

# Variability of *Spartina alterniflora* primary production in the euhaline North Inlet estuary

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**ABSTRACT:** Monthly live and dead aboveground and belowground biomass and decomposition rates of *Spartina alterniflora* were observed spatially and temporally in the North Inlet euhaline marsh-estuarine system. All areas exhibited seasonal patterns, but Creekside live aboveground biomass varied significantly year-to-year. Creekside live biomass was higher during the years following depressed winter-spring salinities in North Inlet. Salinity depression in North Inlet appears to be correlated with increased rainfall. Net aboveground primary production averaged 2188 g m<sup>-2</sup> yr<sup>-1</sup> for Creekside, 724 g m<sup>-2</sup> yr<sup>-1</sup> for Midmarsh and 1295 g m<sup>-2</sup> yr<sup>-1</sup> for Highmarsh. Net belowground primary production was 2363 g m<sup>-2</sup> yr<sup>-1</sup> for Creekside and 5445 g m<sup>-2</sup> yr<sup>-1</sup> for Highmarsh. Total production for *S. alterniflora* was the highest yet reported. Turnover rates ranged from 0.7 to 5.1 yr<sup>-1</sup>, the highest value occurring in the aboveground Highmarsh.

## INTRODUCTION

Primary producers usually control the amount of energy and matter entering an ecosystem and thus form the basis of many food webs. An accurate measurement of primary production is thus essential to the understanding of ecosystem structure and function. In the marsh-estuarine ecosystems of the east coast of the United States, *Spartina alterniflora* Loisel. is often the dominant emergent vascular plant and varies in height from a tall (1.5 m) form at the creekbanks to a short (0.5 m) form high in the marsh near the uplands. Because of their high productivity and location in the rapidly developing coastal zone, *Spartina* marshes have been extensively studied (Keefe 1972, Turner 1976).

In vascular plants, total primary production is the sum of below- and aboveground production. Few studies (Schubauer & Hopkinson 1984) have addressed aerial and belowground production of *Spartina* simultaneously. Because of the labor-intensive aspects of the harvest methods usually employed in emergent macrophyte production studies, statistical accuracy is usually low as sampling is limited to at best 1 yr of monthly observations.

Differences in *Spartina* production exhibited by different height forms within a marsh and similar height

forms in different systems are attributed to variations in soil water movement, tidal range, temperature, insolation, length of growing season, salinity, and nutrient availability (Turner 1976, Shew et al. 1981, Wiegert et al. 1983). As part of a larger ecosystem level study, it is the objective of this study to determine the net primary production of *S. alterniflora* both spatially and temporally in the extensively studied North Inlet, South Carolina marsh-estuarine ecosystem and to identify possible factors which cause year-to-year variability.

## DESCRIPTION OF AREA

North Inlet near Georgetown, South Carolina (Fig. 1) is an extensively studied marsh-estuarine system covering 32 km<sup>2</sup>. *Spartina alterniflora* is the dominant emergent vascular plant in this system and grades from a tall form on the creek banks through a medium form to a short form near the uplands. At mean tide, *S. alterniflora* salt marsh covers 75.2 % of the total area with the remaining area being creeks, oyster reefs and mud/sand flats. The system is ocean-dominated by semi-diurnal tides with a mean range of 1.4 m and maximum range of 2.4 m. There is also an annual cycle of sea level rise and fall due to cycles in sea temperature and atmospheric pressure which result in the

