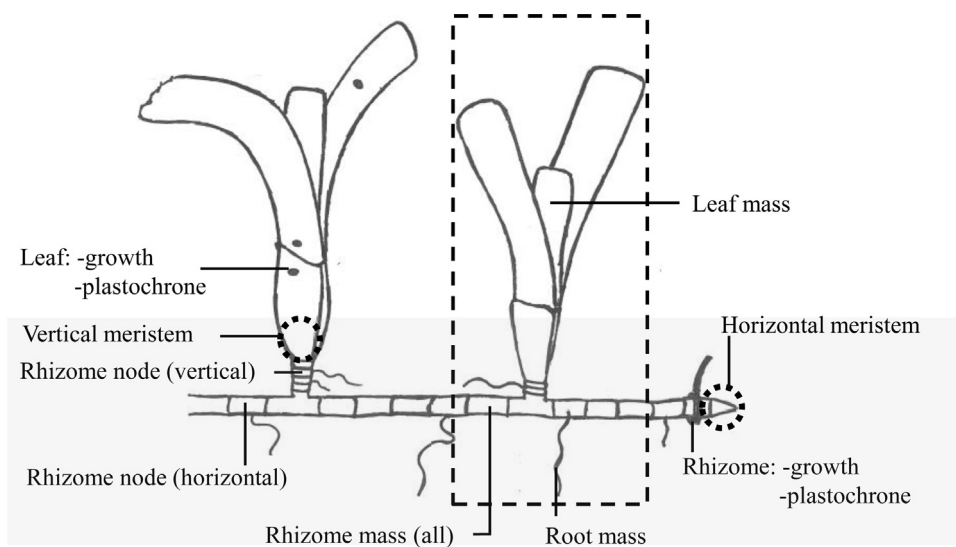


Fig. 2. Overview of seagrass parameters determined for each of the three studied species (*T. hemprichii*, *C. rotundata* and *H. uninervis*). For individual seagrass shoots (marked by dotted line), we determined the mass of leaves, rhizomes and roots. Leaves were marked to quantify leaf growth and plastochrone leaf. Horizontal rhizome meristems were marked to quantify horizontal rhizome growth and plastochrone horizontal rhizomes. Furthermore, shoot density (vertical meristems) and rhizome density (horizontal meristems) were determined.

2.4. Biomass turnover and leaf-to-rhizome ratios

Tropical seagrass meadows maintain a high production year-round (Brouns, 1987; Erftemeijer et al., 1993; Duarte and Chiscano, 1999) and timescales for turnover of seagrass leaf and rhizome biomass were derived assuming a constant production of biomass over time in these meadows. Leaf biomass turnover (T_L ; i.e. time in days required to produce the standing biomass) was calculated as the inverse of the relative leaf growth rate (rel. G_L ; g new leaf g^{-1} leaf mass d^{-1}), thus $T_L = 1/\text{rel. } G_L$. Rhizome biomass turnover (T_R ; days) was calculated by dividing the biomass of rhizomes (B_R) by the total rhizome production (P_R), i.e. $T_R = B_R/P_R$. To quantify the relative importance of aboveground to belowground parts, we calculated the leaf-to-rhizome ratios for the biomass, production and turnover for the three seagrass species. These leaf-to-rhizome ratios (or changes therein) can be considered indicators of the seagrass meadow health state.

2.5. Statistics

Measured seagrass parameters are presented as mean \pm SE values. We expressed the uncertainty for the calculated biomass, production or turnover values as % error, determined as the square root of the summed square relative errors of the multiplied components (here density and mass, growth, or plastochrone). Data were tested for equality of variances and $^{10}\log$ -transformed when necessary before analysis. We used a multivariate design (MANOVA) to analyze the seagrass parameters derived from shoot mass estimations (mass of leaf, rhizome, root), from leaf marking (leaf growth and leaf plastochrone) and from horizontal meristem marking (rhizome growth and plastochrone) to account for correlations between parameters derived from one method and to maintain control over the overall alpha level or type I error (*sensu* Meyers et al., 2005). If significant, separate univariate analyses (ANOVAs) and post hoc Tukey's-b tests were performed for each parameter using the error term of the multivariate analysis to evaluate the F -ratios of these ANOVAs (Meyers et al., 2005). Vertical rhizome node mass and densities for shoots and rhizomes were analyzed using ANOVA, followed by post hoc Tukey's-b tests. Species and meadows were fixed factors in both the MANOVA and ANOVA calculations. All statistics were calculated using IBM SPSS Statistics 20.

