

Scaling of ramet size and spacing in seagrasses: implications for stand development

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Abstract

The scaling between shoot mass and spacer length was examined across 23 seagrass species by compiling field and literature data on architectural and stand features. The distance between shoots programmed in seagrass architecture was scaled at the 0.24 power of shoot mass. The predicted distance between neighboring shoots resulting from the scaling relationship investigated was compared with the spacing observed in 79 crowded natural seagrass stands. Seagrass architecture predicted 50% of the variability of the distance between neighbors observed in natural stands. Moreover, the growth programme of seagrass species predicted 29% of the variance of maximum aboveground biomass developed by seagrass meadows. The close agreement between the shoot density and biomass developed by closed natural stands and that predicted from seagrass architecture suggested that the upper limit to density and aboveground biomass, such as that defined by the self-thinning law, is already imprinted within the basic architecture of seagrasses (i.e. spacer length in between consecutive shoots).

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1. Introduction

Space is a primary resource limiting plant growth (McConnaughay and Bazzaz, 1991; Silvertown and Lovett-Doust, 1993), so that competition for space among neighbors sets an upper limit to the abundance of plant population (Gorham, 1979; Duarte and Kalff, 1987; Duarte et al., 1987; Weller, 1987). As a consequence, the space occupation patterns of a

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species are key traits constraining their competitive ability and the density and biomass of closed stands.

Clonal plants occupy space by reiterating shoots spaced along their growing rhizomes or stolons (Bell and Tomlinson, 1980; Bell, 1991). The spacing between consecutive shoots along the rhizome is very conservative within a seagrass species (e.g. Duarte, 1991; Marbà and Duarte, 1998), as expected from its tight genetic control in clonal plants (Gottlieb, 1986). As a result, the space occupation by clonal plants is tightly regulated and easily modelled (Smith and Palmer, 1976; Bell, 1979; Bell et al., 1979; Bell and Tomlinson, 1980; Duarte, 1995; Callaghan et al., 1990; Klimes, 1992; Cain et al., 1996; Marbà and Duarte, 1998). The spacer length, i.e. the length of rhizome in between consecutive seagrass shoots, sets a minimum distance between neighboring shoots in a stand. Moreover, the negative relationship between shoot mass and density in land (Gorham, 1979) and aquatic (Duarte and Kalff, 1987) plant stands, suggests that spacer length and shoot mass in clonal plants might be positively related. Despite major progress in plant allometry (Niklas, 1994; Duarte, 1991; Marbà and Duarte, 1998), the existence of scaling laws between shoot mass and spacer length is yet to be demonstrated for clonal plants, including seagrasses. The demonstration of a negative relationship between spacer length and the rhizome diameter, a descriptor of size, of seagrasses (Marbà and Duarte, 1998) suggests that spacer length may also be scaled to shoot mass. Such scaling law, if confirmed, would have major implications for the resulting structure and space occupation by seagrass stands.

We examine here the scaling between shoot mass and spacer length of seagrass species. We then use the allometric relationship between shoot mass and spacer length of seagrass species to compare the distance between neighboring shoots predicted by this relationship with the spacing observed in natural closed natural seagrass stands. Lastly, we explore the implications of the scaling laws demonstrated for the biomass development of crowded seagrass stands, and its relationship with expectations resulting from the self-thinning law. These goals are addressed on the basis of published estimates of the architecture and stand structure of a broad range of seagrass species, appended with our own measurements, which allow us to extend the range of species examined and, therefore, the generality of our findings.

2. Methods

Data on seagrass spacer length (i.e. rhizome) and shoot mass (as dry mass, desiccated overnight at 80 °C) were compiled from the literature (Table 1), and amended for *Cymodocea nodosa*, *Posidonia oceanica* and *Ruppia maritima* stands with our own estimates. We used shoot mass values of temperate species measured during summer, the time of the year when shoots are the heaviest. Because seagrass spacer length and shoot mass was examined for a single population for most of the species, we averaged the estimates of architectural features per species when available for several stands.

Another data set compiling published literature reports on the shoot density and above-ground biomass of closed seagrass stands at the time of the seasonal maximum aboveground biomass was also built (Table 2). The average distance between neighbor shoots in the stands was estimated by first calculating the area (m²) per shoot (i.e. shoot per density), and then

Table 1

Seagrass species included in the data base compiling architectural estimates (i.e. shoot mass and rhizome length between connected shoots)

Species	Location	Reference	Number of stands
<i>Amphibolis antarctica</i>	West Australia	Marbà and Walker, 1999	1
<i>Amphibolis griffithii</i>	West Australia	Marbà and Walker, 1999	1
<i>Cymodocea serrulata</i>	The Philippines	Vermaat et al., 1995	1
<i>Cymodocea nodosa</i>	East Spain	Duarte, unpublished	15
	Portugal	Cunha, 1994	5
<i>Cymodocea rotundata</i>	The Philippines	Vermaat et al., 1995	1
<i>Enhalus acoroides</i>	The Philippines	Vermaat et al., 1995	1
<i>Halodule uninervis</i>	The Philippines	Vermaat et al., 1995	1
<i>Halodule wrightii</i>	Mexican Caribbean	Gallegos et al., 1994	1
<i>Halophila ovalis</i>	The Philippines	Vermaat et al., 1995	1
<i>Heterozostera tasmanica</i>	West Australia	Marbà and Walker, 1999	1
<i>Posidonia angustifolia</i>	West Australia	Marbà and Walker, 1999	1
<i>Posidonia australis</i>	West Australia	Marbà and Walker, 1999	1
<i>Posidonia oceanica</i>	East Spain	Marbà et al., 1996a; Marbà et al., unpublished	29
<i>Posidonia sinuosa</i>	West Australia	Marbà and Walker, 1999	2
<i>Ruppia maritima</i>	Southwest Spain	Marbà, unpublished	1
<i>Syringodium filiforme</i>	Mexican Caribbean	Gallegos et al., 1994	1
<i>Syringodium isoetifolium</i>	The Philippines	Vermaat et al., 1995	1
<i>Thalassia hemprichii</i>	The Philippines	Vermaat et al., 1995	1
<i>Thalassia testudinum</i>	Mexican Caribbean	Gallegos et al., 1993	3
<i>Thalassodendron ciliatum</i>	Kenya	Duarte et al., 1996	1
<i>Thalassodendron pachyrhizum</i>	West Australia	Marbà and Walker, 1999	1
<i>Zostera marina</i>	East Spain	Marbà et al., 1996a,b	1
<i>Zostera noltii</i>	East Spain	Marbà et al., 1996a,b	1

computing the average distance between neighbor shoots (d_n , m) as:

$$d_n = \left(4 \times \frac{\text{area}}{\pi} \right)^{1/2}$$

These calculations, which assume that each shoot is in the center of a circular individual surface, represented the more parsimonious approach and yielded results similar (i.e. not statistically different) to those using more complex tessellation.

The scaling between spacer length (Y) and shoot mass (X) was described by fitting allometric equations (cf. Niklas, 1994) of the form $Y = a \times X^b$ using least squares linear regression analyses on log-transformed variables.

3. Results

Seagrass spacer length and shoot mass data were compiled for 72 seagrass stands, encompassing 23 seagrasses species, growing in along the Spanish, Portuguese, Mexican

Table 2

Sources of data on shoot density and aboveground biomass at the seasonal peak of aboveground biomass in seagrass meadows

