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Dynamics of the aboveground and belowground structure of the seagrass *Halodule wrightii*

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ABSTRACT: Dynamics of the aboveground and belowground structure of the seagrass *Halodule wrightii* (Asherson) Asherson was studied from April 1984 to March 1985. Seasonality of plant structure was evident, with the highest abundance of short shoots and belowground structures occurring in June. An inverse relationship between root and rhizome biomass was observed with the former reaching a maximum in February and March, while the latter attained highest values in July and August. The number of short shoots produced per branch varied over the year, ranging from a low of 0.4 to a high of 1.5. The ratio number of branches/rhizome length was relatively constant over the study period with a slight decrease in summer. Examination of underground architecture revealed that, in contrast to plants that have highly branched underground structure, high belowground complexity of *H. wrightii* is achieved by a dense intermingling of many plants with unidirectional rhizomes.

INTRODUCTION

Seagrasses may reproduce predominately vegetatively via underground rhizomes, forming a dynamic belowground system. Although plant ecologists have recently recognized the ecological significance of dynamics of belowground structure and studied the demography, growth and branching patterns of rhizomes and other organs (Sobey & Barkhouse 1977, Bell 1979, Fetcher & Shaver 1983, Room 1983, Hartnett & Bazzaz 1985, Angevine & Handel 1986), little information has been obtained on marine plants. By applying the techniques used primarily in terrestrial systems to marine seagrass beds, information on growth patterns of marine clonal plants can be gathered.

Studies focusing on salt marsh vegetation have provided some information on belowground structures of marine plants; however, a main focus of these investigations has been ratios of aboveground to belowground biomass (e.g. Smith et al. 1979). Another area of interest has been productivity and energy values of belowground plant morphology (Valiela et al. 1976, De la Cruz & Hackney 1977). Schubauer & Hopkinson (1984) examined the belowground biomass of *Spartina alterniflora* Loisel and found an inverse relationship in the peak production times of above- and belowground

biomass, but made no distinction between root and rhizomatous material. In almost all studies of belowground biomass, only combined weights of roots and rhizomes have been reported without quantifying potentially important parameters such as rhizome branching or length which give insight into demography, architecture and energy allocation of clonal plants.

This study focused mainly on the belowground biomass of the seagrass *Halodule wrightii* (Asherson) Asherson, the dominant seagrass in Tampa Bay, Florida. Seasonal changes in biomass of aboveground (short shoot) and belowground (roots and rhizomes) structures were compared over 12 mo. In addition, architecture of rhizome growth and short shoot production was investigated.

MATERIALS AND METHODS

Site. A study site was located on the south side of Courtney Campbell Causeway, Tampa Bay, Florida, USA. This site is in a shallow intertidal zone, often exposed during tidal cycles. The seagrass *Halodule wrightii* is common in Tampa Bay in areas of fluctuating salinity and depths up to 10 m (Dawes 1974). The emergent structure of *H. wrightii* seagrass beds typically senesces in winter with regrowth in spring and

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summer. Annual temperature range is from 19 to 27 °C, and salinity ranges from 21 to 31‰. Mean sediment particle size for the site was 1.33 ϕ (phi units) and organic content was 1.12% over 12 mo of study.

Seagrass morphology. Previous morphological examination of *Halodule wrightii* illustrated that short shoots (tillers) extend upward from an underground rhizome (Fig. 1). Short shoots are 0.5 to 1.0 cm in width and up to 40 cm in length, with rhizomes buried 2 to 9 cm below the surface of the sediment depending upon wave action. The roots of this seagrass extend downward 2 to 5 cm from the rhizome into the sediments, usually attached to the rhizome nodes from which the short shoots extend.

Based upon this information, a sampling and enumeration procedure was devised to determine aboveground biomass, and belowground biomass of rhizomes and roots. In addition, branching pattern of belowground structure and relative position of short shoots to this branching (see Fig. 1) were recorded.