3. Results

3.1. Seagrass mass, growth, and plastochrone

Most of the measured parameters showed significant differences between the three studied seagrass species. *Thalassia hemprichii* was characterized by larger leaf and rhizome mass than the other two species, while differences between *C. rotundata* and *H. uninervis* were relatively small and mainly observed for aboveground parts (Fig. 3a and b). The root mass of *T. hemprichii* was higher (135 ± 14 and 124 ± 9 mg shoot $^{-1}$ in closed and open canopy meadow, respectively) compared to both *C. rotundata* (56 ± 5 and 36 ± 6 mg shoot $^{-1}$) and *H. uninervis* (24 ± 3 and 29 ± 2 mg shoot $^{-1}$).

Growth rates for leaf and rhizome were significantly higher for *T. hemprichii* compared to *C. rotundata* and *H. uninervis* (Fig. 3c and d). Only small differences in the leaf plastochrone (Pl_L) were observed between all species (Fig. 3e). While the plastochrone for horizontal rhizome nodes (Pl_{HR}) was much lower in *T. hemprichii* (Fig. 3f) since this species produced approximately 14 internodes before a new shoot was formed (only 1 internode for *C. rotundata* and *H. uninervis*), the shoot plastochrone (Pl_S) was much larger for the late-successional species *T. hemprichii* (between 43 and 47 days) compared to the early-successional species *C. rotundata* and

H. uninervis (both between 11 and 13 days). For all three species, leaf mass and growth was higher in the closed canopy meadow compared to the open canopy meadow, while no difference between meadows was observed for specific rhizome mass and growth (Fig. 3a and d).

3.2. Density, biomass, and production of meadows

Shoot density was significantly higher in closed compared to the open canopy meadow (ANOVA $F_{1,88} = 69.26$, $p < 0.001$), but no significant difference in horizontal rhizome meristem density was observed (Table 1, Fig. 4). The difference in shoot density between meadows (Fig. 4a) was caused by *C. rotundata* (mean 879 and 378 shoots m^{-2} in closed and open canopy meadow, respectively) and *H. uninervis* (2424 and 1178 shoots m^{-2}), but not by *T. hemprichii* (604 and 799 shoots m^{-2}). No difference was observed between meadows for each species for horizontal rhizome density (Fig. 4b).

Total leaf and belowground biomass was 123 and 652 $g m^{-2}$ in the closed and 69 and 524 $g m^{-2}$ in the open canopy meadow, respectively, showing that the difference in aboveground biomass was not reflected in belowground biomass between the meadows. Biomass of leaves (Fig. 4c) and rhizomes (Fig. 4d) was also only higher for *C. rotundata* and *H. uninervis* in closed compared to open canopy meadows. In the closed and open canopy meadow, total leaf production was 4.9 $g m^{-2} d^{-1}$ and 2.3 $g m^{-2} d^{-1}$, respectively, and total rhizome production was 1.1 $g m^{-2} d^{-1}$ and 0.9 $g m^{-2} d^{-1}$ respectively. Again, the two early succession type species showed higher leaf production (Fig. 4e) and vertical rhizome production (Fig. 4g) in the closed canopy meadow, but not for horizontal rhizome production (Fig. 4f).

3.3. Biomass turnover and leaf-to-rhizome ratios

Comparing turnover timescales between plant parts, species and canopy clearly showed that differences between plant parts were much larger (9–18 times longer turnover) than differences between species (1.07–1.20 times for leaves, 1.52–2.24 times for rhizomes) while differences within species between meadows were relatively smallest (1.01–1.09 times for leaves and 1.03–1.50 times for rhizomes). Estimated seagrass turnover timescales ranged from approximately one month for leaf biomass up to over one year for rhizome biomass (Fig. 5). Leaf biomass turnover, expressed as the time required to produce the standing biomass, was comparable for all three species (25–30 days). Rhizome biomass turnover varied more between species (variation of 52–124%). In general, the rhizome turnover for the early-successional species *C. rotundata* and *H. uninervis* (both < 350 days) was faster compared to the late-successional species *T. hemprichii* (>450 days), with relatively small differences between meadows. Comparing leaf-to-rhizome ratios clearly showed differences between biomass, production and turnover for seagrasses. Although leaf biomass was 1.8–6.8 times smaller than rhizome biomass, leaf production was 2.4–6.3 times higher than rhizome production for the studied species. This resulted in timescales that were on average 1 order of magnitude longer for rhizome turnover compared to leaf turnover.