Species	Location	Reference	Number of stands and/or seasons
<i>Amphibolis antarctica</i>	West Australia	Walker and McComb, 1988	1
<i>Cymodocea nodosa</i>	Northeast Spain	Cebrián et al., 1997	1
	Adriatic Sea	Guidetti et al., 2001	1
		Peduzzi and Vukovic, 1990	3
	Northeast Spain	Pérez, 1989	3
	Southeast Spain	Terrados, 1991	2
<i>Cymodocea rotundata</i>	Papua New Guinea	Brouns, 1987	1
<i>Cymodocea serrulata</i>	Papua New Guinea	Brouns, 1987	1
	North Australia	Moriarty et al., 1990	1
<i>Enhalus acoroides</i>	Papua New Guinea	Brouns and Heijs, 1986	2
<i>Halodule uninervis</i>	Papua New Guinea	Brouns, 1987	1
<i>Halodule wrightii</i>	South Texas, USA	Dunton, 1996	8
	South Texas, USA	Dunton, 1990	3
<i>Halophila ovalis</i>	Papua New Guinea	Brouns, 1987	1
	West Australia	Hilliman et al., 1995	5
<i>Heterozostera tasmanica</i>	South Australia	Bulthuis and Woelkerling, 1983	4
	Chile	Phillips et al., 1983	1
<i>Posidonia oceanica</i>	Northeast Spain	Cebrián et al., 1997	1
	France	Thelin and Giorgi, 1984	1
	France	Bay, 1984	1
	Adriatic Sea	Guidetti et al., 2001	1
	France	Thelin and Giorgi, 1984	2
		Ott, 1980	1
<i>Ruppia maritima</i>	Texas, USA	Dunton, 1990	2
<i>Syringodium isoetifolium</i>	Papua New Guinea	Brouns, 1987	1
<i>Thalassia hemprichii</i>	Papua New Guinea	Brouns, 1987	1
<i>Thalassia testudinum</i>	Florida, USA	Zieman, 1975	1
	South Texas, USA	Kaldy and Dunton, 2000	4
<i>Zostera capricorni</i>	South Australia	Larkum et al., 1984	1
<i>Zostera marina</i>	Japan	Aioi, 1980	4
	Denmark	Wium-Andersen and Borum, 1984	1
	Northeast Spain	Cebrián et al., 1997	1
	Adriatic Sea	Guidetti et al., 1997	1
	Baja California, México	Ibarra-Obando, 1989	1
	France	Jacobs, 1979	1
	The Netherlands	Nienhuis and de Bree, 1980	1
	Denmark	Olesen and Sand-Jensen, 1994	1
	Virginia, USA	Orth and Moore, 1986	3
	Denmark	Pedersen, 1990	1
	East Canada	Robertson and Mann, 1984	1
	Denmark	Sand-Jensen, 1975	1
	Washington, USA	Thom, 1990	3
	Northeast Spain	Cebrián et al., 1997	1
	The Netherlands	Vermaat and Verhagen, 1996	2

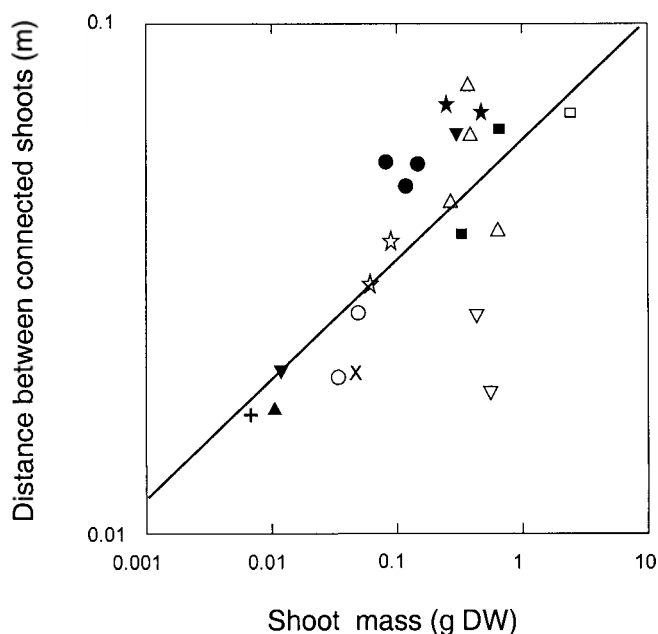


Fig. 1. The relationship between the spacer length and the shoot mass of seagrasses: *Amphibolis* sp. (■); *Cyrtosira* sp. (●); *Enhalus acoroides* (□); *Halodule* sp. (○); *Halophila ovalis* (+); *Heterozostera teasmanica* (×); *Posidonia* sp. (△); *Ruppia maritima* (▲); *Syringodium* sp. (☆); *Thalassia* sp. (★); *Thalassodendron* sp. (▽); *Zostera* sp. (▼). The solid line represents the fitted regression equation (Eq. (1)). The sources of these data are compiled in Table 1.

Caribbean, The Philippines, western Australia, and Kenyan coasts (Table 1). Shoot mass and spacer length spanned four and one orders of magnitude, respectively, among the seagrass stands investigated (Fig. 1). The coefficient of variation of spacer length within individual stands, which reflects the plasticity in this trait, averaged 66% (range 25–133%). About 40% of the variability in spacer length (d_s , m) among the species investigated was associated to the wide differences in shoot mass among the seagrass examined. Regression analysis revealed that seagrasses produce consecutive shoots further apart along their rhizomes as shoot mass (W , g DW) increased (Fig. 1), as described by the equation:

$$d_s = 0.059 W^{0.24 \pm 0.05} \quad (1)$$

$$N = 23; \quad P < 0.0005; \quad R^2 = 0.46$$

which shows the spacer length connecting consecutive shoots along the rhizome to increase as the 1/4 power of shoot mass.

Field estimates on aboveground biomass and shoot density during seasonal peak biomass were obtained for 79 natural closed stands, encompassing 17 seagrass species (Table 2). The distance between neighbor shoots (d_n) in natural seagrass stands at the time of peak biomass was scaled to the 0.29 (± 0.03) power of shoot mass (Fig. 2a), which was remarkably close (t -test, H_0 : slope = 0.24, intercept = 0.059; $P > 0.95$) to the scaling between the spacer

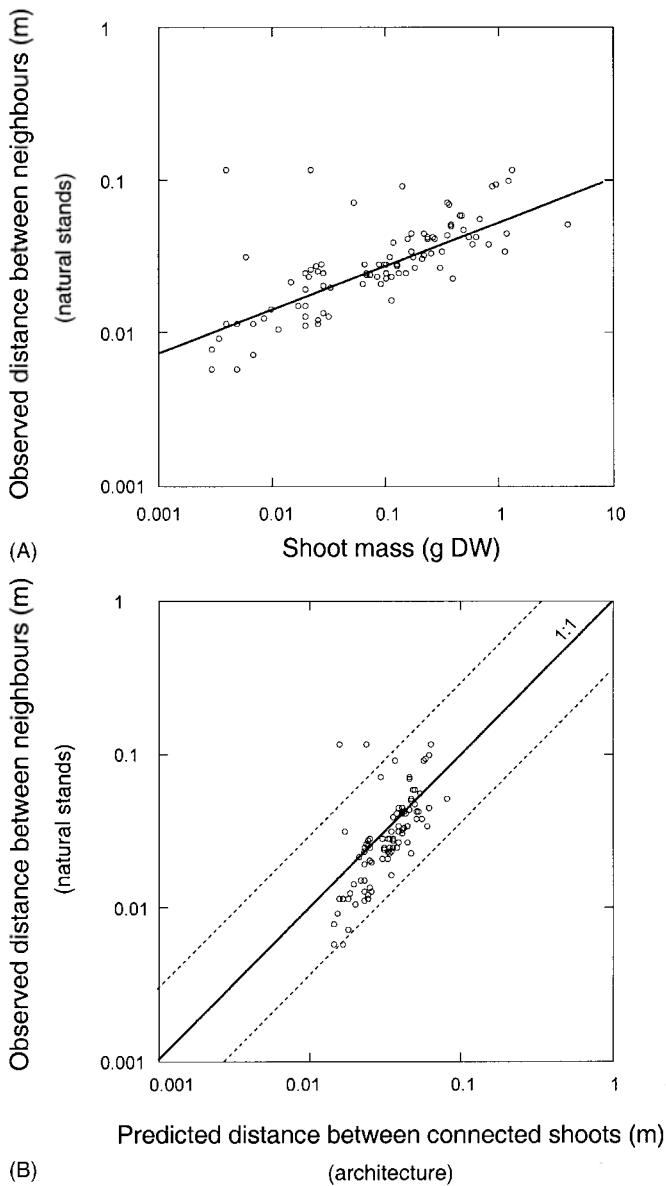


Fig. 2. (A) The relationship between the distance between neighbor shoots during the maximum seasonal above-ground development in monospecific stands of seagrasses. The solid line represents the fitted regression equation: $\text{distance} = 0.06 \text{ shoot mass}^{0.29 (\pm 0.03)}$, $R^2 = 0.50$, $P < 0.00001$, $n = 79$. The sources of these data are compiled in Table 2. (B) Relationship between the distance between neighbor shoots predicted from plant architecture using Eq. (1) (X-axis) and that observed in the seagrass meadows during maximum seasonal aboveground development (Y-axis). The solid line represents the 1:1 relationship between predicted and observed estimates. Dashed lines represent the 95% confidence limits of predicted values.

length (d_s) and shoot mass for consecutive shoots along their rhizomes (i.e. Fig. 2b). Indeed, there was a close relationship between the observed distance between neighbor shoots in natural stands and that predicted from shoot mass using Eq. (1) ($R^2 = 0.50$), with only two of the stands having distances significantly different from those predicted by the architecture (Fig. 2b).