Monitoring of belowground plant biomass was accomplished by collecting eight 14.5 cm² samples from

the intertidal study site approximately monthly from April 1984 to March 1985. Samples were collected with a corer inserted to a depth of 10 cm. The samples were then washed over a 0.5 cm mesh sieve, and returned to the laboratory for analyses. In the lab, each piece of rhizome material was removed from the sieve and the number of short shoots, rhizome internode segments and branches recorded. Rhizomes were then measured and weighed (wet) both with and without their attached roots. Root number was not recorded. The number of branches was then determined as outlined in Fig. 1(B).

RESULTS

The aboveground and belowground abundance data from April 1984 to March 1985 are presented in Figs. 2, 3 and 4. Seasonality in density was evident, with the highest abundance of short shoots, rhizome branches and greatest mean rhizome lengths occurring in June (Fig. 2). The belowground structures showed an inverse relationship between root and rhizome biomass, with July and August being the peak production time of rhizome biomass and February and March yielding the largest biomass of roots (Fig. 3). Although biomass of rhizomes as well as the abundance

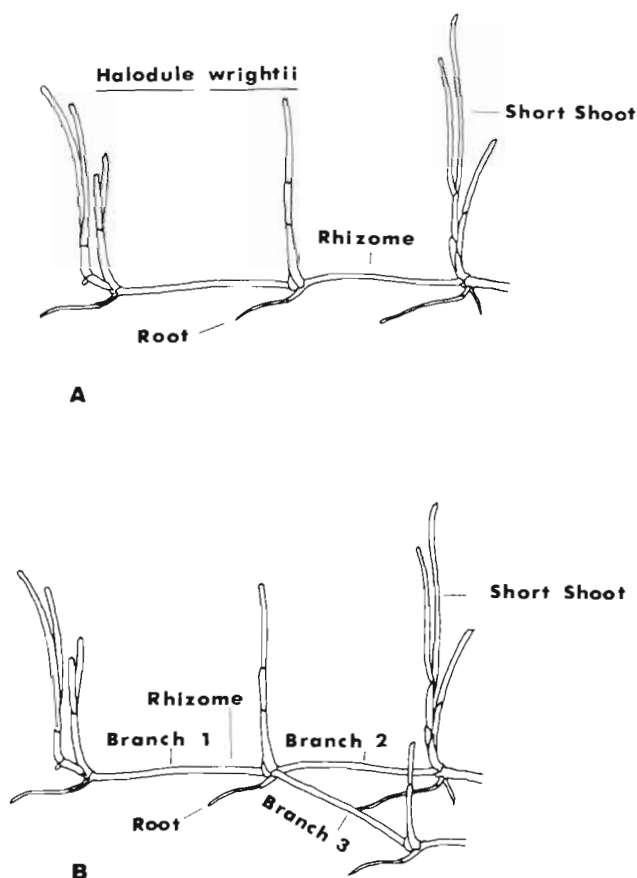


Fig. 1. *Halodule wrightii*. (A) Morphology of seagrass from Tampa Bay, Florida. (B) Specimen with 3 branches and 4 short shoots. Total length = length branch 1 + length branch 2 + length branch 3

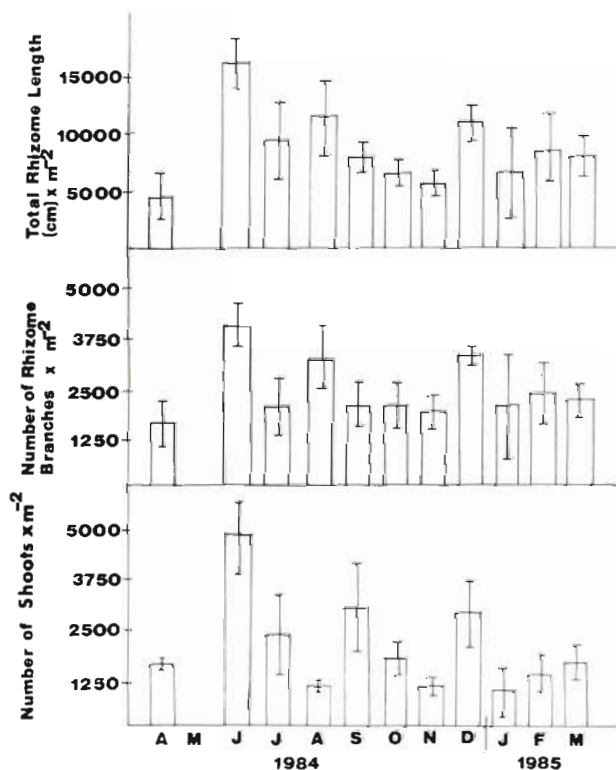


Fig. 2. *Halodule wrightii*. Abundance per m² of short shoots, rhizome branches and rhizome lengths in Tampa Bay from April 1984 to March 1985. All values are shown \pm 1 SE

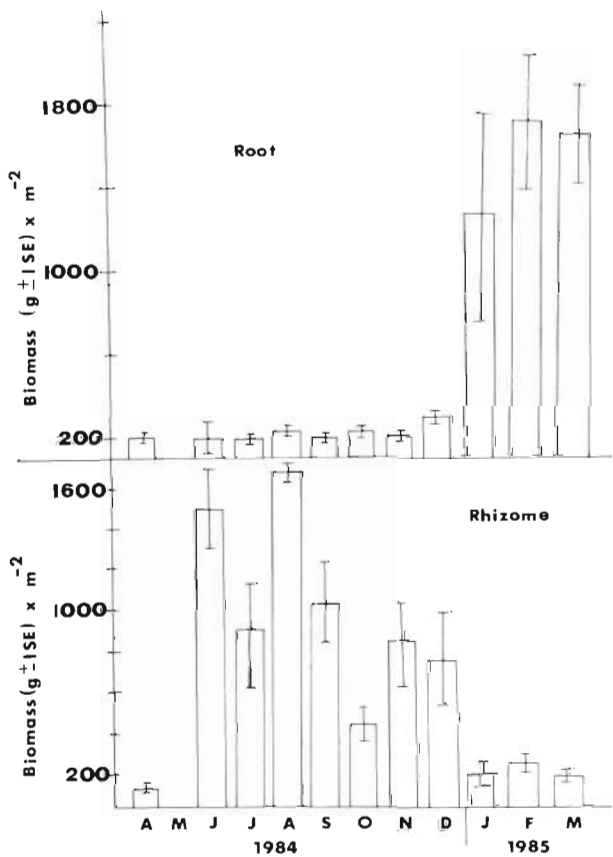


Fig. 3. *Halodule wrightii*. Abundance of root and rhizome biomass per m² from April 1984 to March 1985 in Tampa Bay

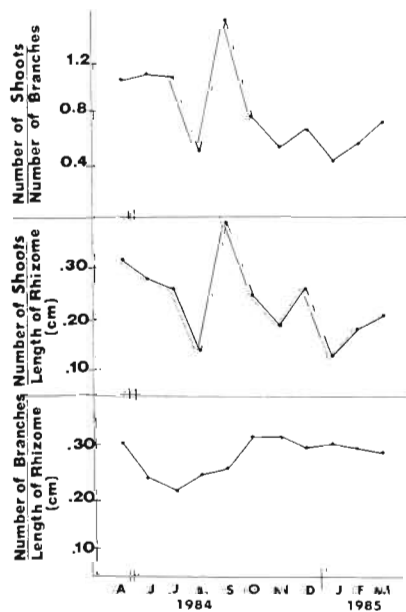


Fig. 4. *Halodule wrightii*. Ratios of above- and belowground components from 1984–1985 in Tampa Bay. All structure is summed for each month for rhizome branches, length and short shoot number

estimates for mean rhizome length, mean branch number and short shoot number were high in June, root biomass values remained among the lowest values recorded at this time.

Monthly ratios between the number of short shoots and number of rhizome branches and length of rhizome, and short shoot and number of branches (Fig. 4) give insight into the dynamics of belowground plant architecture. The maximum short shoot/branch value of 1.5 indicates, for example, that for each branch in September, one and a half short shoots are produced. The ratio of number of short shoots produced per branch varied from a low of 0.4 (January) to a high of 1.5 (September) over the year. The maximum short shoot/length value of 0.39 indicates that on average, a short shoot is initiated approximately every 3 cm along the rhizome system. The ratio between the number of branches and rhizome length remained fairly constant year round in the seagrass bed, with a slight depression in summer (Fig. 4).

DISCUSSION

Plant architecture

The results obtained from this 1 yr study indicate a seasonality in both aboveground and belowground plant structure. An inverse relationship existed between peaks of abundance for root and rhizome biomass (Fig. 3). An inverse relationship between root and rhizome biomass for the salt marsh grass *Spartina alterniflora* (Valiela et al. 1976, Livingstone & Patriquin 1981, Schubauer & Hopkinson 1984) has also been reported. The pattern found by these authors are similar to those found in the seagrass *Halodule wrightii* system which shows a rapid production of both above- and belowground parts in June, an increase in rhizome biomass in August, followed by an increase of root productivity in January, February and March.

Much of the variation in belowground abundance of plant structures may be related to seasonal patterns in the allocation of energy sources. The rhizomes of the seagrasses *Thalassia testudinum* König ex Banks, *Halodule wrightii*, and *Syringodium filiforme* Kützing have been shown to contain high levels of soluble carbohydrates in the fall and low amounts in the spring, which precedes rhizome extension and increased short shoot growth (Dawes & Lawrence 1980, 1983). Thus a relative shift from assimilation of biomass and production to translocation and storage in the rhizome could occur with a subsequent re-allocation to root production to support spring and summer growth.

Branching patterns, lengths, numbers and diameters of rhizomes are important determinants of below-

ground structural complexity (architecture, *sensu* Bell 1979). Terrestrial plant ecologists have repeatedly examined rhizome growth and branching patterns in relation to the morphology of clonal growth and demographic characteristics. Smith & Palmer (1976) and Bell (1974, 1979) focused on the branching angles of rhizomatous species. Their work suggests that highly geometric branching patterns allow for an efficient means of exploration and exploitation of the surrounding substrate and a highly predictable underground architecture. Bell & Tomlinson (1980) identified 3 basic types of branching patterns in clonal plants: based on (1) a 60° branching angle, (2) a 45° angle and (3) those with a predominately linear (unidirectional) component. Most seagrasses fall into the latter category (Tomlinson & Vargo 1966, Tomlinson 1974). This concurs with the pattern observed for *Halodule wrightii* (Figs. 1 and 4).

Little information is available on the belowground characteristics of seagrass species. Kuo & Cambridge (1978) examined the morphology, anatomy and histochemistry of the Australian seagrass *Posidonia australis* Hook f., although no ecological information was included in their study. The observations made in the present and previous studies (e.g. Bell & Tomlinson 1980) revealed no orderly geometric patterns to the belowground architecture of *Halodule wrightii* as compared to those found in *Syringodium filiforme* or many terrestrial clonal perennials. However, despite the lack of any organized geometric pattern, a high short-shoot and rhizome abundance with intertwining of the rhizome systems of adjacent plants was observed in the present study. This suggests that the belowground parts of *H. wrightii* nevertheless form a dense and complex underground structural network. High belowground complexity can be achieved by a single plant with a highly branched underground system (Bell 1979) as well as by the dense intermingling of many unidirectional rhizomes (Hartnett 1983) as was true for *H. wrightii*.

The physical structure or architecture of rhizome systems and other underground parts has several ecological consequences. First, patterns of rhizome growth and branching influence the population dynamics, growth patterns, and persistence of plant clones (e.g. Harper 1977, Hartnett & Bazzaz 1985). Also, patterns of rhizome development are important in substrate stabilization, enabling many clonal plants to colonize unstable substrates in disturbed sites (Fetcher & Shaver 1979). In addition, the physical structure or architecture of vegetation which has been shown to influence the organization of animal communities associated with aboveground vegetation in terrestrial systems (Southwood et al. 1979, Stinson & Brown 1983) may also apply to belowground systems. The relation-

ship between belowground vegetation structure and associated fauna has yet to be adequately explored. This is especially true in marine systems where the architecture and dynamics of the rhizome system or other belowground parts have also been largely ignored.

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