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# Growth patterns and demography of pioneer Caribbean seagrasses *Halodule wrightii* and *Syringodium filiforme*

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ABSTRACT: The shoot demography and rhizome growth of *Syringodium filiforme* Kütz. and *Halodule wrightii* Aschers. were studied, based on plant dating techniques, to account for their role as pioneer in the succession sequence of Caribbean seagrasses. Results demonstrated that these species are able to develop dense meadows, supporting biomasses in excess of 500 g DW m$^{-2}$ They produced more than 2000 g DW m$^{-2}$ yr$^{-1}$ due to their high leaf (5.0 to 8.5 yr$^{-1}$) and rhizome (2.0 to 3.3 yr$^{-1}$) turnover. Rhizome growth and branching rates were very high, allowing these seagrasses to rapidly occupy the space they colonise. The rapid rhizome turnover involved, however, a high shoot mortality rate and low life expectancy (average shoot life expectancy 100 to 180 d). This implies that, while these pioneer species are able to rapidly occupy the space they colonise, their established shoots cannot occupy that space for as long as the more long-lived species *Thalassia testudinum*. We suggest, therefore, that the role of seagrass species as pioneer or climax species is independent of their capacity to support dense, productive populations, and is closely related to shoot longevity and rhizome turnover.

KEY WORDS: Rhizome growth · Shoot age · Biomass · Production

The seagrasses *Syringodium filiforme* Kütz. and *Halodule wrightii* Aschers. occupy an important role as pioneer species in the Caribbean Sea (den Hartog 1971, Patriquin 1975). They colonise denuded sediments following perturbations, preceding the climax community of *Thalassia testudinum* Banks ex König in the successional sequence of Caribbean seagrasses (den Hartog 1971, Patriquin 1975, Williams 1987, 1990). *S. filiforme* and *H. wrightii* also develop mono-specific meadows in the area (Gilbert & Clark 1981, Iverson & Bittaker 1986, Van Tussenbroek 1994), so that, in addition to their role as pioneer species, they may also be important primary producers (Zieman et al. 1989, Short et al. 1993). Most studies on these species have focused on leaf biomass and production (Virnstein 1982, Fry 1983, Barber & Behrens 1985, Iverson & Bittaker 1986, Eleuterius 1987, Williams 1987, Fry & Virnstein 1988, Zieman et al. 1989, Van Tussenbroek 1994), but reports of their rhizome growth and demography are as yet few (Eleuterius 1987, Zieman et al. 1989, Duarte 1991). Knowledge of their rhizome growth rates and demographic dynamics would, however, help to interpret the dynamics and maintenance of the meadows these species develop (Duarte & Sand-Jensen 1990a, b).

On the basis of data obtained using plant dating techniques (Patriquin 1973, Gallegos et al. 1993, Duarte et al. 1994, Marbà et al. 1994), we describe the biomass, and rhizome and shoot dynamics of monospecific *Syringodium filiforme* and *Halodule wrightii* meadows in the Mexican Caribbean.

**Methods.** We studied shallow (1.0 to 1.5 m) monospecific meadows of *Syringodium filiforme* and *Halodule wrightii* on the reef lagoon near the town of Puerto Morelos (21° N, 87° W, Yucatán Peninsula, Mexico; Marbà et al. 1994), using the approach described by Gallegos et al. (1993). In August 1991, the time of maximum seagrass biomass in the area (Van Tussenbroek 1994), we randomly collected 6 and 3 cores (20.5 cm internal diameter) from the *S. filiforme* and *H. wrightii* meadows, respectively. The cores were pushed 40 cm into the sediment to collect the shoots down to their insertion in the rhizomes, which was needed to esti-

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mate shoot age (cf. Gallegos et al. 1993). Sediment (coarse carbonate sand) was then carefully washed off the samples, all the living shoots and the standing leaves they supported were counted, and the presence of flowers or fruits recorded. We also noted the number of branches in the horizontal rhizomes as well as the number and length of rhizome internodes between consecutive shoots and those in the entire sample, to estimate rhizome growth (cf. Gallegos et al. 1993).

