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Seagrass leaf element content: A global overview

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ABSTRACT

Knowledge on the role of seagrass leaf elements and in particular micronutrients and their ranges is limited. We present a global database, consisting of 1126 unique leaf values for ten elements, obtained from literature and unpublished data, spanning 25 different seagrass species from 28 countries. The overall order of average element values in seagrass leaves was Na > K > Ca > Mg > S > Fe > Al > Si > Mn > Zn. Although we observed differences in leaf element content between seagrass families, high intraspecific variation indicated that leaf element content was more strongly determined by environmental factors than by evolutionary history. Early successional species had high leaf Al and Fe content. In addition, seagrass leaf element content also showed correlations with macronutrients (N and P), indicating that productivity also depends on other elements. Expected genomes of additional seagrass species in combination with experiments manipulating (micro)nutrients and environmental drivers might enable us to unravel the importance of various elements to sustain productive and flourishing meadows.

1. Introduction

The functions of elements in seagrasses have been examined in various contexts across the world. Seagrass elemental composition has been intensively studied for the macronutrients nitrogen (N) and phosphorus (P) as drivers for productivity and in relation to nutrient limitation and disturbances such as eutrophication (e.g. Duarte, 1990; Fourqurean and Zieman, 2002). Metal content such as copper, nickel and lead have been studied in relation to metal accumulation and the role of seagrass in predicting water quality as bioindicator (Prange and Dennison, 2000; Govers et al., 2014b; Bonanno and Di Martino, 2016). The potential importance of some other nutrients for the productivity and nutrient dynamics of seagrasses has been acknowledged (e.g. for Fe; Romero et al., 2006; Van Tussenbroek et al., 2006), but has only been sparsely investigated (e.g. Duarte et al., 1995; Van Katwijk et al., 2011).

Elements, and micronutrients in particular, have various known functions in plant physiology and metabolism (see Marschner, 2011 for an extensive overview). For seagrasses, knowledge on the functions of various elements besides N and P that may act as nutrients is more limited, yet, several studies have reported on some of these functions (Table 1). Like in all submerged macrophytes, potassium (K), sodium

(Na) and calcium (Ca) are especially important for osmosis regulation (e.g., Touchette, 2007; Olsen et al., 2016). Magnesium (Mg) and iron (Fe) are essential elements involved in photosynthesis, and while Mg is generally abundantly available in seawater (Pilson, 2013), Fe availability can be limited especially in carbonate sediments (Duarte et al., 1995). Zinc (Zn) is involved in protein synthesis (Malea et al., 1995) and manganese (Mn) is important in various redox processes (Jagtap, 1983). Sulphur (S) is used in cell walls as part of sulphated polysaccharides (Olsen et al., 2016) and can accumulate in seagrass tissue (Holmer et al., 2005). Finally, leaf aluminium (Al) and silicon (Si) content have been reported (Malea, 1993; Herman et al., 1996), although no specific functions for these elements are known in seagrasses.

In general, plant stoichiometry is highly variable, plastic, and dependent on the environment (Sternier and Elser, 2002; Marschner, 2011). Plant element ratios closely reflect dominant environmental conditions and potential mechanistic adaptations of how plants deal with adverse environmental conditions (Ågren and Weih, 2012). For example, like all vascular plants growing in seawater, seagrasses have to deal with a medium that contains high ion concentrations. Salt tolerant plants have active uptake mechanisms for certain elements to withstand osmotic pressure and/or to excrete elements that negatively influence cell functioning (Flowers et al., 1977; Subbarao et al., 2003;

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Table 1
Overview of known functions of the studied elements in seagrasses.

Element	Functions in seagrasses	References
K	Elevated levels of K in seagrass tissue balance the osmotic potential in order to prevent dehydration in a saline environment.	Touchette, 2007
Na	Na is elevated in seagrasses, primarily in the vacuoles, to maintain the osmotic potential. At high environmental concentrations Na can replace K for binding sites, so antiporters in the membrane minimize Na accumulation.	Carpaneto et al., 1997; Touchette, 2007; Olsen et al., 2016
Ca	Calcium carbonate is produced by calcifying epiphytes on the seagrass leaves, and by the seagrass itself both internally in the cell wall and on the leaf surface. Calcium is also involved in osmoregulation by reducing Na uptake and increasing K and Ca uptake.	Marbà et al., 2006; Hadi and Karimi, 2012; Enríquez and Schubert, 2014
Mg	Mg is the central atom of the chlorophyll molecule, and therefore essential in photosynthesis. Mg is generally not limiting in seagrass ecosystems. High environmental concentrations can become toxic.	Marschner, 2011; Thangaradjou et al., 2013
S	Toxic sulphide in marine sediments is re-oxidized by seagrass and can be accumulated as elemental sulphur in their tissue. Sulphated polysaccharides in the cell wall facilitate ion and water retention.	Holmer et al., 2005, 2009; Olsen et al., 2016
Fe	Important in electronic transport chain for photosynthesis, about 80% of the total iron is localized in chloroplasts, in case of deficiency PS I drops first. Fe can become limiting especially in tropical carbonate sediments.	Duarte et al., 1995; Marschner, 2011;
Mn	Important in redox processes because of the high number of oxidation states, toxic effects to seagrasses are unknown.	Jagtap, 1983; Thangaradjou et al., 2013
Zn	Important in protein synthesis, high concentrations of Zn can induce seagrass leaf mortality.	Malea et al., 1995; Marschner, 2011;
Al	Seagrasses are commonly unaffected by toxic Al^{3+} concentrations because they have a cytoplasmic pH above 6.0 at which Al is harmless.	Thake et al., 2003
Si	Unknown, but reported limiting in environments where terrestrial runoff is lacking. Si improves the rigidity of macrophytes in dynamic environment and could be involved in salt tolerance.	Herman et al., 1996; Liang et al., 2007; Schoelynck and Struyf, 2016

Hadi and Karimi, 2012). Adaptations of seagrasses to marine conditions might be correlated to evolutionary lineages. Seagrasses made the transition from freshwater to saltwater environments at least three times during evolutionary history (78–40 million years ago) and the four seagrass families together thus form an ecological group rather than a monophyletic clade (Les et al., 1997; Den Hartog and Kuo, 2006). Recent research to the complete genome of *Zostera marina* (Zosteraceae) revealed some of the genes responsible for the physiological and structural adaptations for its return to sea (Olsen et al., 2016). Members from the other seagrass lineages can have evolved similar physiological adaptations, however, differences in leaf element content can be indicative that other lineages have developed alternative mechanisms to flourish under these challenging conditions.

To investigate the role and importance of (micro)nutrients for seagrass physiology and functioning we aimed to provide a global overview of the leaf elemental content (Al, Ca, Fe, K, Mg, Mn, Na, S, Si, Zn) of seagrasses. We therefore collected data for species that belong to the four seagrass families (Zosteraceae, Cymodoceaceae, Posidoniaceae and Hydrocharitaceae) and discuss the potential role of these (micro)nutrients in seagrass physiology and their role in adaptations of seagrass species through evolutionary history. Data were collected from both literature and unpublished field datasets. Since seagrass species distribution often covers a substantial amount of the globe and plants are exposed to a high variety of environmental conditions (e.g. Green and Short, 2003), we hypothesized that environmental conditions drive seagrass element content and expect large variation within and between species. Evolutionary adaptations were expected to be reflected by clear differences in leaf element content between seagrass families (e.g. Broadley et al., 2004). Additionally, differences in leaf element content in species of different successional stage (i.e. climax and colonizer species) could indicate the importance of elements for seagrass productivity. Finally, relations between leaf elements were derived from correlations between the ten studied elements and between these elements and the macronutrients N and P.

2. Materials and methods

2.1. Literature search

Seagrass leaf element data were collected from Web of Science (ISI; search: “seagrass” AND (Sodium OR Potassium OR Calcium OR Magnesium OR Sulphur OR Silicon OR Iron OR Zinc OR Aluminium OR

Manganese)) and Google Scholar®, accessed Dec. 2016. We collected element contents derived from graphs, tables and text of 84 studies (see Supplement 1). Measurements from the same study were averaged if sampled < 1 km apart (measured in Google maps®), if located in the same bay, or if sampled at different seasons. Seagrasses growing in known polluted or impacted sites have been omitted from our database and only natural or reference location have been included. Only leaf element content was used and all values were converted to % dry weight of leaf, yielding in total 605 unique data points. Data included in our database spanned a 40-year period, from 1975 up to 2016. The constructed literature database consisted of seagrass habitats on all continents where seagrasses occur (all but Antarctica); ranging from 59° northern to 36° southern latitudes (Fig. 1). Literature data was obtained for 25 different seagrass species from 28 countries.

2.2. Leaf element analysis

In addition to obtaining data on leaf elemental content from literature, we analysed leaf elemental content of field samples, including nitrogen, phosphorus and carbon (C). In total, 318 leaf samples were collected from twenty locations spanning nine different countries and twelve species belonging to three seagrass families (Table S4). Leaves were carefully cleaned from epiphytes, rinsed and dried (60 °C, 48 h). Dried material was transported back to the Netherlands and ground. Prior to elemental analyses, samples were digested in pressure tubes using H_2O_2 and HNO_3 in an autoclave for 30 min at 121 °C as described by Smolders et al. (2006). Total concentrations of Al, Ca, Fe, K, Mg, Mn, Na, S, Si, Zn and P in seagrass leaf tissue were measured by inductively coupled plasma emission spectrometry (ICP-MS, IRIS Intrepid II, Thermo Electron Corporation, Franklin, USA). Leaf C and N content in this ground leaf material was analysed using an elemental analyser (Type NA 1500 Carlo Erba Thermo Fisher Science, USA), coupled online via an interface (Finnigan Conflo III) to a mass spectrometer (Thermo Finnigan Delta Plus, USA).

2.3. Constructed databases

We constructed a *global seagrass leaf element database* (Supplement 1) based on obtained literature values and from analysed leaf elements. We merged analysed elements of seagrass leaf samples from nearby locations (< 1 km) before adding these average values to the global database (reference “authors’ data” in Supplement 1). The data points

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