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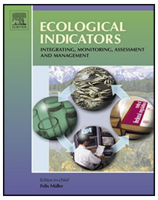

What lies beneath: Why knowledge of belowground biomass dynamics is crucial to effective seagrass management

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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.

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 CO_2 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

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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 Erftemeijer, 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. Erftemeijer 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 m^2 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