4. Discussion

In general, *C. rotundata* and *H. uninervis* have similar biomass and production rates and could be modelled as a single group, however, *T. hemprichii* has quite different parameters and would have to be considered separately in most cases. Modelling leaf dynamics would be the only exception, since the influence of variation induced by differences between species is relatively small for leaf turnover (<20% variation between species). Thus when modelling leaf dynamics for these multi-species meadows the species can be

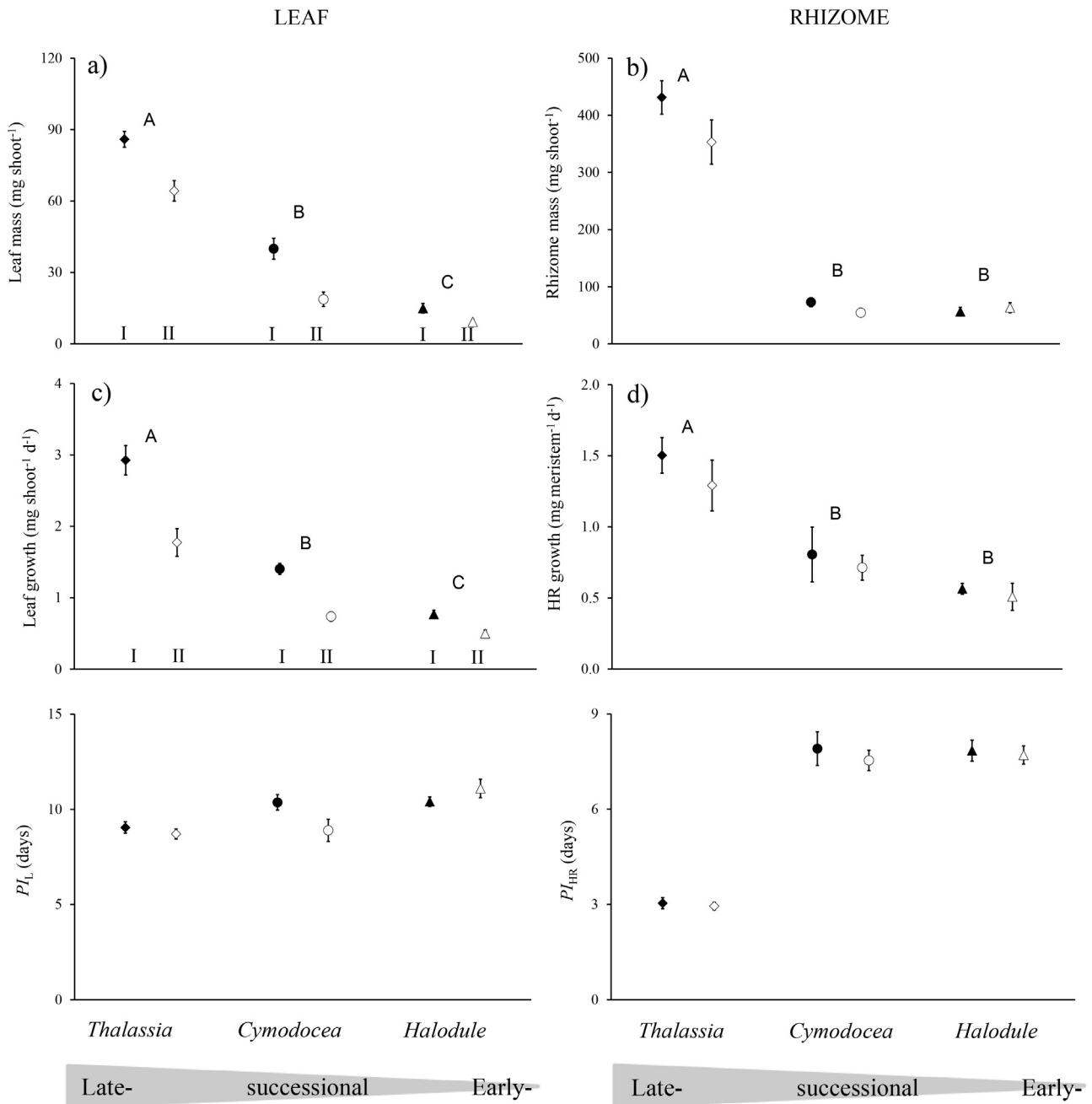


Fig. 3. Mean (\pm SE) seagrass parameters for leaf (left column) and rhizome (right column). Seagrass mass for leaf (a) and rhizome (b), growth of leaf (c) and horizontal rhizome (HR; d), and plastochrone for leaf (PL_L ; e) and horizontal rhizome (PL_{HR} ; f) of *T. hemprichii* (diamonds), *C. rotundata* (circles), *H. uninervis* (triangles) in both closed canopy (closed symbols) and open canopy (open symbols) meadows. Significant differences are denoted (see Table 1) between Species (capitals), Meadows (Roman numerals) or interaction between Species and Meadows (letters).

considered a single functional group and no added complexity is needed in the models in comparison to single species meadows (e.g. Van der Heide et al., 2007; Carr et al., 2010). However much larger variation between species was observed for rhizome turnover (up to >100%), reflecting differences in growth form with larger species characterized by longer rhizome life span, higher storage capacity, and slower growth (Vermaat, 2009). Modelling belowground biomass dynamics would need including parameters for all seagrass species growing within the meadow, resulting in enhanced model complexity and uncertainty.

The largest differences in turnover timescales were observed for the different plant parts, i.e. between leaves and rhizomes. Due to higher biomass and slower production, rhizome turnover was 9–18