The age of living (i.e. bearing green leaves) and dead (i.e. devoid of green leaves) shoots was estimated as the sum of the number of leaf scars and standing leaves (Patriquin 1973, Cox & Tomlinson 1988, Gallegos et al. 1993). Dead shoots were dated only if they ended in a rounded tip, indicating that the shoot was not broken (Gallegos et al. 1993). The age units obtained were plastochrone intervals (PIs), which represent the average time interval between the initiation of 2 successive leaves on a shoot (Erickson & Michelini 1957, Brouns 1985). Using a dissecting microscope, we examined the time course of vertical internodal length of the oldest shoots sampled, to identify annual cycles in the length of vertical internodes (cf. Duarte et al. 1994, Marbá et al. 1994). The inverse of the number of internodes in a cycle (number of leaves yr$^{-1}$) corresponds to the annual average PI (cf. Duarte et al. 1994, Marbá et al. 1994) which was used to convert PIs into absolute time units.

The data set obtained in August 1991 was complemented with information on flowering frequency, maximal shoot age, and additional sequences of internodal length for old shoots. These were obtained during 2 more visits in the spring of 1992 and 1993 (sample sizes about 2000 and 4000 shoots for *Syringodium filiforme* and *Halodule wrightii*, respectively).

The PI of horizontal rhizomes was calculated by regressing the number of rhizome internodes between shoots along the rhizome against their age difference (Patriquin 1973, Gallegos et al. 1993). The rate of vertical growth of *Syringodium filiforme* and *Halodule wrightii* shoots was also calculated by regressing shoot length against age (Gallegos et al. 1993). Shoot age structure was described using data on living and dead shoots (Gallegos et al. 1993, Duarte et al. 1994). The average age of living shoots represents the overall age of the shoot population, but it does overestimate their life expectancy, which is best represented by the age at death (Gallegos et al. 1993, Duarte et al. 1994). Shoot mortality ($K$, in natural logarithm units time$^{-1}$; cf. Duarte & Sand-Jensen 1990b) was calculated from the age distribution of dead shoots (Gallegos et al. 1993, Duarte et al.

1994) by fitting the equation

$$N_t = N_0 e^{-kt}$$

which describes the exponential decline in shoot number ($N$) in increasingly older age classes with time ($t$) from the onset on mortality ($t = 0$). Shoot recruitment rates were then calculated as the natural logarithm of the inverse of the fraction of the shoot population older than 1 yr (Duarte & Sand-Jensen 1990b).

**Results.** *Halodule wrightii* and *Syringodium filiforme* developed lush monospecific stands in the reef lagoon, reaching a high shoot density and high biomass of shoots and rhizomes (Table 1). Rhizome internodes of *S. filiforme* were thicker and longer than those of *H. wrightii* (30.6 ± 0.25 and 20.2 ± 1.0 mm internode$^{-1}$, respectively), and the 2 species formed a dense network of 228.5 m and 216.8 m of rhizome m$^{-2}$, respectively. Shoot density closely resembled rhizome internode density (Table 1), because both species produce 1 short shoot at each rhizome internode. The number of internodes between connected shoots and their age difference were closely correlated (p < 0.0001). The slope of the regression equations describing these relationships indicated that *H. wrightii* and *S. filiforme* produce 1.81 ± 0.17 and 2.81 ± 0.27 internodes PI$^{-1}$, respectively. Shoot vertical growth was calculated from regression analysis between shoot length and shoot age to be 0.56 ± 0.13 and 0.12 ± 0.01 cm PI$^{-1}$ for *S. filiforme* and *H. wrightii*, respectively (Fig. 1). The distinct seasonal pattern in the sequence of vertical internodal length (Fig. 2) allowed calculation of the average number of vertical internodes (= number of leaves) produced per shoot per year, and the average PI for the 2 species (Table 1), which were used to calculate annual rates of rhizome elongation from rates per PI (Table 1). Rhizomes branched in 3.2 % and 9.3 % of the rhizome