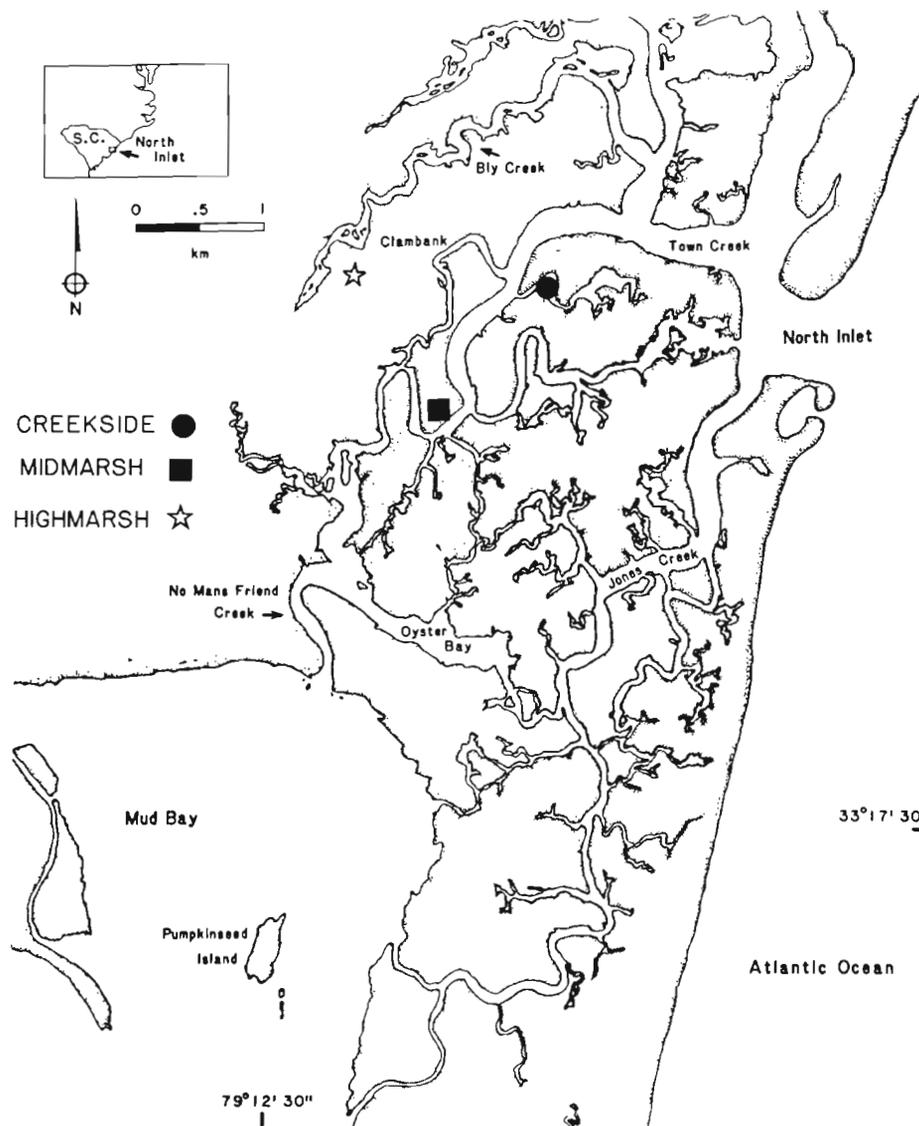


Fig. 1. Location of sample sites within the North Inlet marsh-estuarine system

marsh being covered by water 42 % of the time in October compared to 27 % of the time in January with an average coverage of 30 % (Kjerfve et al. 1978). Salinity is near-oceanic, having a yearly-average salinity of 34.6 ppt. Fresh water input from groundwater, surface runoff and rainfall is generally low (Kerfve et al. 1982).

#### METHODS

Because of the spatial variation in height forms, 3 sites (Fig. 1) with near-homogeneous distributions of stands of tall, medium and short *Spartina alterniflora* were chosen for study. The Creekside site covered by tall *S. alterniflora* encompassed the edges of Bread and Butter Creek to a horizontal distance of 3 m from the Creek edge. The Midmarsh site covered by medium

height *S. alterniflora* is located off Town Creek (40 m × 100 m) and the Highmarsh site covered by short *S. alterniflora* is located at the upper reaches of Bly Creek (30 m × 70 m). The sites were sufficiently large to ensure no sample plot would be resampled over the duration of the study.

**Aboveground methods.** The harvest method of Shew et al. (1981) was used to determine net aboveground primary production (NAPP). In this method, it is assumed that (1) the study sites are homogenous with respect to plant distribution and height, (2) the removal of dead material has no effect on the mortality of live plants and (3) there is no loss of material from a site between samplings. The first assumption was justified by choosing sites based on uniformity of plant size, distribution and monospecificity. Initial experiments showed  $\frac{1}{4}$  m<sup>2</sup> sample plofs were equivalent to  $\frac{1}{2}$  m<sup>2</sup>

plots in determining live biomass estimates, thus the smaller size was used. These observations also indicated that 10 Creekside, 15 Midmarsh and 5 Highmarsh replicates provided mean estimates with less than 20 % variability. Sites with sufficient area were selected so that 10 % of the total site area would be cut in 5 yr of monthly sampling. The validity of the second assumption was verified by comparing growth data from plots containing dead material to plots in which dead material had been removed (Dame unpubl.). The final assumption was satisfied by utilizing 1.5 m tall screen cages (1 mm mesh) to minimize tidal influences and litter bags to estimate decomposition between samplings.

NAPP was determined monthly from June 1981 to October 1985 utilizing the methods of Shew et al. (1981) as follows: 2 replicates (A and B) were designated at the first visit. Plot A was clear cut on the initial visit with all plant material and detritus removed. This material was later divided into live plant, dead plant parts, and other dead material. Dead material is defined subjectively as plant material which is less than 10 % green. On the initial visit, Plot B was cleared of all standing dead plants and detritus, but not attached dead parts, then a screen cage open at the top was placed over Plot B. On the return visit about 1 mo later, the screen cage was removed and Plot B was clear cut with material divided into live and dead. All samples were refrigerated (not frozen) until sorted. The sorted samples were dried in an oven at 100 °C for 48 h and weighed to the nearest 0.1 g.

Beginning in September 1982, decomposition rates of leaves and shoots were estimated for 5 samples from each zone each month. Initial live material was washed, air dried for 48 h, weighed, and subdivided into 2 portions. One portion was returned to the appropriate site in 1 mm mesh bags and the other portion was oven dried for 48 h at 100 °C and weighed. After about 25 d the initial bagged portion was collected, washed and oven dried as before. The percent decomposition or disappearance was determined by dividing the difference between the initial and final weights by the initial weight and multiplying by 100.