times longer compared to leaf turnover for all three studied species. Replacement of rhizome biomass will thus occur over more than a year, instead of less than a month for leaf biomass. Thus including only aboveground seagrass parameters in modelling (e.g. Van der Heide et al., 2010) could result in different predictions for meadow dynamics compared to models that include both above- and belowground biomass. By modelling the interactions between turtles and seagrasses, Christianen et al. (2014) showed that meadows were stable when only aboveground grazing was considered; however, including belowground grazing in the model showed a collapse of the seagrasses due to a lack of regeneration from its belowground biomass. Since aboveground biomass and turnover was also not directly related to belowground biomass and turnover, we

Table 1
Differences in seagrass parameters between species and meadows were analyzed using (M)ANOVA for each type of measurement: (A) seagrass mass, (B) leaf growth and plastochrone for leaf (Pl_L), (C) horizontal rhizome (HR) growth, and plastochrone horizontal rhizome (Pl_{HR}), (D) vertical rhizome node mass, (E) shoot density and (F) rhizome density. (Number of samples analyzed for each combination of species and meadow denoted between brackets; significant differences in bold.)

Response	Effect R^2	Error	Species		Meadow		Species * meadow	
	(Adj.)	MS	MS	<i>p</i>	MS	<i>p</i>	MS	<i>p</i>
<i>(A) Seagrass mass (n = 10)</i>								
Leaf (mg shoot ⁻¹)	0.863	0.021	3.411	<0.001	0.724	<0.001	0.048	0.113
Rhizome (mg shoot ⁻¹)	0.857	0.025	4.322	<0.001	0.052	0.158	0.041	0.210
Root (mg shoot ⁻¹)	0.822	0.020	2.511	<0.001	0.033	0.201	0.100	0.010
<i>(B) Leaf marking (n ≥ 11)</i>								
Leaf growth (mg shoot ⁻¹ d ⁻¹)	0.765	0.022	1.894	<0.001	1.070	<0.001	0.101	0.622
Pl_L (d; = Pl_{VR})	0.258	0.004	0.041	<0.001	0.007	0.172	0.013	0.037
<i>(C) Horizontal rhizome marking (n = 5)</i>								
HR growth (mg meristem ⁻¹ d ⁻¹)	0.596	0.020	0.430	<0.001	0.023	0.291	0.001	0.931
Pl_{HR} (d)	0.950	0.002	0.547	<0.001	0.001	0.477	0.001	0.960
<i>(D) Vertical rhizome node mass (n = 5)</i>								
Node (mg)	0.304	0.062	0.417	0.005	0.223	0.070	0.021	0.718
<i>(E) Aboveground density (n = 45)</i>								
Shoots (# shoots m ⁻²)	0.328	0.188	5.697	<0.001	8.331	<0.001	2.922	<0.001
<i>(F) belowground density (n = 15)</i>								
Rhizome (# meristems m ⁻²)	0.180	0.497	5.638	<0.001	0.437	0.352	0.251	0.606

consider it important to include both compartments when modelling productivity, turnover and dynamics in seagrass meadows.

Differences in characteristics between the three species reflected their successional type (Brouns, 1987; Vermaat et al., 1995). *T. hemprichii*, *C. rotundata* and *H. uninervis* represent a late-successional species and two early-successional species, respectively. The late-successional species *T. hemprichii* had a slower rhizome biomass turnover compared to the early-successional species *C. rotundata* and *H. uninervis*. However this was not reflected in leaf turnover timescales which were on average comparable between the three species, with only slightly longer turnover for *T. hemprichii* compared to both other species (~10% and ~20% longer turnover in closed and open canopy meadow, respectively). This indicates that successional type only induced a small variation in leaf turnover for these three seagrasses growing in mixed meadows. The specific shoot mass of these species varies around 1 order of magnitude. Only when taking a much larger range of size classes (3 orders of magnitude i.e. from *Halophila* spp. up to *E. acoroides*), Duarte (1991) observed a decrease in leaf turnover rates with increasing seagrass size. Although these two species occurred in the study area, their density was too low and patchy to be included in this study.

In contrast to leaf turnover, rhizome turnover timescales showed on average large variation between species. Therefore, we conclude that modelling belowground biomass turnover in these mixed-species meadows using rhizome parameters from a single genus would introduce large uncertainty in belowground meadow productivity and turnover timescales. Rhizome turnover timescale was 1.5–2.2 times longer for *T. hemprichii* compared to the other species. The short rhizome turnover timescale calculated for *C. rotundata* in the open canopy meadow resulted in large differences between meadows for this species (50%), while only small differences were measured for the other species (<5%). As for many studies, due to the lower sampling intensity and larger variation in samples of belowground plant parts we had larger uncertainty around calculated rhizome turnover values compared to leaf turnover values. *Cymodocea* was also the species with the largest relative difference in rhizome biomass between the meadows (>300% in closed canopy compared to open canopy meadow).

Rhizome biomass was 3.7–5.4 times larger than leaf biomass in the meadows, however, leaf production was 2.5–4.2 times faster than rhizome production. A meta-analysis by Duarte and

Chiscano (1999) showed that turnover rates of seagrass aboveground biomass averaged 2.6% per day (median value 1.7%) and belowground biomass averaged 0.77% per day (median value 0.57%). We observed on average fast aboveground turnover rates (3.3–4.0% per day) and slow rhizome turnover rates (0.20–0.46% per day) in our studied meadows. Since seagrass production increases slower than population biomass (Duarte and Chiscano, 1999), this can lead to a slower biomass turnover of dense compared to sparse seagrass meadows. No such general pattern was observed for the three studied species in our meadows. We observed faster rhizome turnover rates for *C. rotundata* in the open canopy meadow (0.46% per day) compared to the closed canopy meadow (0.31% per day). However, for the other early successional species (*H. uninervis*) as well as the late successional species (*T. hemprichii*) no differences were observed between the studied meadows (on average ~0.30% per day and ~0.20% per day, respectively, in both meadows).

The large number of feedbacks and interactions in seagrass systems that can span multiple spatial and temporal scales provides challenges to assess seagrass dynamics (Kendrick et al., 2008). For example, the shoot-specific leaf mass and production of *T. hemprichii* was smaller in the open canopy meadow, compared to the closed canopy meadow. Since no differences in sediment composition or grazing intensity had been observed between the meadows (Vonk, 2008) and there was no difference between belowground biomass and production for *T. hemprichii*, differences in growth strategy were not induced by belowground competition for nutrients nor by herbivory (e.g. Van Tussenbroek et al., 2006). The shoot density of *T. hemprichii* was comparable in both meadows and close to maximum densities observed for other *Thalassia* meadows (cf. Duarte and Chiscano, 1999), while the main difference in species composition between the meadows was the different density of the two smaller species. The main differences between the meadows were thus induced by uncomprehended spatial and temporal feedback mechanisms.