The non-linear increase of spacer length with shoot size suggests that the ground area per unit shoot mass of ideal closed seagrass stands should increase slower as the plants develop larger shoots (i.e. $A_s \sim D_s^2 \sim (W^{1/4})^2 \sim W^{1/2}$). This was confirmed by the analysis of the ground area per shoot in the natural stands examined (i.e. scaling exponent between A_s and $W = 0.57 \pm 0.06$, $R^2 = 0.50$). Similarly, the biomass (B , g DW m²) developed by an ideal seagrass stand (i.e. one that preserves the average distance between neighbors equal to the spacer length) could be calculated as the ratio of the shoot mass and the ground area per shoot, and is, therefore, expected to scale as $W^{1/2}$ (i.e. $B = WA_s^{-1} = W(W^{1/2})^{-1} = W^{1/2}$). Hence, the biomass of dense seagrass stands developed from the simple iteration of their spacing between connected shoots is, therefore, predicted to increase with increasing shoot mass. This prediction was also consistent with the scaling of aboveground biomass and shoot mass in the natural seagrass stands (scaling exponent between B and $W = 0.39 \pm 0.06$, $R^2 = 0.29$; Fig. 3a), and allowed the prediction of the biomass of closed seagrass stands from allometric equations based on seagrass architecture (Fig. 3b).

4. Discussion

Our results confirm the hypothesized relationship between the spacer length and the shoot mass of seagrass species. The relationship, however, contained substantial scatter, which may partially result from morphological plasticity. Intraspecific plasticity of spacer length has been demonstrated for *Posidonia oceanica* (Marbà et al., 1996a,b), and *Cymodocea nodosa* (Duarte unpublished results), where the spacing between shoots along rhizomes may vary up to four-fold within a species. The intraspecific plasticity in spacer length has been shown to be of adaptive significance in clonal plants, allowing the plants to respond to spatial variability in resources (Slade and Hutchings, 1987a,b; Sutherland, 1987).

The relationship between spacer length and shoot mass was similar to that between the realized average distance between neighbor shoots and shoot mass in natural seagrass stands. This remarkable similarity strongly indicates that the internal packaging of shoots within closed seagrass stands is largely the result of the basic growth programme of these clonal plants, so that the allometric scaling between spacer length and shoot mass is preserved in the distance between neighbor shoots in developed, closed seagrass stands. This similarity is remarkable provided the broad range of species included in the analysis.

The results obtained suggest that the basic clonal architecture of seagrass species, imprinted on the spacing of shoots along their rhizomes, is projected onto developing stands during growth. The clonal architecture of seagrass allows the prediction of the structure of ideal stands where the area and biomass per capita is not significantly different to that maintained in the natural stands during crowding conditions. The observation that