The calculated aboveground values were: change in live material ( $\Delta L$ ), mortality (M), and net aerial primary production (NAPP). Change in live material was the difference in mean live standing crop at time  $t_1$  and time  $t_2$  for the same site. Mortality was estimated by subtracting the dead parts in Plot A from the dead material in the return Plot B over the monthly interval. Decomposition (D) was calculated by multiplying the dead biomass in each plot by the appropriate decomposition rate determined above. For the time before September 1982, average decomposition rates from observed months were utilized for the appropriate

sites. The value for NAPP was the sum of  $\Delta L$ , and M, and D. To maintain statistical consistency, both positive and negative values for  $\Delta L$ , M and D were utilized.

*Belowground methods.* Belowground biomass and production were estimated every other month from July 1983 to September 1984 for the Creekside and Highmarsh sites. Statistical analysis indicated 8 cores from Creekside and 12 cores from Highmarsh were necessary to obtain no more than 20 % variability about the mean. Cores were taken within 10 d from plots harvested the previous month for aboveground productivity. The coring device was a plastic pipe 10.2 cm in diameter (0.00817 m<sup>2</sup>) and 40 cm long with the edge sharpened at one end. The core samples were washed, sieved (1 mm pore size), animals were removed, and live root/rhizome material was separated from dead material by color and texture (Valiela et al. 1976). The live and dead samples were dried separately at 100 °C for 48 h and then weighed. Because of the large quantity of sand present in the dead Highmarsh samples, subsamples of this material were burned in a muffle furnace at 550 °C for 6 h to estimate sediment content in order to correct the biomass measurements.

Yearly net belowground primary production (NBPP) was calculated by the Smalley (1959) method which considers change in live and dead material, without determining decomposition rates. Computation of NBPP per sampling interval was as follows: (1) if changes in both live and dead material are positive for a time interval, NBPP equals the sum of those changes; (2) if changes in both live and dead material are negative, then production is zero; (3) if live biomass decreased through the interval and dead material increased, and if their algebraic sum is positive, then NBPP equals that value, however if the algebraic sum is negative, NBPP is zero; and (4) if live material increased and dead material decreased through the interval, NBPP equals the live biomass value. The values for each time interval are summed to provide an estimate of annual NBPP (Shew et al. 1981).

## RESULTS AND DISCUSSION

The amount of live aboveground material was highest at the Creekside site, varying from 75 to 1150 g m<sup>-2</sup> (Fig. 2). Live aboveground biomass was lowest at the Midmarsh site ranging from 25 to 310 g m<sup>-2</sup> (Fig. 2). The amount of live leaf and shoot biomass was intermediate in value at the Highmarsh site varying from 25 to 350 g m<sup>-2</sup> (Fig. 2).

Spatial heterogeneity in aboveground density, height, and production has long been observed in *Spartina alterniflora* marshes. There is usually a gra-

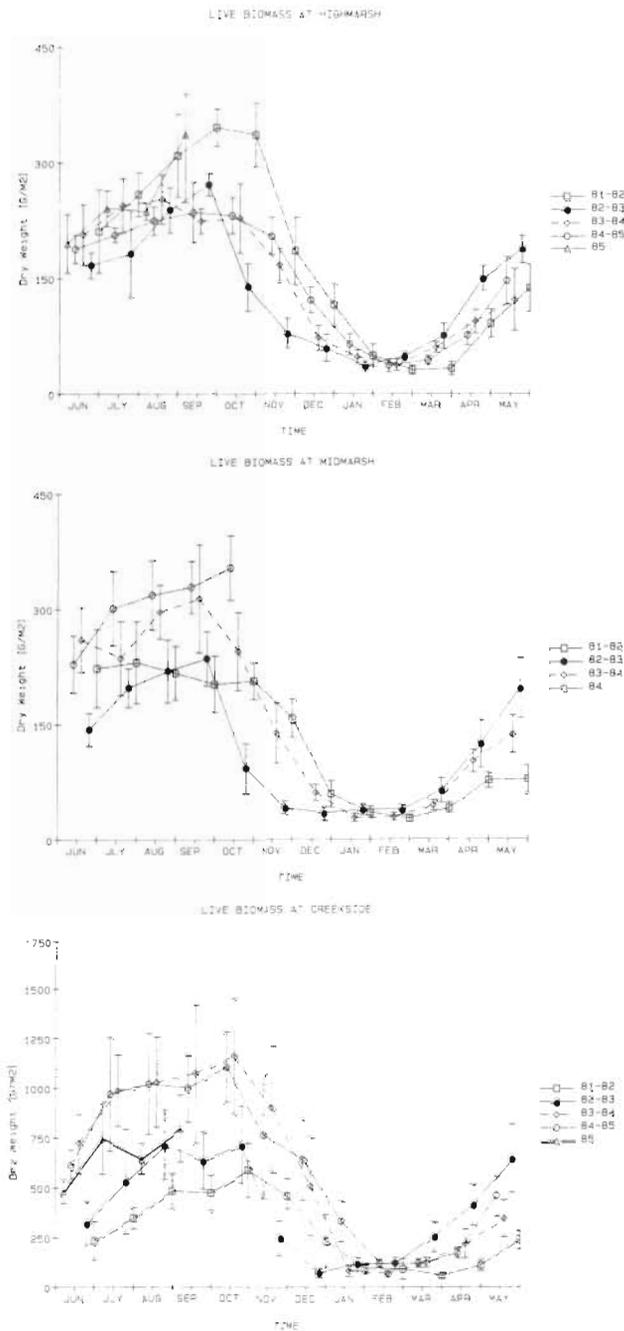


Fig. 2. Monthly aboveground live biomass at the Highmarsh, Midmarsh and Creekside sites. Vertical bars: 95 % CI

gradient in plant size from Creekside to Highmarsh, but in North Inlet, biomass  $m^{-2}$  is lower at the Midmarsh site. These low values at the Midmarsh site seem to be a function of an abundance of relatively light (weak) individuals with a low density distribution (Table 1). While we did observe a high-to-low gradient of stem height, no gradient was observed for productivity with very low NAPP in the Midmarsh and higher production in Creekside and Highmarsh. From our observations,