Under disturbance such as heavy grazing and desiccation, seagrass collapse is prevented by continued regeneration from its belowground biomass (roots and rhizomes), counterbalancing aboveground losses (Stapel et al., 1997; Christianen et al., 2013). The rate and ability of regeneration is determined by the turnover rate and biomass of belowground parts. High fragmentation of the meadow with abundant bare gaps, often induced by anthropogenic disturbances and less common by intense grazing on rhizomes,

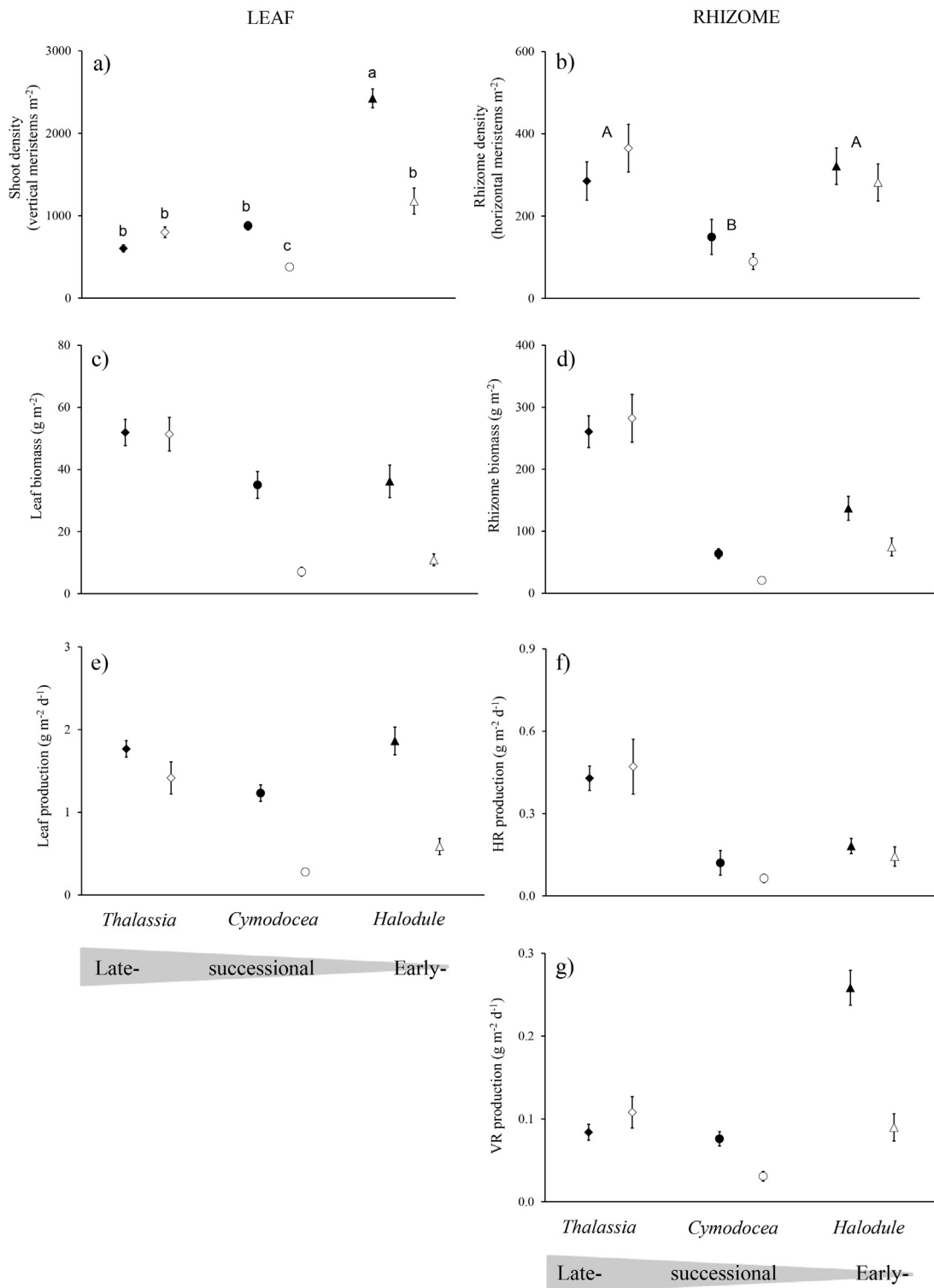


Fig. 4. Overview of aboveground (leaf; left column) and belowground (rhizome; right column) seagrass parameters of the meadows. Measured density of vertical meristems (shoots; a) and horizontal meristems (rhizomes; b), calculated biomass of leaf (c) and rhizome (d), and biomass production of leaf (e), horizontal rhizome (HR; f) and vertical rhizome (VR; g) for *T. hemprichii*, *C. rotundata* and *H. uninervis* in closed and open canopy meadows (symbols as in Fig. 3; panels a–b mean \pm SE, panels c–g mean \pm error).

can enhance erosion by waves and wind and reduce regrowth (Patriquin, 1975; Fonseca and Bell, 1998). This could potentially lead to complete collapse of the seagrass habitat (Christianen et al., 2014). Once completely degraded to open sediments, seagrass recovery can take decades; however, when donor sites are nearby and vegetative growth into the open areas is possible this recovery can be faster (Di Carlo and Kenworthy, 2008; Waycott et al., 2009).

Due to slower growth and longer turnover, Di Carlo and Kenworthy (2008) observed that belowground biomass in disturbed sites (propeller scars) was still 50% lower than in undisturbed sites even after full recovery of aboveground biomass. This indicates that areas that appear to be recovered (i.e. similar aboveground biomass) can still have large differences in rhizome biomass. It can thus be argued that for many (disturbed) seagrass meadows, aboveground biomass

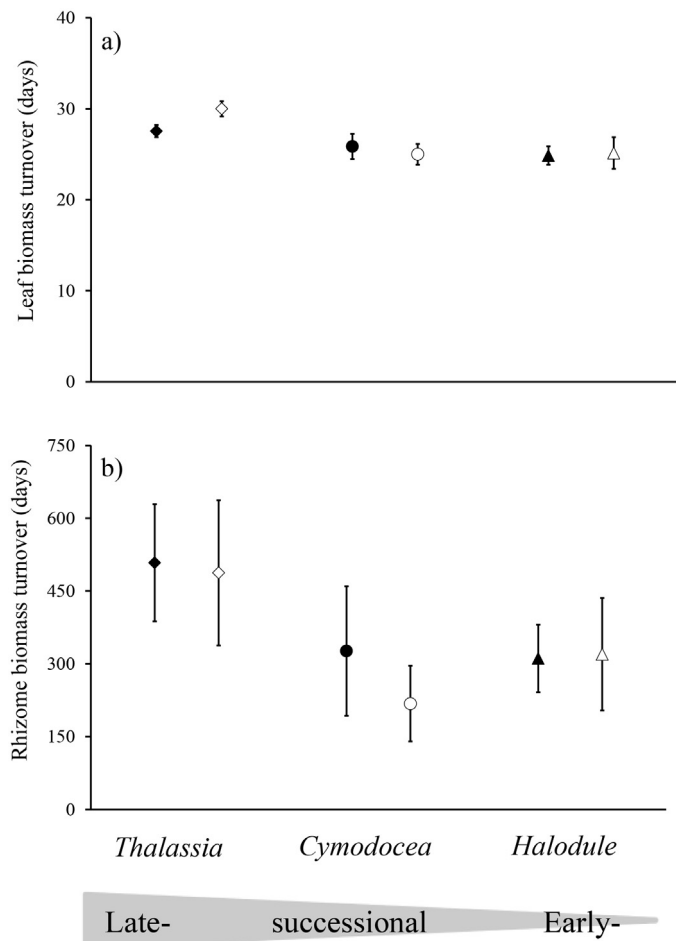


Fig. 5. Seagrass turnover timescales related to leaf biomass (a) and rhizome biomass (b) for *T. hemprichii*, *C. rotundata* and *H. uninervis* in closed and open canopy meadows (symbols as in Fig. 3; mean \pm error).

is no clear indicator of belowground biomass, as also observed in our studied meadows (also vice versa: similar belowground biomass, different aboveground biomass).

