

Direct effects of current velocity on the growth, morphometry and architecture of seagrasses: a case study on *Zostera noltii*

Gloria Peralta^{1,2,*}, Fernando G. Brun^{1,2}, J. Lucas Pérez-Lloréns², Tjeerd J. Bouma¹

¹Netherlands Institute of Ecology (NIOO-KNAW), Center for Estuarine and Marine Ecology, PO Box 140, 4400 AC Yerseke, The Netherlands

²Department of Biology, University of Cadiz, 11510 Puerto Real (Cadiz), Spain

ABSTRACT: Hydrodynamics affect and are affected by the presence of seagrasses. Previous studies have suggested that such effects could modify the capacity of these marine plants to cope with adverse environmental conditions. However, the direct impact of hydrodynamics on seagrass performance remains undemonstrated. In this study, the direct effects of current velocity on seagrasses were examined by cultivating single plants of *Zostera noltii* in 12 flume tanks with contrasting current velocities (0.01, 0.10 and 0.35 m s⁻¹), while avoiding differences in other abiotic factors. Our results demonstrated that current velocity directly affects (1) dynamic plant parameters such as growth, elongation, recruitment and plastochrone index (*PI*), (2) the morphometry of leaves, rhizome and roots and (3) the architecture of *Z. noltii* plants. Growth, elongation and recruitment rates increased significantly with increasing velocities, whereas the *PI* was significantly reduced. The resulting morphotypes appeared to represent acclimation to hydrodynamic stresses: they had (1) an improved anchoring system and (2) a reduced risk of shoot breakage. That is, at high velocity, the root system was enlarged, the aboveground/belowground biomass ratio (AG/BG ratio) was reduced and the cross sections of leaves and rhizomes increased.

KEY WORDS: Seagrass · Hydrodynamics · Acclimation · Plant morphometry · Growth · Flume tank

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INTRODUCTION

Seagrass meadows have been widely recognized as highly important coastal systems that provide valuable ecosystem services (Costanza et al. 1997) and make a significant contribution to the net ecosystem production of coastal areas (Duarte & Cebrian 1996). An important component of the ecosystem services provided by seagrasses is related to the way they affect hydrodynamic forces. Seagrasses may reduce current velocity (Gambi et al. 1990, Koch & Gust 1999) and attenuate wave energy (Koch & Gust 1999) by extracting momentum from the water within the canopy. The extent of this energy reduction has been previously related to the architectural properties of the meadow. Characteristics such as shoot density (Gambi et al.

1990, Bouma et al. 2005a), shoot stiffness (Bouma et al. 2005a) and the volume of the water column occupied by seagrasses (Koch 2001) are the main variables that have been related to the loss of hydrodynamic energy within vegetation.

Less intensively studied, but a potentially equally important aspect, are the feedback effects that the reduced hydrodynamic energy within seagrass beds may have on the performance of these marine plants (see references in Koch 2001). On one hand, it is well known that hydrodynamic energy from waves or currents that is too high will restrict seagrass distribution (e.g. see Fonseca & Bell 1998, van Katwijk & Hermus 2000, Schanz & Asmus 2003), and on the other hand, that some water movement is needed to sustain growth (Ackerman & Okubo 1993, Koch 1994, Thomas & Cornelisen 2003). However, the ef-

*Email: gloria.peralta@uca.es

fects of intermediate ranges of velocities are not well understood. Both positive and negative effects have been described for changes within a moderate range of water velocity. For example, moderate decreases in velocity may indirectly increase light availability by reducing self-shading on undeflected canopies and by increasing water transparency as sediment deposition increases (see references in Koch 2001). However, moderate increases in hydrodynamics may directly favor the leaf uptake rates by reducing the diffusive boundary layer (DBL) at leaf surfaces, which is considered an important limiting step for seagrass primary production in sheltered waters (Koch 1994, Stapel et al. 1996, Thomas & Cornelisen 2003).