Table 1. *Spartina alterniflora*. Comparison of mean  $\pm$  standard error of stem weight, height and density in Creekside, Midmarsh and Highmarsh zones in North Inlet in August 1982

Parameter	Zone		
	Creekside	Midmarsh	Highmarsh
Weight (g)	$5.1 \pm 0.5$	$1.6 \pm 0.1$	$0.3 \pm 0.02$
Height (cm)	$158.2 \pm 5.4$	$96.9 \pm 4.0$	$50.2 \pm 4.2$
Density (no. $m^{-2}$ )	$120.4 \pm 9.7$	$154.4 \pm 7.6$	$1068.6 \pm 101.6$

the Midmarsh site appeared to have more standing water. This may be due to the fact that the Midmarsh site is lower than the Creekside levees and also lower than the Highmarsh. Thus it is possible that stagnant conditions (standing water) resulted in low aerial biomass and in turn low NAPP for Midmarsh. Two types of hypotheses based on genetic and environmental variation have been proposed to explain the observed differences in these parameters. Electrophoretic studies by Shea et al. (1975) and transplant studies by Valiela et al. (1978) have failed to show genetic differences between plants from different zones. Wiegert et al. (1983) proposed that stagnant water reduces iron availability and increases free hydrogen sulfide. The latter accumulates in stagnant conditions and may reduce nitrogen uptake by the plants. Anoxia may also influence root function.

Similar seasonal cycles in abundance of aboveground live and dead biomass were observed each year at each site. The quantity of live material reached a maximum in late summer and early fall. Although the relative biomass was larger, the same seasonal pattern was observed at Sapelo Island, Georgia (Schubauer & Hopkinson 1984). The abundance of dead material (Fig. 3) reached a maximum in winter and was about 6 mo out of phase with respect to live material. The variations in abundance of dead material in North Inlet exhibited a much more defined seasonal pattern than Sapelo Island. This pattern may be the result of colder winters at the more northern location causing more complete die-back in aboveground vegetation.

The Creekside site showed a large amount of variation in live biomass from summer to summer with 1983 and 1984 biomass being significantly higher than 1981, 1982 and 1985. The variation in aboveground biomass at Creekside and possibly Midmarsh may be attributable to changes in the environment. Numerous studies (Adams 1963, Haines & Dunn 1976, Mendelsohn & Marcellus 1976, Zedler et al. 1980, Linthurst & Blum 1981, Linthurst & Seneca 1981) have shown that aerial growth rates in *Spartina alterniflora* are reduced

as salinity increases. At high salinities, it is thought that more energy is expended by the plants on metabolic regulation and internal ion balance than on growth process (Haines & Dunn 1976). However, Longstreth & Strain (1977) concluded from laboratory studies that the effects of salinity stress in *S. alterniflora* growth can be offset by increased illumination.

Aerial growth of Creekside *Spartina alterniflora* increased rapidly during the first half of 1983 and 1984

(Fig. 2). Monthly measurements of salinity and the amount of rainfall in the North Inlet area during the study period are given in Fig. 4. From these data, it is suggested that there was much more rain and thus lower salinities in North Inlet during the late winter and spring (January to May) of 1983 and 1984. The coincidence of the periods of reduced salinity with that of high growth in Creekside *S. alterniflora* suggests that elevated amounts of rainfall and concurrent reduction in salinities due to upland runoff and rainfall may lead to changes in primary productivity. Adams (1963) noted that rainfall decreased soil salinity for varying periods of time in North Carolina marshes. Although rain fell over the entire marsh, the Creekside area has higher infiltration into its sediments (Wiegert et al. 1983) and is also covered by the tides a greater proportion of the time. This site might therefore be more likely to show a response to reduced salinities than the corresponding Highmarsh or Midmarsh sites. A concurrent study (Wolaver pers. comm.) of soil salinity profiles indicated lower salinities in the Creekside marsh soils at this time.

Monthly decomposition rates of aerial biomass are shown in Fig. 5. Month-to-month variations in the rate of biomass disappearance from the mesh bags varied from not detectable to 35 %. A seasonal variation in the rates was also observed; the summer decomposition proceeding faster than that of the winter. These rates are comparable to those reported by Kirby & Gosselink (1976) in Louisiana, Kruczynski et al. (1978) in Florida, and Odum & De La Cruz (1967) in Georgia *Spartina alterniflora* marshes. Unlike Marinucci (1982), who concluded that rates of decomposition were higher with increasing tidal inundation, we found increasing decomposition rates from Creekside to Highmarsh. McKee & Seneca (1982) observed a similar occurrence in several North Carolina marshes and attributed lower rates of decay in Creekside plants to greater amounts of stem tissue.

The monthly measurements of NAPP were summed to yield yearly values (Table 2). In the harvest method, NAPP integrates accumulated biomass over long periods of time. Mean NAPP was highest at Creekside ( $2069 \text{ g m}^{-2} \text{ yr}^{-1}$ ), then Highmarsh ( $1113 \text{ g m}^{-2} \text{ yr}^{-1}$ ) and finally lowest at Midmarsh ( $649 \text{ g m}^{-2} \text{ yr}^{-1}$ ). Year-to-year NAPP varied about 25 % for Creekside, 12 % for Midmarsh and 3 % for Highmarsh, i.e. within our 20 % variability limits for sampling live biomass.

The validity of comparing NAPP values in salt marshes is confounded by the lack of a universally accepted technique and suitable intercalibration experiments. Shew et al. (1981) related their method to a number of previously reported methods by comparing calculated turnover rates with turnover rates determined from longevity experiments (Table 3). Because

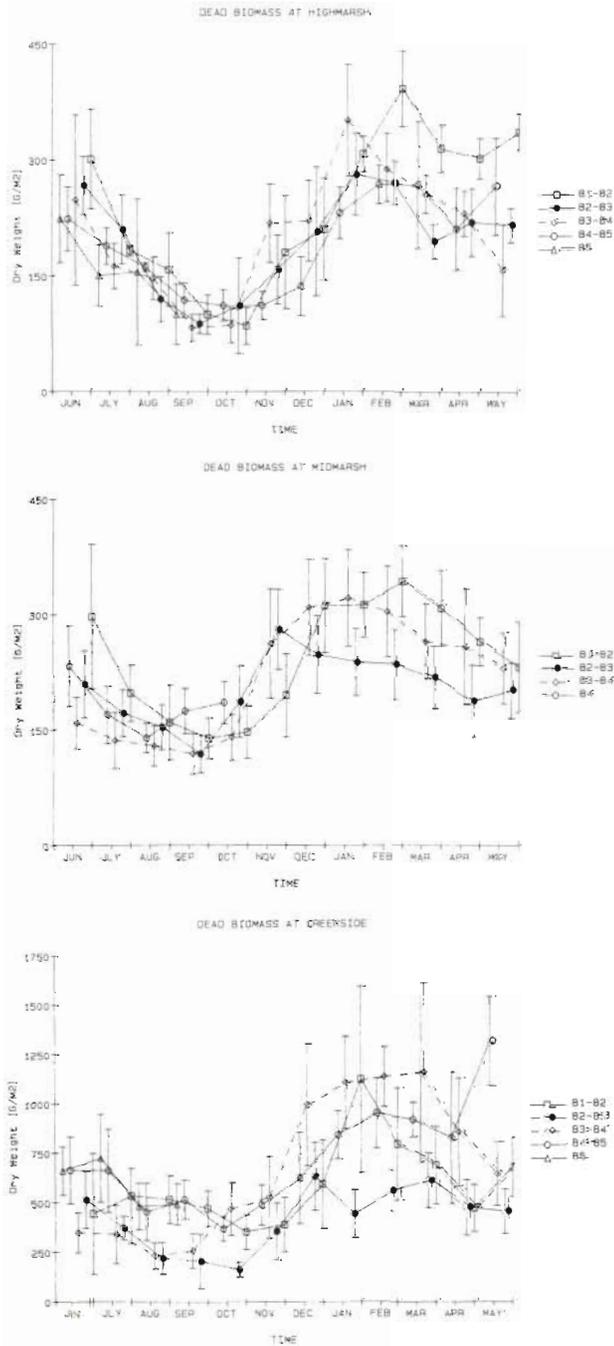


Fig. 3. Monthly aboveground dead biomass at Highmarsh, Midmarsh and Creekside sites. Vertical bars: 95 % CI

NAPP was also known for the various studies, the turnover data also implied under- or overestimates of NAPP. In general, the peak standing crop methods of Milner & Hughes (1968) and Smalley (1959) lead to underestimates, while the methods of Wiegert & Evans (1964) and Lomnicki et al. (1968) lead to overestimates. The modified Lomnicki et al. (1968) or Shew et al. (1981) method utilized in this study is thought to be a slight overestimate. Within the limits of the data, it appears that the Highmarsh NAPP ( $1284 \text{ g m}^{-2} \text{ yr}^{-1}$ ) for North Inlet is a higher NAPP than that determined by Shew et al. (1981) for a North Carolina highmarsh ( $454 \text{ g m}^{-2} \text{ yr}^{-1}$ ). In contrast, estimates of NAPP for North Inlet Creekside ( $2031 \text{ g m}^{-2} \text{ yr}^{-1}$ ) and Highmarsh ( $1284 \text{ g m}^{-2} \text{ yr}^{-1}$ ) are lower than those reported for Sapelo Island, Georgia ( $3700$  and  $1538 \text{ g m}^{-2} \text{ yr}^{-1}$ , respectively) by Gallagher et al. (1980) utilizing a modified Wiegert & Evans (1964) method.

Unlike aboveground live biomass, belowground live biomass in North Inlet was greatest at the Highmarsh site, ranging from  $2500$  to  $5000 \text{ g m}^{-2}$  (Fig. 6). Live material varied from  $1500$  to  $3300 \text{ g m}^{-2}$  at the Creekside site (Fig. 6).

The amount of live material belowground in North Inlet was less than that observed in Georgia (Schubauer & Hopkinson 1984) and Massachusetts (Valiela et al. 1976). Seasonal cycles in the abundance of live and dead belowground material were also observed in North Inlet. The amount of live material reached a maximum in the fall. The amount of below-

Table 2. *Spartina alterniflora*. Net aerial primary production ( $\text{g m}^{-2} \text{ yr}^{-1}$ ) for the different zones in the North Inlet marsh

Time	Creekside	Midmarsh	Highmarsh
Jun 81–May 82	1755	778	1313
Jun 82–May 83	2350	817	1301
Jun 83–May 84	2460	729	1272
Jun 84–May 85	1602		1250

Table 3. *Spartina alterniflora*. Turnover or P/B rates (times  $\text{yr}^{-1}$ ) for aboveground and belowground marsh. Aboveground values are means for 3 yr; all ratios computed with peak live and peak dead values

	Creekside		Midmarsh		Highmarsh	
	Live	Dead	Live	Dead	Live	Dead
Aboveground	2.1	2.2	2.3	2.1	5.1	3.2
Belowground	0.7	1.1	–	–	1.1	1.4

ground dead material reached a maximum in winter and spring at the Creekside site and in summer at the Highmarsh site. The greatest maximum in live biomass occurred at similar times above and belowground at both Creekside and Highmarsh. These results contrast with those of Schubauer & Hopkinson (1984) who found a temporal asynchrony between belowground and aboveground biomass abundance in Georgia

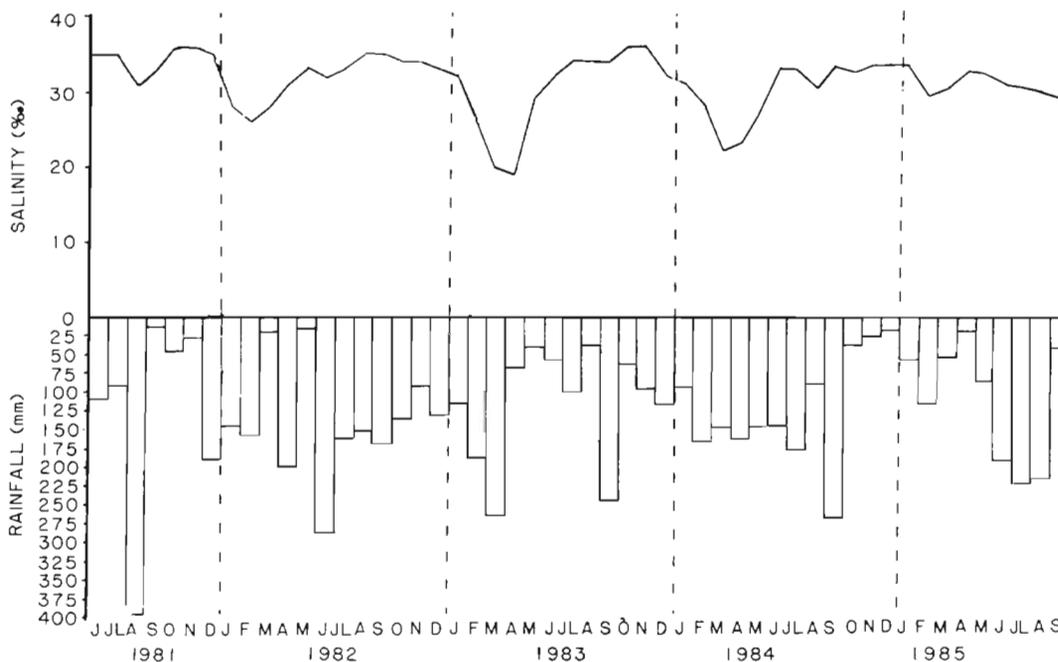


Fig. 4. Monthly accumulated rainfall from Hobcaw Plantation near Georgetown, South Carolina, and mean monthly salinities of daily water samples taken at Clambank in North Inlet (Fig. 1)

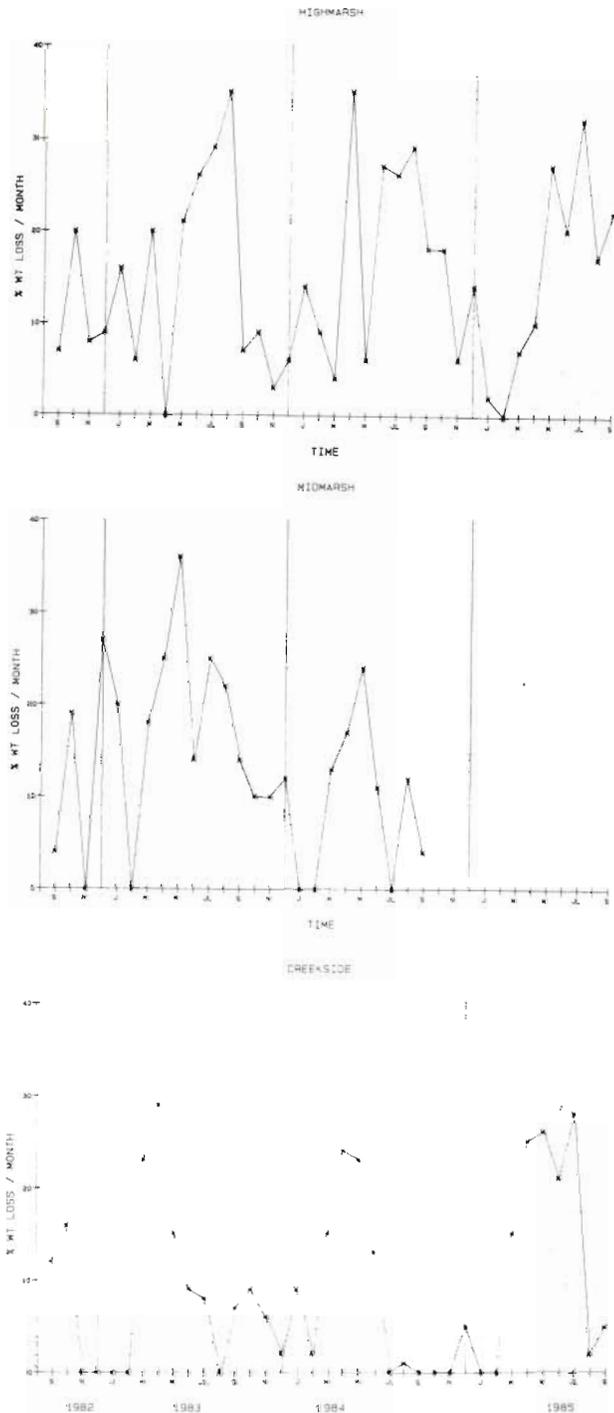


Fig. 5. Aboveground decomposition rates of macrodetritus in North Inlet

marshes. They interpreted their data to mean aboveground organic material was being stored belowground in winter and then utilized for growth in spring.

Net belowground primary production (NBPP) of *Spartina alterniflora* in North Inlet ranged from 2,363 g m<sup>-2</sup> yr<sup>-1</sup> at Creekside to 5445 g m<sup>-2</sup> yr<sup>-1</sup> at High-

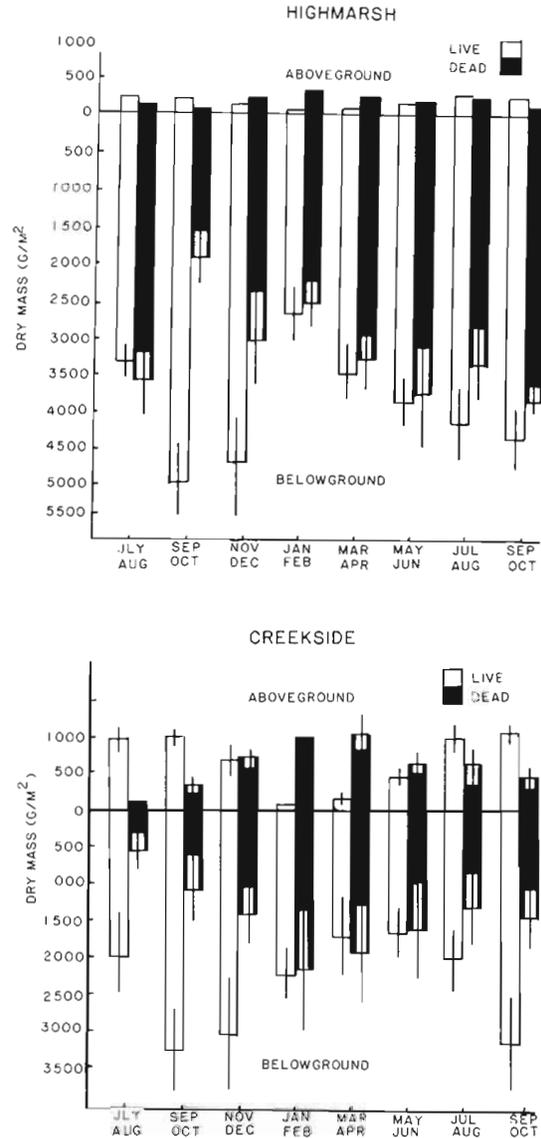


Fig. 6. Above- and belowground live and dead biomass with 95 % CI for Highmarsh and Creekside, 1983-1984

marsh site and are among the highest values reported (Table 4). However, our observed NBPP of *S. alterniflora* in North Inlet was below the theoretical limits of belowground production (6500 g C m<sup>-2</sup> yr<sup>-1</sup>) for Sapelo Island, Georgia, as estimated by Morris et al. (1984). We utilized the Smalley (1959) method to calculate NBPP; it is thought to be a slight underestimate of net primary production because this method, although advocated by Schubauer & Hopkinson (1984), does not take into account loss of biomass by decomposition.

Total net primary production for *Spartina alterniflora* in 1983-1984 varied from 4833 g m<sup>-2</sup> yr<sup>-1</sup> at Creekside to 6717 g m<sup>-2</sup> yr<sup>-1</sup> at Highmarsh. These values are similar to the previously reported high of 7620 g m<sup>-2</sup> yr<sup>-1</sup> for medium *S. alterniflora* in Georgia

(Schubauer & Hopkins 1984). The method we used to estimate NAPP is generally thought to give lower values than the preceding authors', although we utilized essentially the same NBPP methods.

Turnover rates offer estimates of how fast a given component is being replaced within a system, providing information on the dynamic aspects of that component. The turnover rates (NAPP/maximum biomass) of aboveground live *Spartina alterniflora* in North Inlet ranged from 2.1 times  $\text{yr}^{-1}$  at Creekside and Midmarsh to 5.1 times  $\text{yr}^{-1}$  in Highmarsh (Table 3). Year-to-year variation within a given site was 21 to 30 %. The North Inlet turnover rates encompass those reported by Hopkinson et al. (1978) of 3.5 times  $\text{yr}^{-1}$  in Louisiana and are higher than those of Shew et al. (1981) of 1.9 times  $\text{yr}^{-1}$  for a Highmarsh in North Carolina. The turnover rates for dead aerial material were similar, ranging from 2.1 to 3.2 times  $\text{yr}^{-1}$ . Belowground turnover rates for live material range from 0.7 times  $\text{yr}^{-1}$  for Creekside to 1.1 times  $\text{yr}^{-1}$  for Highmarsh. Dead belowground material turnover rates were 1.1 and 1.4 times  $\text{yr}^{-1}$  respectively. In contrast to North Inlet, turnover rates for dead marsh materials in Georgia (Schubauer & Hopkins 1984) and Massachusetts (Valiela et al. 1976) were always lower than those for live materials.

The magnitudes of the ratio of live belowground to aboveground material (root-to-shoot ratio) are thought to be reflections on the stressfulness of the environment on plants (Valiela et al. 1976). High values of this ratio indicate more stress. These ratios vary seasonally in North Inlet from near 2 in summer to 32 in winter (mean 18.3) for Creekside plants. Highmarsh plants had even higher ratios ranging from 6 to 76 (mean 35.2). Summer values for Creekside compare favorably with that of 1.7 found by Schubauer & Hopkins (1984) for a Sapelo Island, Georgia salt marsh. The

ratio of below to aboveground net primary production was 1.0 for Creekside and 4.3 for Highmarsh.

In environments made harsh by the presence of anoxia, nutrient scarcity, and high salinity, etc., reduced water and nutrient uptake per unit root may be overcome by a greater investment of biomass in roots (Hopkinson & Schubauer 1984). In North Inlet, the higher root-to-shoot ratios for *Spartina alterniflora* than in other areas, notably Georgia, may be the result of the higher average salinities this estuarine system normally experiences.

The conversion of solar energy via photosynthesis into *Spartina* biomass available to heterotrophs is an important aspect in the dynamics of the salt marsh system. For North Inlet, the rate of light incidence for 1982–1983, a rainy year, was  $125675 \text{ ly yr}^{-1}$  ( $1.26 \times 10^2 \text{ kcal cm}^{-2} \text{ yr}^{-1}$ ). Utilizing values of 3.2 and 2.6  $\text{kcal g}^{-1}$  the solar conversion efficiencies at Creekside (0.55 %) and Highmarsh (0.28 %) were calculated (Nixon & Oviatt 1973). When belowground net primary production is included, the solar conversion efficiencies are 2.3 % for Creekside and 2.2 % for Highmarsh. Turner (1976) found that the efficiency of solar conversion for aboveground *Spartina* was 0.20 and 0.35 %, with slightly lower values for Highmarsh than for Creekside. On a global scale, Odum (1983) reports an average solar conversion efficiency of 0.1 % and a maximum of 4.0 %.

The spatial heterogeneity of plants in the salt marsh is closely associated with the sediment they live in and the varying influence of tidal inundation. The spatial differences in primary production may be continuous (Wiegert et al. 1983), but for conceptual reasons the marsh is usually divided into specific areas or zones. In North Inlet Highmarsh, numerous small aerial shoots and a large belowground biomass combine for high net

Table 4. *Spartina alterniflora*. Comparison of aboveground and belowground productivity ( $\text{g m}^{-2} \text{ yr}^{-1}$ ) according to location and height form

Area	Height form	Net primary production			Source
		Above	Below	Total	
Nova Scotia	NR	803	1051	1851	Livingstone & Patriquin 1981
Massachusetts	NR	420	3500	3920	Valiela et al. 1976
New Jersey	Short	500	2300	2800	Smith et al. 1979
North Carolina	Short	650	460	1110	Stroud 1976, Stroud & Cooper 1968
	Tall	1300	500	1800	Stroud 1976, Stroud & Cooper 1968
South Carolina	Short	1272	5445	6717	This study
	Medium	775	—	—	This study
	Tall	2460	2363	4833	This study
Georgia	Short	1350	2020	3370	Gallagher & Plumley 1979
	Medium	2840	4780	7620	Schubauer & Hopkins 1984
	Tall	3700	2110	5810	Gallagher & Plumley 1979

NR: Not reported; Short = Highmarsh; Medium = Midmarsh; Tall = Creekside

primary production. Creekside marsh is typified by large less numerous plants with an equivalent below-ground biomass which also yields high net primary production. Midmarsh with weak sparse plants in a water-logged environment has lower NAPP. