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Root architecture of six tropical seagrass species, growing in three contrasting habitats in Indonesian waters

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ABSTRACT

Although several recent studies point at the importance of seagrass roots for nutrient acquisition in oligotrophic tropical ecosystems, remarkably little is known about the root architecture of tropical seagrasses. The present study provides a detailed description of the root architecture of six seagrass species that were extracted from three sites differing in sediment type and nutrient availability (i.e., except for one species that was not present at one of the sites). Number of roots per node, order of root branching, length and diameter per root order, root hair density and length were determined and used to calculate a topological index for the different species and habitats. Root architecture differed strongly between species. The relatively long-lived and slowly-growing species *Thalassia hemprichii* and *Enhalus acoroides* were characterised by short internodes with relatively few unbranched roots per node and a high root hair density. More fast growing species such as *Cymodocea rotundata*, *Cymodocea serrulata* and *Syringodium isoetifolium* had many roots per node, the majority of which were branched. Surprisingly, differences in sediment type and nutrient availability, as present between locations, had little effect on root architecture. We expect this to be due to a relatively homogeneous nutrient distribution at the small scale within water saturated sediments. Overall, all seagrass species had relatively simple branching (topological index > 0.7), comparable to angiosperms of the low temperate salt marsh. We speculate that relatively simple root architecture of plants in flooded systems reflects the need for a minimal path length for oxygen transport from shoots to roots.

1. Introduction

Seagrasses are ecologically well studied and economically important vegetations, that often occur in oligotrophic coastal ecosystems (Duarte and Chiscano, 1999; Costanza et al., 1997; Orth et al., 2006). In such oligotrophic ecosystems, seagrasses have a continuous need for nutrients due to their relatively low efficiency in reusing internal nutrient pools (Stapel and Hemminga, 1997; Hemminga et al., 1999; Romero et al., 2006). Calculations on nutrient balance constraints (Erftemeijer and Middelburg, 1995) and recent observations on nutrient uptake from (particulate) organic matter that is trapped within the sediment (Evrard et al., 2005; Barron et al., 2006; Vonk et al., 2008a; but see Kilminster et al., 2006), underline the importance of seagrass roots for acquiring nutrients in addition to foliar uptake. Moreover, nutrient limitations have been shown to enhance root development (Pérez et al., 1994). However, until now, little work has focused on the form and functioning of seagrass roots (Duarte, 1999).

Architecture (Fitter, 1987, 1991; Fitter et al., 1991, 2002; Bouma et al., 2001a), plasticity (Campbell et al., 1991; De Kroon and Mommer, 2006; but see Kembel and Cahill, 2005) and longevity (Eissenstat and Yanai, 1997; Bouma et al., 2001b) have been identified as important factors in determining the overall nutrient capture and efficiency (nutrient gain per carbon expenditure) of root systems. Root architecture and root plasticity may offer seagrass species advantages in acquiring nutrients in contrasting sediment types that differ in nutrient availability, such as e.g. carbonaceous nutrient-poor sediments as well as in more muddy and nutrient-rich sediments (Erftemeijer and Middelburg, 1993; Kamp-Nielsen et al., 2002). However, roots are also important for anchoring seagrasses and below-ground biomass distributions are

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known to respond to substrate stability and hydrodynamic exposure (Peralta et al., 2006; Di Carlo et al., 2007). Thus, for seagrasses, root architecture could be determined by other factors than nutrient availability. So far published basic descriptions on seagrass root architecture (e.g., Kuo and McComb, 1989; Duarte et al., 1998; Cambridge, 1999; Oliva et al., 2007) lack necessary quantitative detail. Hence, the primary objective of our study was to provide a detailed quantitative description of the root architecture for six seagrass species that are commonly found in oligotrophic tropical environments.

Root architecture is commonly characterised using a link-based topological model, as introduced by Fitter (1987). This model allows root branching to be classified as herringbone (or monopodial) vs. dichotomous (or sympodial, Fitter and Stickland, 1991). According to the theory (Fitter, 1991), a herringbone branching is favourable to slow-growing species living in nutrient poor environments, as such branching minimizes inter-root competition. Dichotomously branched roots are less expensive to construct, but will cause more inter-root competition. Hence, dichotomously branched roots are considered to be favourable to fast-growing species from nutrient-rich habitats (cf. Fitter and Stickland, 1991; Berntson and Woodward, 1992; Taub and Goldberg, 1996). Thus we hypothesise that the roots of slow-growing seagrass species that inhabit oligotrophic environments will have herringbone branching, whereas faster growing seagrass species may have more complex root branching to facilitate soil exploration.