Table 1. *Syringodium filiforme* and *Halodule wrightii*. Average (± SE) shoot and rhizome biomass, density, production, and shoot recruitment and mortality rates for the populations studied

| Variable | S. filiforme | H. wrightii |
|---|---|---|
| Shoot biomass (g DW m$^{-2}$) | 446.9 ± 48.4 | 519 ± 86 |
| Shoot density (shoots m$^{-2}$) | 7139 ± 1366 | 14872 ± 2444 |
| Rhizome biomass (g DW m$^{-2}$) | 233 | 97 |
| Rhizome density (internodes m$^{-2}$) | 7468 | 10732 |
| Leaf plastochrone interval (d) | 60.8 | 16.5 |
| Leaves shoot$^{-1}$ yr$^{-1}$ | 6 | 22.1 |
| Rhizome elongation (cm yr$^{-1}$ apex$^{-1}$) | 51.6 | 80.9 |
| Vertical growth (cm yr$^{-1}$ shoot$^{-1}$) | 3.36 | 2.65 |
| Shoot recruitment (ln units yr$^{-1}$) | 0.77 | 4.18 |
| Shoot mortality rate (ln units yr$^{-1}$) | 2.04 ± 0.39 | 3.54 ± 0.37 |
| Leaf production (g DW m$^{-2}$ yr$^{-1}$) | 2234 | 4619 |
| Rhizome production (g DW m$^{-2}$ yr$^{-1}$) | 466 | 320 |
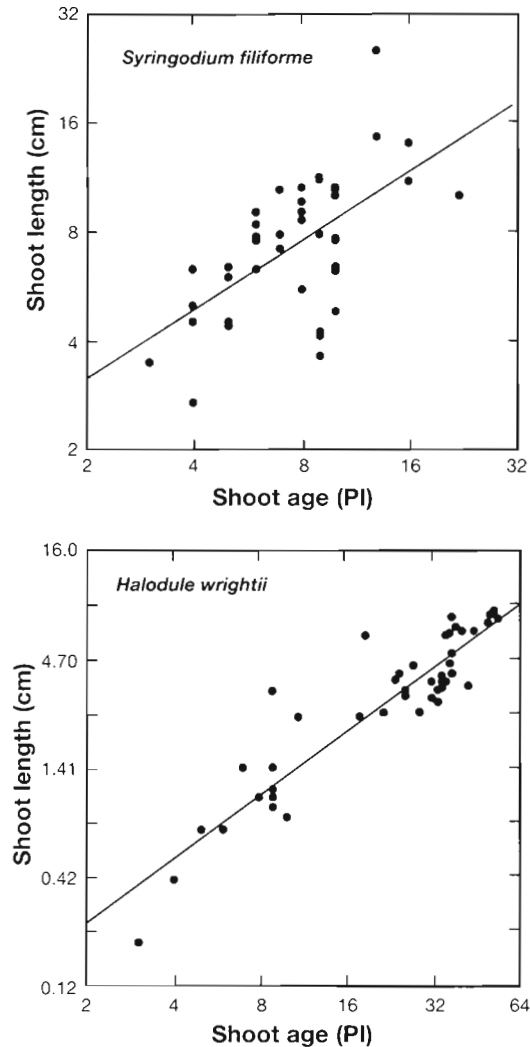
Fig. 1. *Syringodium filiforme* and *Halodule wrightii*. Relationship between the length of vertical rhizomes and the age of shoots
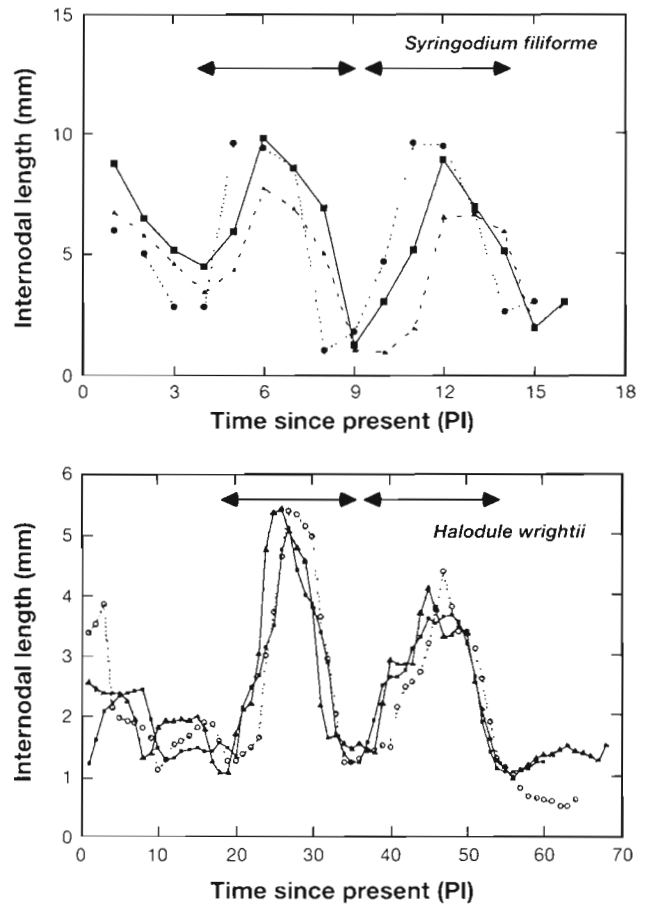


Fig. 2. *Syringodium filiforme* and *Halodule wrightii*. Sequence of internodal length recorded for the oldest shoots sampled. Arrows indicate annual cycles

internodes examined for *S. filiforme* and *H. wrightii*, respectively.

The average age of *Syringodium filiforme* shoots was ca 1 yr ($6.7 \pm 0.1$ PIs), and most of the shoots had been produced within the current year (i.e. age <7 PIs; Fig. 3), indicative of a high shoot recruitment rate (Table 1). The age distribution of dead shoots (Fig. 3) showed a clear exponential decline in survival with increasing age that allowed calculation of mortality rates (Table 1). The average life expectancy of *S. filiforme* shoots was found to be about half a year ($3 \pm 0.16$ PIs) and the oldest *S. filiforme* shoot found was about 7 yr (46 PIs, n > 2000). Almost all of the living *Halodule wrightii* shoots had been produced within a year (Fig. 4), indicating very high shoot recruitment rates (Table 1). High rates are needed to compensate

for their high mortality rate (Table 1), as reflected by the rapid exponential decline in shoot abundance with increasing shoot age (Fig. 4). The life expectancy of *H. wrightii* shoots is, therefore, only about 3 mo or $6.9 \pm 0.4$ PIs, and the longest-lived shoot found was only 3 yr (70 PIs, n > 4000).