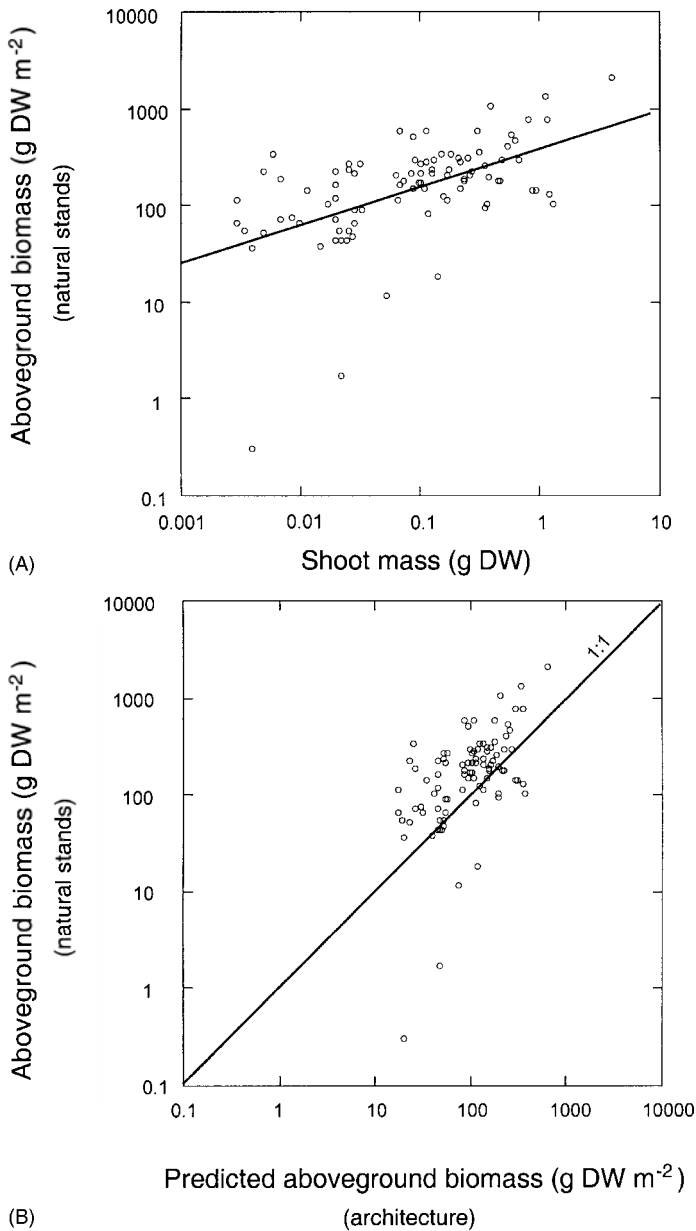


Fig. 3. (A) The relationship between the aboveground biomass (B) and individual shoot mass (W) at the time of maximum seasonal aboveground development in seagrass stands. The solid line represents the regression equation: $B = 389 W^{0.39 (\pm 0.06)}$. The sources of these data are compiled in Table 2. (B) The relationship between the aboveground biomass of closed seagrass stands predicted from the monotonous iteration of their architecture and that observed in the field during maximum seasonal aboveground development. The solid line represents the 1:1 relationship between predicted and observed estimates.

the upper limit to plant abundance of closed seagrass stands is similar to that predicted from the simple iteration of the spacing between connected shoots, assigns a dominant role to the clonal architecture of seagrasses in the configuration of their packaging in closed stands.

The scaling between the maximum biomass realized in closed seagrass stands is similar to that predicted from the monotonous iteration of their shoots following the growth programme imprinted onto their basic architecture. The resulting shoot density of natural seagrass stands is similar to the shoot weight-dependent upper boundary to plant abundance described for even-aged populations (Gorham, 1979; Duarte and Kalff, 1987; Niklas, 1994). Indeed, the increase in maximum stand biomass with increasing shoot weight demonstrated here is similar to the square root power scaling of shoot mass to aboveground biomass predicted by the self-thinning law (Weller, 1987), and departs from the law of constant yield, which would have resulted in a linear scaling between biomass and shoot mass (Harper, 1977). Whether clonal plants undergo self-thinning during the development of closed stands has been subject to debate, for the structure of close stands of clonal plants has been often shown to conform to the predictions derived from this law (Hutchings, 1979; Pitelka, 1984; Duarte and Kalff, 1987), as also indicated here (Fig. 3a), while the self-thinning law involves mortality as the stands develop, which does not make evolutionary sense for clonal plant. Our finding that the scaling between aboveground biomass and shoot mass described by the self-thinning law is already built onto the basic architecture of seagrasses (Fig. 3b) does suggest a possible explanation to reconcile these opposing views, for it does suggest that seagrasses can reach the upper boundary to shoot mass described by the self-thinning law without undergoing density-dependent mortality (Hutchings, 1979; Olesen and Sand-Jensen, 1994; Room and Julien, 1994). Our results do, therefore, suggest that the upper limits to density and aboveground biomass defined by the self-thinning law are already imprinted within the basic clonal architecture of seagrasses (i.e. spacer length in between consecutive shoots). Moreover, crowded stands of clonal plants may remain at the upper limit to density and biomass by decreasing shoot recruitment or rhizome growth (Hutchings, 1979; Schmid, 1990) or shoot size (Pitelka, 1984) once the limit is reached, thereby avoiding competition for space through the physiological integration of the clone.

In summary, the results obtained demonstrate the existence of an allometric scaling between spacer length and shoot weight in seagrasses that is preserved on the average density between neighbors of the stands they form. The close agreement between the aboveground biomass developed by closed natural seagrass stands and that predicted from the monotonous iteration of their architecture demonstrates that the structure of the stands seagrass develop is, to a large extent set by the growth program imprinted in their architecture, and explains the observation of size-dependent differences in the maximum aboveground biomass developed by different species (Duarte and Chiscano, 1999). The minimum distance between neighbors allowing shoot survivorship and the upper limit to the aboveground biomass of seagrass stands is, therefore, programmed within their architecture. This finding suggests that the efficient occupation of space must be a strong component of fitness and, thus, a main factor in the evolution of seagrasses, and provide additional evidence of the power of allometric approaches (Duarte, 1991; Niklas, 1994; Marbà and Duarte, 1998) for the comparative analyses of seagrass ecology.

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