Root branching and root plasticity have been found to be negatively correlated with flood resistance (Bouma et al., 2001a; Jansen et al., 2005), suggesting that aquatic plant species may have a relative simple and conservative root architecture. The latter may

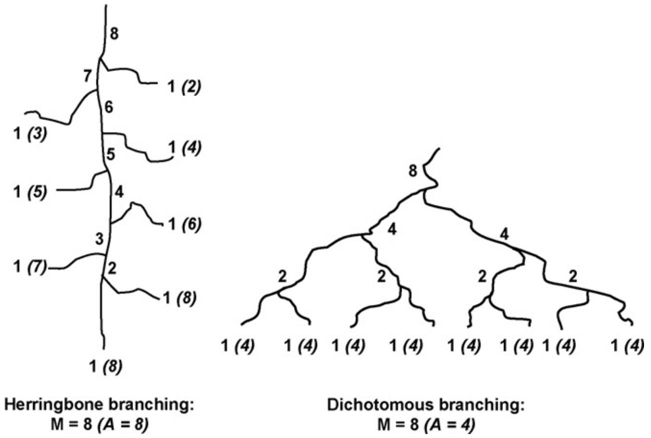

Fig. 1. Schematic representation of a link-based method to describe root topology (cf. Fitter, 1987, 1991). A link is defined as a piece of root between two branching points (interior link) or between a branch and a meristem (exterior link). The magnitude (*M*) of an individual link within the root system represents the total number of root segments connected to the shoot through that specific link (indicated by numbers outside parentheses). Because exterior links do not connect any other root segment, their magnitude is by definition 1. The magnitude of an interior link equals the sum of the magnitudes of the two links that are joined together. The magnitude of the overall root system will thus represents the total number of meristems in a root (i.e., equal to the total number of exterior links). The altitude of the overall root system (*A*) describes the number of links in the longest path from an exterior link to the most basal link of the root system (i.e., where the root connects to the shoot). The altitude can also be calculated for individual root branches, as indicated by italic numbers within parentheses. The topological index of a root system is defined as Log altitude/Log magnitude.

Table 1
p values as obtained by analysis of variance (ANOVA) for all parameters shown in Table 3 and Figs. 2–7. For each parameter, we tested for a species effect, a sediment effect and the interaction term. The degrees of freedom (df) are indicated.

Parameter	Data presented in	Species effect		Sediment effect		Species × Sediment interaction		df residuals
		df	*p*	df	*p*	df	*p*	
C content (%)	Table 3	4	0.0001	2	0.0001	8	0.0001	70
N content (%)	Table 3	4	0.0001	2	0.0001	8	0.0001	70
P content (%)	Table 3	4	0.0001	2	0.1625	8	0.0078	70
CNratio	Table 3	4	0.0001	2	0.0001	8	0.0001	70
CPratio	Table 3	4	0.0001	2	0.0506	8	0.0092	70
Nodes with roots (fraction)	Fig. 2	4	0.0001	2	0.0062	8	0.0001	46
Branched root (fraction)	Fig. 2	4	0.0001	2	0.1695	8	0.1097	45
Maximum branching order	Fig. 2	4	0.0001	2	0.7954	8	0.678	47
Branched roots per node	Fig. 3	4	0.0001	2	0.0001	8	0.0001	47
Unbranched roots per node	Fig. 3	4	0.0001	2	0.8045	8	0.4145	47
Length branched roots (cm)	Fig. 3	1	0.0001	2	0.0001	2	0.0001	18
Length unbranched roots (cm)	Fig. 3	3	0.0001	2	0.2976	6	0.0001	34
RL main axis relative length (%)	Fig. 4	4	0.0001	2	0.1453	8	0.0455	109
1st-order lateral relative length (%)	Fig. 4	1	0.1034	2	0.1339	2	0.6428	42
2nd-order lateral relative length (%)	Fig. 4	1	0.0017	2	0.8149	2	0.2444	31
1st-order lateral length (cm)	Fig. 4	1	0.0006	2	0.0257	2	0.4499	42
2nd-order lateral length (cm)	Fig. 4	1	0.0787	2	0.4049	2	0.0852	33
Topological index	Fig. 5	1	0.0001	2	0.9948	2	0.092	42
Main axis diameter (mm)	Fig. 6	4	0.0001	2	0.0033	8	0.0001	108
1st-order diameter (mm)	Fig. 6	1	0.0001	2	0.2426	2	0.4319	42
2nd-order diameter (mm)	Fig. 6	1	0.0192	2	0.0089	2	0.8681	31
3rd-order diameter (mm)	Fig. 6	0		1		1		11
Main axis – root hair density (mm^{-1})	Fig. 7	4	0.0001	2	0.1341	8	0.0008	103
1st-order – root hair density (mm^{-1})	Fig. 7	1	0.0001	2	0.0142	2	0.0001	41
2nd-order – root hair density (mm^{-1})	Fig. 7	1	0.0001	2	0.0001	2	0.0011	29
3rd-order – root hair density (mm^{-1})	Fig. 7	0		1		1		9
Main axis – root hair length (mm)	Fig. 7	4	0.0001	2	0.0138	8	0.0029	103
1st-order – root hair length (mm)	Fig. 7	1	0.0026	2	0.0003	2	0.1317	41
2nd-order – root hair length (mm)	Fig. 7	1	0.1243	2	0.0002	2	0.0069	29
3rd-order – root hair length (mm)	Fig. 7	0		1		1		9