The average shoot life expectancies estimated (182 and 110 d for *Syringodium filiforme* and *Halodule wrightii*, respectively) will, in a stable population, correspond to their shoot turnover time (Gallegos et al. 1993), which are, therefore, about 2.0 and 3.3 yr$^{-1}$. These estimates should also be close to the average rhizome turnover rates (Gallegos et al. 1993), because shoot turnover is maintained by a parallel rhizome turnover (i.e. 1 internode is formed for each shoot produced). An estimate of the average number of leaves that a shoot produces per year, together with the average number of standing leaves per shoot ($2.6 \pm 0.1$ and $1.2 \pm 0.03$ leaves shoot$^{-1}$), allows the leaf turnover to be calculated as 8.5 and 5.0 yr$^{-1}$ for *H. wrightii* and *S. filiforme*, respectively. Hence, leaf turnover is about twice
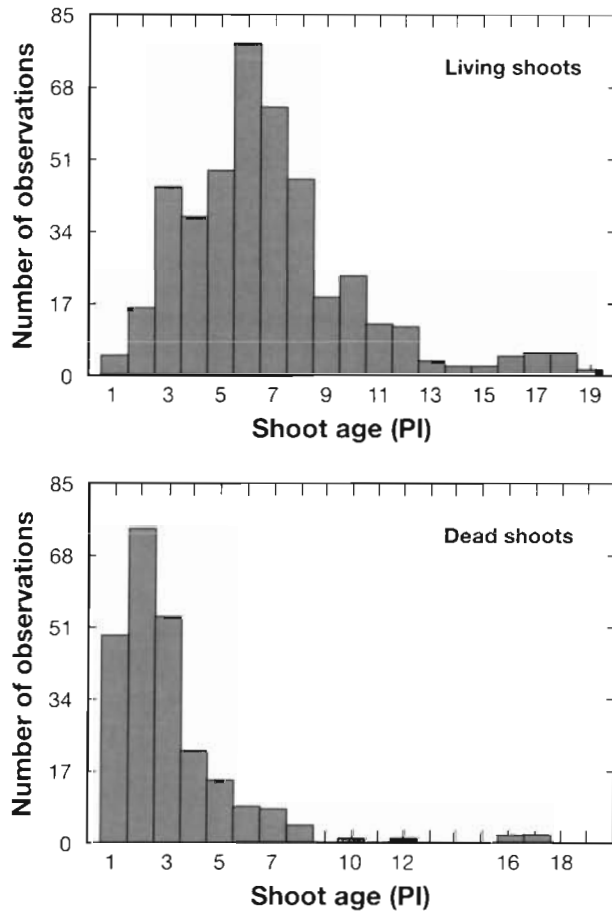
Fig. 3. *Syringodium filiforme.* Age distribution of living and dead shoots



Fig. 4. *Halodule wrightii.* Age distribution of living and dead shoots

as fast as rhizome turnover. The calculated turnover rates combined with the biomass of leaves and rhizomes (Table 1), which show little seasonal variation in this area (Van Tussenbroek 1994), reveal the production of the 2 species to be nearly 3 and 5 kg DW m$^{-2}$ yr$^{-1}$, respectively (Table 1).

*Syringodium filiforme* and *Halodule wrightii* flowered in spring, and 6.4% and 10.5%, respectively, of their shoots had flowered in spring 1993, representing about 300 and 1500 flowering shoots m$^{-2}$, respectively. Flowering shoots had an average age of 8.4 ± 0.8 PI for *S. filiforme* and 29.3 ± 2.7 PI for *H. wrightii*, which indicates flowering to be more frequent for shoots older than 1 yr. In August 1991, 366 fruiting *H. wrightii* shoots m$^{-2}$ were found, with each fruit-bearing shoot having 2 fruits, which indicates that only about 20% of the flowering shoots set fruit.

**Discussion.** The results obtained showed that the 2 species are able to develop lush, highly productive meadows in the Mexican Caribbean (Table 1). The shoot density and biomass were greater than values
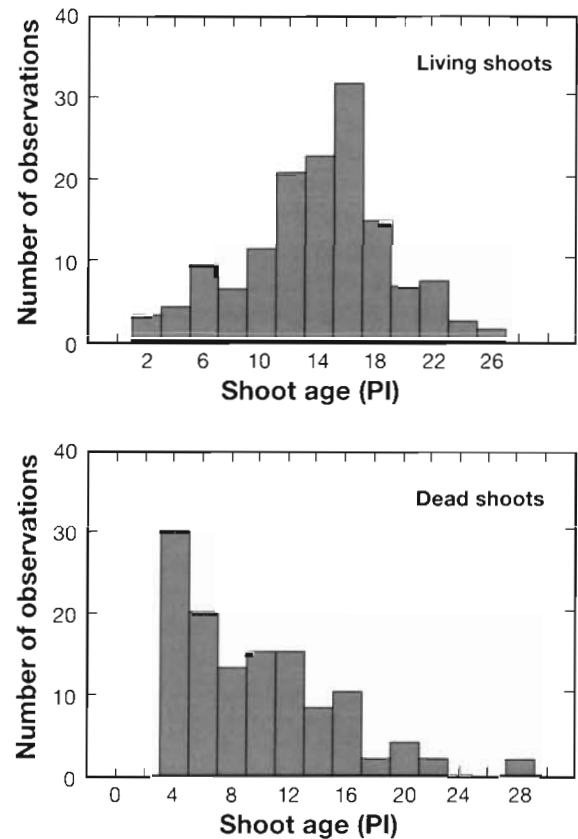
reported to date for the Gulf of Mexico (e.g. Eleuterius 1987) and the Atlantic Ocean (Short et al. 1993), although *S. filiforme* has been observed to produce even larger biomasses, close to 1 kg DW m$^{-2}$, in the Mexican Caribbean (Van Tussenbroek 1994). The biomass and production of *S. filiforme* and *H. wrightii* (Table 1) were each comparable to that of *T. testudinum*, the climax species, in this area (Gallegos et al. 1993).

The 2 populations of *Syringodium filiforme* and *Halodule wrightii* studied had higher horizontal elongation rates (Table 1) than those reported in the northern Gulf of Mexico (Eleuterius 1987), although *S. filiforme* rhizomes grew at rates similar to that reported for the Indian River Lagoon (Florida, USA; Short et al. 1993). Rhizome growth rates for the species investigated were 2- to 4-fold greater than those of *Thalassia testudinum* in the Caribbean (22.3 cm yr$^{-1}$; Gallegos et al. 1993). In addition to their higher growth rate, *S. filiforme* and *H. wrightii* also branched at every 94 and 21.8 cm, respectively, whereas *T. testudinum* produces 1 branch for every 6300 cm of horizontal rhizome (Gallegos et al. unpubl.). Hence, *S. filiforme* and *H. wrightii* are able to colonise and occupy space much faster than

*T. testudinum.* Moreover, the density of flowering *H. wrightii* and *S. filiforme* shoots is about 10- to 50-fold greater than that of *T. testudinum* (Gallegos et al. 1992, 1993), further contributing to the ability of these species to colonise unvegetated sediments faster than the climax species.

The high growth rate and associated high mortality rate of *Syringodium filiforme* and *Halodule wrightii* (Table 1) imply that these pioneer species must have high nutrient requirements (Fourqurean et al. 1992, Short et al. 1993, Duarte 1994). The rapid loss of *S. filiforme* and *H. wrightii* material, which represents the bulk of the abundant seagrass material washed onto the shoreline, associated with the short life-span of their leaves and shoots, must also reduce their capacity for nutrient storage and internal recycling. In contrast, *Thalassia testudinum* grows slower and lives much longer (Gallegos et al. 1993), and should, accordingly, have lower nutrient requirements (Fourqurean et al. 1992, Duarte 1994), and be better able to store and recycle nutrients (Patriquin 1972).

These observations help explain why *Thalassia testudinum* is the climax species in the Caribbean, and why the dense meadows developed by *Syringodium filiforme* and *Halodule wrightii* are eventually replaced by meadows of the longer-lived climax species in oligotrophic Caribbean ecosystems. Our results also demonstrate important differences in the reproductive output and rhizome growth of the 2 pioneer species. The areal density of *H. wrightii* flowering shoots was 5-fold greater than that of *S. filiforme*, which also had a slower rhizome growth and turnover. Hence, *S. filiforme* presents an intermediate reproductive effort, rhizome turnover, and shoot longevity between *H. wrightii* and *T. testudinum*, and indeed occupies an intermediate position in the Caribbean seagrass successional sequence (den Hartog 1971, Williams 1990).

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