In addition to the aforementioned hydrodynamic effects on processes that may affect growth, previous studies also revealed that hydrodynamics may influence plant allometry. For example, seagrass plants were found to develop larger root/rhizome systems when growing in environments with higher hydrodynamic energy (Fonseca & Bell 1998, Peralta et al. 2005). Leaf size may also change in response to changes in hydrodynamic conditions. For example, the fast-growing seagrass species *Zostera noltii* developed a small-leaved morphotype after local hydrodynamics increases (Schanz & Asmus 2003, Peralta et al. 2005). Of course, such morphological changes will directly affect the growth efficiency of seagrass plants by altering the ratio between photosynthetic and non-photosynthetic tissues. This ratio is of crucial importance for seagrass plants' ability to cope with adverse environmental conditions (Hemminga 1998), and such morphological changes may make seagrass more vulnerable to light stress. Hence, it would be useful to obtain a better understanding of the effect of hydrodynamics on seagrass growth and allometry.

Although it is well recognized that hydrodynamics can affect the growth, architecture and allometry of seagrasses, the direct or indirect nature of this effect remains undemonstrated. Previous data originated from field observations and/or field manipulations, where many external variables remained uncon-

trolled. Therefore, these studies cannot be used to confirm whether hydrodynamics have a direct role on seagrasses, i.e. by affecting the seagrass ecophysiology, or an indirect role via other abiotic variables. Hence, the objective of the present study was to assess if hydrodynamics may have a direct effect on the growth, morphology and architecture of seagrasses. For clarity, we define indirect effects as those effects that are caused by the modification of abiotic conditions in response to current velocity (e.g. velocity effects on nutrient concentrations in the water column, turbidity effects on light availability etc); direct effects are defined as those effects that are directly related to hydrodynamics (e.g. drag forces, thickness of the boundary layer etc). We used *Zostera noltii* as a model species because of its high growth rate and large morphometric plasticity (Peralta et al. 2005).

We hypothesize that, below the limit of plant detachment, hydrodynamic conditions are important for seagrass performance, and cause plants to change morphotype as an acclimative response to ambient hydrodynamics. We tested our hypothesis by growing single plants of the small and fast growing seagrass *Zostera noltii* under 3 contrasting hydrodynamic regimes, while all other physico-chemical variables were constant. Subsequently, architectural and dynamic properties of the *Z. noltii* plants were compared. The implications of the acclimative response are discussed in a broad context, including possible interactions with other abiotic variables and the conditions necessary to extrapolate plant-based results to the population level.

MATERIALS AND METHODS

Experimental design. Twelve small flume tanks (Fig. 1a) were used to expose *Zostera noltii* plants over a period of 4 wk to 3 contrasting current velocities (i.e. 4 flume tanks per current velocity). The low (LV), medium (MV) and high velocities (HV) were adjusted to approximately 0.01, 0.10 and 0.35 m s⁻¹, respec-

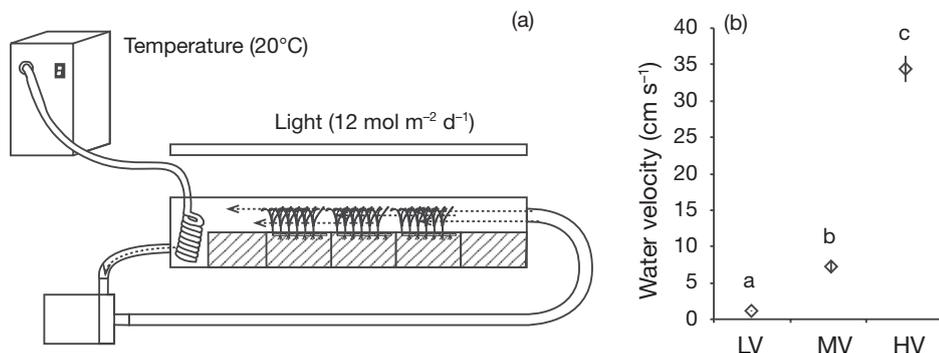


Fig. 1. (a) Schematic of flume tank set-up used to obtain contrasting current velocities. (b) Velocities achieved in low (LV), medium (MV) and high (HG) current velocity treatments