Leaf biomass monitoring can be performed at large scales (Knudby and Nordlund, 2011; Lyons et al., 2013) and provides direct information about changes in meadow extent. However, leaf biomass can quickly be replaced for the studied tropical species and observed changes persist only at a short timescale. This can result in a scenario in which a meadow is indicated as a disturbed site, while the seagrasses can recover quickly from this short-term disturbance as long as the belowground biomass is not disturbed (Fig. 6, bottom right panel). No or limited action is needed to support recovery of these meadows and monitoring of recovery will be sufficient. Rhizome biomass has a much longer turnover and changes in rhizome biomass therefore reflect effects on seagrass meadows on a much longer timescale. This could thus result in a scenario in which no change is yet observed in aboveground biomass, while the belowground biomass is already reduced due to long-term disturbances (Fig. 6, top left panel). Only when the aboveground biomass will decline too (Fig. 6, bottom left panel), problems will be detected and measures will be applied. However, recovery of seagrasses in meadows with strongly declined above- and belowground biomass is often very slow (Di Carlo and Kenworthy, 2008) if occurring at all (Irwing, 2013). We therefore support the plea by Christianen et al. (2013) to include also belowground biomass as a proxy for ecosystem services and estimation long-term impact on seagrass meadows. For this purpose, more detailed studies on

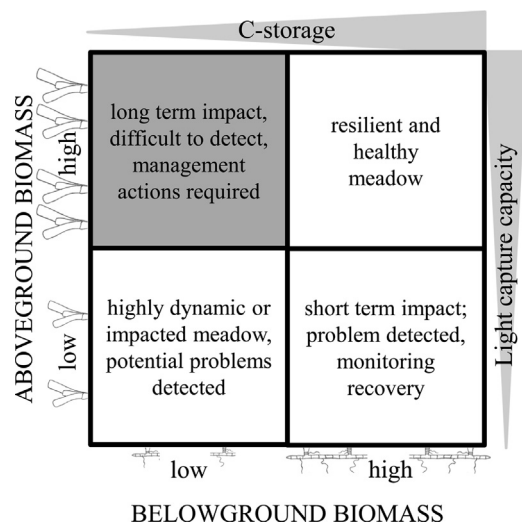


Fig. 6. Ratio between aboveground and belowground biomass reflects impact on seagrass meadows. Productive and resistant meadows are characterized by a high light capture capacity (leaf biomass) and large storage of carbon (rhizome biomass; top right panel). In cases with co-occurring decrease in above- and belowground biomass (or low density meadows like *Halodule* spp.), the leaf-to-rhizome ratio remains comparable, while changes are easily detected and management actions can be applied (bottom left panel). Short term decline of leaf biomass while rhizome biomass is unaffected results in the detection of a potential problem while recovery would not require management actions (bottom right panel). On the other hand, a slow decline in belowground biomass can occur unnoticed, i.e. without a decline in leaf biomass (top right panel). The natural ability of these meadows to recover is diminished and makes them vulnerable to short-term perturbations and a collapse of seagrass biomass and cover.

the aboveground to belowground ratios in undisturbed and disturbed meadows are needed. Since it takes a relatively long time to restore declines in rhizome biomass, we propose that changes in belowground biomass are the most suitable indication to assess prolonged impact of adverse environmental conditions on seagrass meadows.

5. Conclusions

Leaf turnover timescales were comparable for all three species growing in the mixed meadows. For all three species, ranging from early- to late-successional seagrasses, rhizome turnover timescales were much longer compared to leaf turnover. Besides, large differences in rhizome turnover were observed between the late-successional species and the early-successional species. We therefore conclude that for modelling of mixed-species seagrass meadows estimations for belowground indicators are needed for the individual species. Seagrass productivity depends on species and monitoring should include species composition and specific densities to come to a reliable area estimation of production. Modelling seagrass meadows using only aboveground indicators (i.e. leaf biomass or production) will miss important features of meadow dynamics and relative importance of species, since these tropical seagrass species showed much larger differences in belowground indicators (i.e. rhizome biomass and production) compared to aboveground. The slow turnover of belowground parts could provide more insight into seagrass meadow health and ability to withstand prolonged adverse conditions, and we therefore stress the importance of adding belowground parts in seagrass modelling and management programmes.

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