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Effects of light and biomass partitioning on growth, photosynthesis and carbohydrate content of the seagrass *Zostera noltii* Hornem

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Abstract

Plants of the seagrass *Zostera noltii* were cultured in the laboratory (mesocosms) for two weeks to assess the effect of above: below-ground (AG/BG) biomass ratios and light on growth, photosynthesis and chemical composition. Experimental plant units (EPUs) with different proportions between AG and BG biomass were obtained from plants of the same size (containing 6 shoots and 5 internodes) by excising 0–5 shoots. The EPUs maintained the proportions in AG/BG biomass ratios during the experiment. While growth rate was unaffected by biomass partitioning at high light, maximum growth at low light was recorded in plants with low AG/BG ratios. The production of shoots and rhizomes showed a compensatory morphological response depending on the initial AG/BG proportions regardless of the light level. While shoot production, estimated as shoot appearance rate, was high at low AG/BG ratios and minimal under high AG/BG values, rhizome production, estimated as internode appearance rate and internode elongation rate, was maximal under high AG/BG proportions and decreased towards lower AG/BG ratios. This rhizomatic response was observed for secondary rhizomes and not for primary ones. In contrast to morphological response, no significant differences were detected in maximum electron transport rates (ETRm) among the different shoots in the plant. However, mean values of ETRm in plants were affected by biomass partitioning and light. EPUs grown in low light increased the sucrose stored in shoots as the AG/BG biomass ratios decreased; however, EPUs grown at high light showed no effect of biomass partitioning on sucrose levels. In conclusion, shoots excision by experimental manipulation caused a compensatory morphological response in plants while photosynthetic performance remained almost unaffected.

Keywords: Apical dominance; Biomass partitioning; Clonal integration; Growth; Light; *Zostera noltii*

1. Introduction

Seagrasses are aquatic angiosperms that may complete their life-cycle fully submerged in seawater (Arber, 1920; Hemminga and Duarte, 2000). They represent an ecologically important structuring element of the ecosystem and a major source of primary production in shallow waters worldwide (Hemminga and Duarte, 2000). The possession of a root–rhizome system offers seagrasses competitive advantages compared to seaweeds: (1) anchorage in soft substrata, (2) assurance of a nutrient supply from sediment pool, and (3) resource

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storage (Hemminga, 1998). However, since below-ground tissues are heterotrophic (i.e. sinks) they depend exclusively on light-driven basipetal translocation of photosynthates and oxygen (Smith et al., 1984; Kraemer and Alberte, 1993; Zimmerman and Alberte, 1996).

Plant responses to light encompass a mixture of adaptations at biochemical (Wiginton and McMillan, 1979; Alcoverro et al., 1999; Moore and Wetzel, 2000; Brun et al., 2003a) and physiological (Abal et al., 1994; Grice et al., 1996) levels. Furthermore such adaptations frequently affect growth rate and plant architecture (i.e., individual morphological features), meadow morphological characteristics (i.e., canopy height, shoot density, above to below-ground (AG/BG) biomass ratios, etc.) and seagrass distribution (Backman and Barilotti, 1976; West, 1990; Fitzpatrick and Kirkman, 1995; Krause-Jensen et al., 2000; Brun et al., 2002, 2003b; Peralta et al., 2002, 2003).

Experimental studies on seagrass shoot responses to light are relatively common (see references cited above). In comparison, those focussed on below-ground (rhizome–roots) growth and branching pattern (plant architecture) are scarce (Olesen and Sand-Jensen, 1993; Peralta et al., 2002; Brun et al., 2006b) or observational and poorly documented (Hemminga and Duarte, 2000; Brun et al., 2003b, in press). Besides space occupation role of the rhizomes, the biomass partitioning (i.e. AG/BG ratio) becomes essential for seagrass carbon budgets because below-ground tissues are the main storage compartments but, as heterotrophic tissues, they rely on photosynthates provided by shoots. Thus, several studies have revealed that the seagrass *Zostera noltii* has a relatively high capacity to cope with environmental stress by adapting its morphology (Vermaat and Verhagen, 1996; Peralta et al., 2002, 2005, 2006; Brun et al., 2003c, 2006b). However, morphological plasticity has several costs and risks, since it may increase the fitness of the phenotype to some environmental stresses but may reduce the fitness in other underlying traits (de Witt et al., 1998). For instance, a great reduction in the AG/BG ratio of *Z. noltii* was recorded as a response to human-induced increase in hydrodynamic conditions. This change in biomass partitioning improved the anchoring capacity of the plants but may imbalance the source/sink ratio for carbon, and thus, to increase the vulnerability of plants under sudden low light conditions (Peralta et al., 2005). As light is the main driving force involved in this process, the benefit of having a root–rhizome system becomes a drawback when the quantity of light reaching the canopy decreases and the sediment becomes anaerobic (Hemminga, 1998). To what extent seagrasses are able to respond to reduced light through changes in the biomass partitioning between shoots and root–rhizomes is still unknown (Hemminga, 1998).

The response of a seagrass plant (usually composed by a variable number of shoots and internodes) to light may depend on the number of shoots recruited by the plant, because connected shoots share resources among them (Tomasko and Dawes, 1989; Marbà et al., 2002). Furthermore, apical shoot influences the nutrient status of adjacent-connected shoots due to its higher metabolic activity and hormone levels (Phillips, 1975; Cline, 1997). Consequently, the interrelation between both clonal traits (clonal integration and apical dominance) may modify the response of the whole plant and individual elements (shoots and internodes) against the same environmental stimulus. The acclimation of *Z. noltii* to environmental stress involves several plant-properties (apical dominance, clonal integration, and plant morphological variability) at different organization levels (leaves, shoots, and whole plant) that must be considered when studying acclimation processes.

The aim of this work was to assess the combined effect of light and AG/BG biomass ratios (artificially generated) on growth, photosynthetic estimators and biochemical composition of the seagrass *Z. noltii* taking into account the apical dominance and the clonal integration. The results showed a compensatory morphological response between above (AG) and below-ground (BG) parts that can be an important adaptation to cope with variable AG/BG ratios.

2. Materials and methods

2.1. Plant material

Z. noltii Hornem. plants were collected from an intertidal sand bed at El Bajo de la Cabezuela, Cádiz (36° 32′ N, 6° 15′ W) in summer when *Z. noltii* is in its maximum growth phase (Brun et al., 2003a). Plants were gathered carefully to keep below-ground parts intact and transported to the laboratory in an ice-chest. Previous to any experimental manipulation, plants were gently rinsed in seawater and visible epiphytes were removed by scraping. Eighty plants, with 6 shoots and 5 internodes, were selected and acclimated to the laboratory conditions in a clear aquarium for 24–48 h. All plants were sized and weighted on fresh basis (FW). Twenty plants, of the 80, were randomly chosen as representative of the initial experimental conditions (initial plants).

2.2. Experimental design

The effects of light availability and biomass partitioning (i.e. above to below-ground biomass ratio, AG/BG)