tively, using individual water pumps for each flume. The selected velocities were a good approximation of the lowest and highest velocities that might be found at vegetated intertidal areas in the Oosterschelde estuary, south-west Netherlands (Bouma et al. 2005b). The flume tanks were constructed as independent rectangular stainless-steel containers (13 × 26 × 130 cm) that could each hold 5 stainless-steel pots (12 × 12 × 25 cm) (Fig. 1a). All pots were completely filled with a homogeneous mix of clay, sand and gravel, to obtain a smooth surface area. In each flume, *Z. noltii* units (see next section) were cultured in the 3 central pots. Light and temperature conditions were constant over the duration of the experiment (12 mol photons m⁻² d⁻¹ and 20°C). To prevent any differences in water column nutrient availability due to current velocity effects on sediment flux, all sediment was thoroughly washed and the water column frequently renewed in each flume tank (max. 2 d) using 2 µm filtered Oosterschelde water. Over the course of the experiment, current velocities were measured on top of each pot for each flume, using an Acoustic Doppler Velocimeter (Nortek). These measurements confirmed that the experimental treatment worked well (Fig. 1b).

Biological variables. *Zostera noltii* plants were cultured in the 3 central pots of every flume tank, using 6 plant units per pot (i.e. 18 plants per flume tank). As a plant unit, we initially selected an apical shoot with its first rhizome segment (i.e. first internode). The overall growth period of the experiment was 4 wk. For fast growing *Z. noltii* plants, this represents a significant growth period that should allow more than a 100% increase in biomass, and represents approximately 20% of the length of the growth season in The Netherlands. At the beginning and end of the experiment, morphometric measurements of the plant units were taken, including: length, width and thickness of every leaf, length and 2 main diameters on internodes, and total length on every root. At the end of the experiment, we measured for each plant the dry weight (DW) of corresponding modules (i.e. leaves, rhizome and roots), which allowed the aboveground/ belowground biomass ratio (AG/BG ratio) to be calculated.

For leaves and rhizomes, the cross-sections were estimated according to Eqs. 1 and 2:

$$L_{\text{sec}} = \frac{LW}{2} \cdot \frac{LTh}{2} \cdot \pi \quad (1)$$

$$I_{\text{sec}} = \frac{D_1}{2} \cdot \frac{D_2}{2} \cdot \pi \quad (2)$$

where L_{sec} is leaf cross-section (mm²), I_{sec} is internodal cross-section (mm²), LW is leaf width (mm), LTh is leaf thickness (mm), and D_1 and D_2 are the 2 main diameters of the internode. From previous measurements,

architectural and dynamic properties of the *Zostera noltii* plants were estimated according to Peralta et al. (2000) using the following equations:

$$LER = \frac{\sum_{i=1}^n [(LL_{i,f} - LL_{i,0}) > 0]}{t_f - t_0} \quad (3)$$

$$LLR = \frac{\sum_{i=1}^n [(LL_{i,f} - LL_{i,0}) > 0] - \sum_{i=1}^n LL_{i,0}}{t_f - t_0} \quad (4)$$

$$IER = \frac{\sum_{i=1}^n (IL_{i,f} - IL_{i,0})}{t_f - t_0} \quad (5)$$

$$RER = \frac{\sum_{i=1}^n (RL_{i,f} - RL_{i,0})}{t_f - t_0} \quad (6)$$

$$PI = \frac{t_f - t_0}{\sum NL_a} \quad (7)$$

where (Eq. 3) LER is leaf elongation rate (cm plant⁻¹ d⁻¹), LL is leaf length (cm) and n is number of modules (leaves in this case) at the end of the study period ($t_f - t_0$); (Eq. 4) LLR is leaf loss rate (cm plant⁻¹ d⁻¹) and m is number of leaves lost during the study period ($t_f - t_0$); (Eq. 5) IER is internodal elongation rate (mm plant⁻¹ d⁻¹), IL is internodal length and n the number of modules (internodes in this case) between the punched leaf and the apical meristem during the study period ($t_f - t_0$); (Eq. 6) RER is root elongation rate (mm plant⁻¹ d⁻¹), RL is root length resulting from the sum of all roots presents at node i , and n is the number of modules (nodes in this case) between the punched leaf and the apical meristem; (Eq. 7) PI is plastochrone index, calculated as the number of days elapsed between the appearance of 2 consecutive leaves from the apical meristem (NL_a).

Elongation rates of leaves (LER), rhizome (IER) and roots (RER) were transformed into biomass growth rate (GR , mg DW plant⁻¹ d⁻¹), using the length/DW ratio of each plant:

$$GR = \left(LER \cdot \frac{DW}{LL} \right) + \left(IER \cdot \frac{DW}{IL} \right) + \left(RER \cdot \frac{DW}{RL} \right) \quad (8)$$

where DW/LL , DW/IL and DW/RL are the DW/length ratios for leaves, internodes and roots, respectively.

Finally, a shoot recruitment rate (SRR ; shoots shoot⁻¹ mo⁻¹) was estimated:

$$SRR = \frac{\sum M_A}{\sum M_0} \cdot \frac{30}{(t_f - t_0)} \quad (9)$$

where $\sum M_A$ is the number of new meristems activated during the studied period ($t_f - t_0$), and $\sum M_0$ the number

Table 1. *Zostera noltii*. Nested ANOVA of architectural and dynamic variables and experimental hydrodynamic conditions (effect shown: velocity treatment). Where necessary, transformation of date indicated as log, $\sqrt{\quad}$, $\sqrt{\log}$ or $\sqrt{x^{-1}}$. * $p < 0.05$, ns: not significant

Variables	Data transformed	F, df	p
Water velocity	$\sqrt{\quad}$	2292.9, 2	*
Leaf length (LL)		1.50, 2	ns
Leaf cross section (L_{sec})	log	9.45, 2	*
Internodal length (IL)		3.68, 2	ns
Internodal cross section (I_{sec})		17.52, 2	*
Root length (RL)		4.43, 2	*
Total root length (TRL)	log	14.09, 2	*
AG/BG	$\sqrt{\log}$	5.29, 2	*
Leaf elongation rate (LER)	log	6.65, 2	*
Internodal elongation rate (IER)	log	8.79, 2	*
Root elongation rate (RER)	log	11.60, 2	*
Growth rate (GR)	log	30.63, 2	*
Plastochrone index (PI)	$\sqrt{x^{-1}}$	7.24, 2	*
Leaf loss rate (LLR)		2.37, 2	ns
Shoot recruitment rate (SRR)	$\sqrt{\quad}$	8.20, 2	*

of meristems existing at time zero (t_0). The activation of a new meristem was recognized by the appearance of a second leaf at the same node.

To assess the existence of dependence between the AG/BG ratio and PI, maximum values of AG/BG ratio

were plotted against the integer values of PI. For this plot, the characteristics of individual plants were grouped by similar PI. Each group included plants within an integer range of PI values, i.e. for $PI = 5$ d, all plants for which $5 \leq PI < 6$ d were grouped. Subsequently, the maximum value of the AG/BG ratio was obtained by adding SD to mean AG/BG ratios for each group of similar PI.

Statistical analysis. The effects of the current velocity treatment were tested using nested ANOVA, followed by post hoc Tukey tests, or Tukey's unequal N Honestly Significant Difference (HSD) test for multiple comparisons when necessary (Sokal & Rohlf 1995) (Table 1). In the nested ANOVA, the sources of variation were (1) velocity treatment and (2) flume tank. The source of variation 2 (flume tank) was considered as the random variable and was nested in the source of variation 1 (velocity treatment). Therefore, results shown only correspond to Variable 1 (Table 1). Heteroscedastic data were transformed when necessary (see Table 1). In all cases, the significance level was set at 5% probability.

RESULTS

The flume design (Fig. 1a) allowed us to culture *Zostera noltii* plants under strongly contrasting hydro-

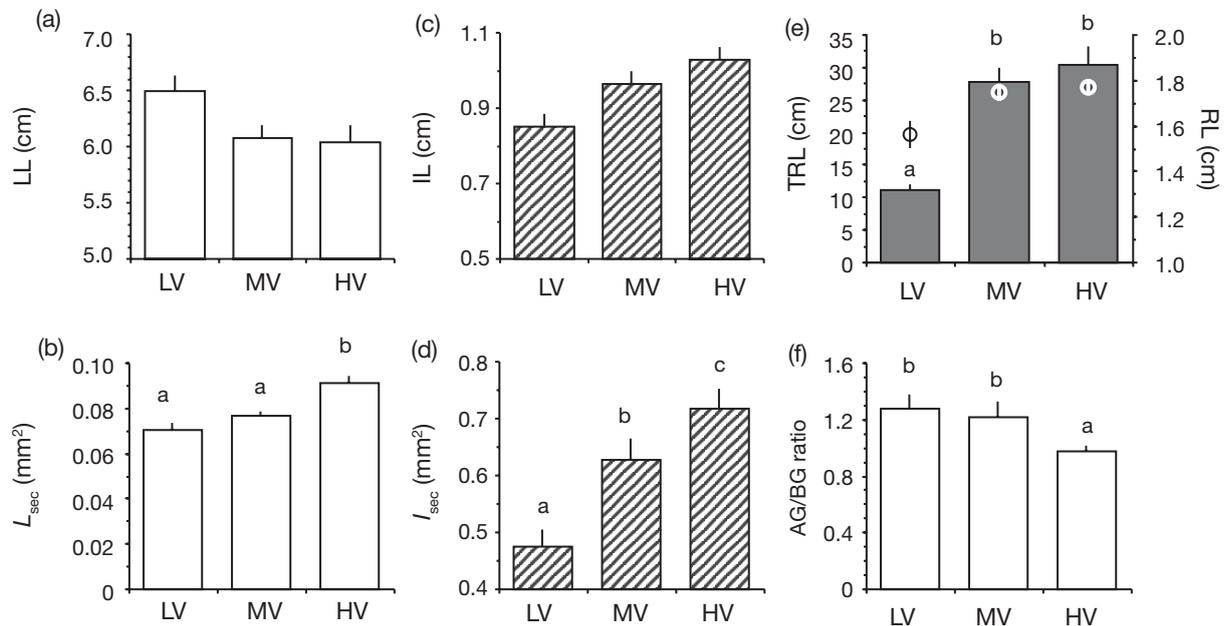


Fig. 2. *Zostera noltii*. Architectural properties of plants cultivated in LV, MV and HV treatments. Averaged (a) leaf length (LL), (b) leaf cross section (L_{sec}), (c) internodal length (IL), (d) internodal cross section (I_{sec}) (e) sum of root length per plant (TRL: columns) and root length (RL: ϕ), (f) aboveground/belowground ratio (AG/BG ratio). Bars: SE; a,b,c: significant differences among treatments (see Table 1)

dynamic conditions, by significantly altering the current velocity (Table 1) while maintaining other environmental variables (e.g. light availability, water temperature and nutrient concentrations) at similar levels in the water column. For the LV, MV and HV treatments, averaged values of water velocity were 0.01, 0.07 and 0.34 m s⁻¹ respectively (Fig. 1b). Our detailed growth analysis revealed that a 4 wk exposure to these contrasting current regimes was enough to induce significant differences in the leaf, rhizome and root morphology in *Z. noltii* (Table 1, Fig. 2) as well as within the variables that describe dynamic plant growth (Table 1, Fig. 3).

The leaves of the plants growing in MV and HV treatments tended to be slightly shorter than those growing in the LV treatment, but only plants growing at HV showed a significantly larger leaf cross section (Table 1, Fig. 2a,b). The root/rhizome system showed a clear increase in its morphometric parameters with increasing water velocity. The cross section of the internodes was most responsive to current velocity, increasing significantly from LV to HV (Table 1, Fig. 2c,d). The roots were significantly longer and more numerous at MV and HV than at LV (Table 1, Fig. 2e). The combination of all these morphometric differences (leaves, internodes and roots) resulted in a significantly lower AG/BG ratio at HV than at LV or MV (Table 1, Fig. 2f).

The observed changes in morphology were supported by growth differences at all levels. The elongation rates of leaves, rhizomes and roots increased significantly with increasing water velocity, whereas *PI* showed a significant decrease at HV (Table 1, Fig. 3a,e). In contrast, leaf loss rate was not significantly affected (Table 1), and exhibited low values (mean ± SE) of 0.81 ± 0.03, 1.01 ± 0.04 and 0.96 ± 0.06 cm plant⁻¹ d⁻¹ for LV, MV and HV respectively. Elongation patterns were similar for leaves, rhizomes and roots: elongation tended to increase from LV to HV (Fig. 3a,c). Similar to observations of morphology, rhizomes were most sensitive to changes in current velocity with significant differences evident among the 3 velocity levels (Fig. 3b). Differences in elongation rates agreed with observed differences in *GR*. The *GR* was significantly differ-

ent between every treatment level, increasing from LV to HV (Table 1, Fig. 3d). However, only plants growing at HV showed a significantly lower *PI* and a significantly higher shoot recruitment (Table 1, Fig. 3e,f).

Despite the evident contribution of every module (i.e. leaf, rhizome or roots) to the decrease in the AG/BG ratio in the HV treatment, *PI* and shoot recruitment were the only dynamic variables that exhibited exactly the same pattern as that observed for the AG/BG ratio. Despite all significant differences found at dynamic and morphometric levels, HV plants were only significantly different to both the LV and MV plants when *PI*, shoot recruitment and AB/BG ratio were compared (Table 1, Figs. 3 & 4). Accordingly, we observed a strong positive correlation between the maximum threshold for the AB/BG ratio and *PI* (Fig. 4).

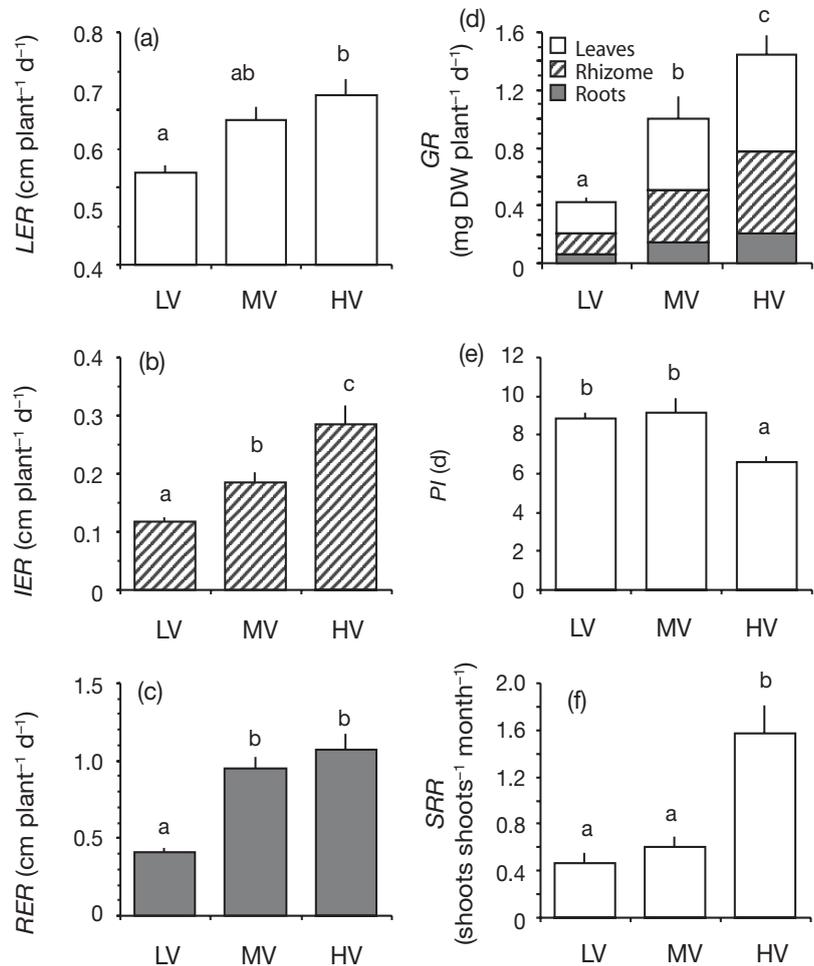


Fig. 3. *Zostera noltii*. Dynamic properties of plants cultivated in LV, MV and HV treatments. Averaged values of (A) leaf elongation rate (*LER*), (b) internodal elongation rate (*IER*), (c) root elongation rate (*REL*), (d) plant growth rate (*GR*), (e) plastochrone index (*PI*), (f) shoot recruitment rate (*SRR*). Bars: SE; a,b,c: significant differences among treatments (see Table 1)

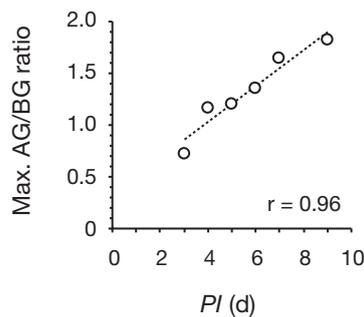


Fig. 4. *Zostera noltii*. Correlation between maximum AG/BG ratio and *PI*. Maximum values of AG/BG ratio were obtained as mean + SD of individual plants grouped by similar *PI* values (see 'Materials and methods')

DISCUSSION

This study demonstrated for the first time the direct effects of hydrodynamics on seagrass growth and morphology, achieved using flume tanks that excluded indirect effects of nutrient concentration and light availability. In the following, we discuss in a broader and more general context (1) which seagrass properties may be affected by altered hydrodynamic conditions, (2) the possible mechanism that may be involved in inducing these changes and (3) the possible consequences of such changes for tolerating (at the population level) other abiotic conditions, which in the field may co-vary with current velocity.

Plant responses to current velocity: dynamic variables, morphometry and architecture

Increased current velocity affected several dynamic plant variables by enhancing growth rates, elongation rates and shoot recruitment rates and by reducing the *PI*. A stimulation of seagrass growth in environments with increased hydrodynamics was previously reported for other seagrass species (e.g. *Thalassodendron ciliatum*; Bandeira 2002). The beneficial effects of increased hydrodynamics on seagrass growth is also supported by the observation that the most productive seagrass community yet studied is one of the typically exposed genus *Phyllospadix* (Ramirez-Garcia et al. 1998). In particular for *Zostera noltii*, optimum growth conditions were previously associated with decreases in *PI* (Brun et al. 2003, Peralta et al. 2005) and/or recruitment events (Vermaat & Verhagen 1996, Peralta et al. 2005). The combination of a stimulated *GR* with a reduced *PI* and increased shoot recruitment thus underlines that, within the range of velocities used in the present study, increased current velocity has a positive effect on *Z. noltii*, provided that other vari-

ables are not limiting. An increase in belowground systems in high hydrodynamic environments, as was observed in this study, was previously described *in situ* for *Z. noltii* (Peralta et al. 2005), *Zostera marina* (Fonseca & Bell 1998), *Halodule wrightii* (Fonseca & Bell 1998) and *Phyllospadix* spp. (Cooper & McRoy 1988).

The present study demonstrates that, when external resources are not limiting, the morphometry of the plants responds to increased current velocity by enhancing the chance of survival and reducing the chance of damage via (1) reduction of the AB/BG ratio and (2) increase of the leaf cross section (see below). The reduced AG/BG ratio in the HV treatment is in agreement with observations of fresh water plant species (Puijalón et al. 2005) and wind exposed terrestrial species (Telewski 1995), and clearly benefits acclimation by increasing the anchorage strength of plants. Increased leaf cross section may benefit acclimation to HV by decreasing the risk of shoot breakage. Shoot breakage risk has been positively related with the second moment of area (*I*) (Koehl 1986); that is, lower values of the second moment of area indicate stronger leaves. For *Zostera noltii* leaves, the second moment of area was previously calculated as $I = 1(12 \times L_{\text{width}} \times L_{\text{diameter}}^3)^{-1}$, with L_{width} being leaf width and L_{diameter} leaf diameter (Bouma et al. 2005a). This equation predicts that the observed increase in leaf cross section at higher velocities will decrease the second moment of area, with a corresponding reduction in leaf breakage risk. Our observation of a reduced leaf loss rate in the HV treatment supports this (Table 1, see 'Results').

Mechanisms to explain plant responses to current velocity

Leaf detachment was previously suggested to be the main mechanism for variable leaf morphometry among environments with contrasting hydrodynamic conditions (van Katwijk & Hermus 2000, Schanz & Asmus 2003, Peralta et al. 2005). In our study, this mechanism was unlikely to have affected leaf morphometry: reduced leaf loss rate was observed in all the treatments. On the contrary, the observed effects were most likely related to interactions with (1) environmental conditions (i.e. current velocity), (2) effects on plant uptake and biomass allocation and (3) corresponding plant feedbacks.

On one hand, the growth of *Zostera noltii* was limited in the LV treatment owing to restricted access to resources in the water column. Access to water column resources is generally severely restricted by the DBL around the leaves (Koch 1994, Stapel et al. 1996). Reduced current velocity increases the thickness of the DBL, where the transport of molecules is 10^{11} -fold

slower than in adjacent layers with turbulent flow (Denny 1988). A relative large investment in above-ground tissues seems an effective response of *Z. noltii* to compensate for growth limitations (Peralta et al. 2002, 2005). This is comparable to the well documented shift in carbon investments in root vs. shoot material when terrestrial plants are nutrient vs. light limited (Ericsson et al. 1996). For HV plants, the situation should be just the opposite, with plants having a higher capacity to access external resources in the water column. Good accessibility to water column resources, combined with the need to withstand larger drag forces in HV conditions (see previous section), accounts for why a reduced AG/BG-ratio is beneficial in HV conditions.

Accessibility to water column resources may also account for the maximum *GR* observed in HV plants. However, the effect of *GR* is by itself insufficient to fully explain the changes in morphometry and recruitment observed at HV, because these changes will require an additional modification of biomass allocation pattern (Brun et al. 2006). According to the model developed by Brun et al. (2006), the divergences observed in this study between growth and recruitment patterns (Fig. 3 d,f) can be explained by the combination of *GR* and *PI* changes. Moreover, intensive events of shoot recruitment in *Zostera noltii* have been previously associated with important decreases in *PI*, which is considered as an indicator of highly favorable growth conditions (Vermaat & Verhagen 1996, Peralta et al. 2005). Our results support this hypothesis, but also support the hypothesis that *PI* reduction could be partly responsible for the decrease in AG/BG ratio at HV (see Fig. 4). In agreement with Brun et al. (2006), the correlation observed in Fig. 4 between *PI* and the relative maximum production of photosynthetic tissue suggests that there is a mechanism that modifies the AG/BG ratio. This hypothesis also agrees with previous studies of *Z. noltii*, where significant reductions in *PI* were accompanied by strong reductions in the AG/BG ratio (Peralta et al. 2005). Although further studies are necessary to fully demonstrate the mechanistic control of *PI* on the morphometry and architecture of seagrasses, our results highlight the importance of this variable to morphometric acclimation of the small seagrass *Z. noltii*.

Overlapping responses to abiotic conditions: consequences, limitations and alternatives

From the results presented in this study, the most relevant effects of current velocity on seagrasses at the population level appear to be (1) the decrease in the AG/BG ratio of *Zostera noltii* plants and (2) the

increase in the rate of shoot recruitment. In most ecosystems, (anthropogenic) changes in hydrodynamic regimes will generally be correlated with changes in other abiotic conditions. To evaluate the vulnerability of a seagrass meadow to these kinds of changes in abiotic environment, it is necessary to consider the following 2 aspects: (1) the plant responses to each of the external variables and (2) density-dependent feedbacks. To illustrate the importance of both aspects, we focus on the role that current velocity could have on the vulnerability of the meadow to light reduction. A decreased AG/BG ratio in response to strong current velocities can have negative consequences for the population when light is limiting. In case of light deprivation, respiratory costs of below-ground tissues may induce a negative C balance (Hemminga 1998). However, light deprivation and current velocity seem to have opposite effects on plant morphometry, as light deprivation increases the *PI* and the leaf length of *Z. noltii* (Vermaat & Verhagen 1996, Peralta et al. 2005). Regarding the opposing effects of high currents and light limitation, it is necessary to evaluate the relative magnitude of each factor in order to draw conclusions at the plant level. In addition, the relative magnitude of both variables will change within the meadow as a consequence of gradients caused by vegetation density (Brun et al. 2003, 2006). Hence, shoot density and the corresponding density dependent feedbacks must be accounted for in order to evaluate the effects of abiotic parameters like current velocity and light availability at the population level.

When considering the complexity of density gradients and density dependent feedbacks, we believe it is necessary to use spatially-explicit models for studies at the population level. These models should describe the physical environment perceived by each plant in the population, in combination with plant responses to abiotic factors, as identified in the present study. In the case of fast growing species such as *Zostera noltii*, our study suggests that the predictive capacity of these models will, to a large extent, be determined by the knowledge of factors that control the *PI*. This study conclusively demonstrates for the first time that, in addition to light and nutrients, current velocity can also strongly affect the *PI* of seagrasses, and thereby the morphometry and architecture of these plants.

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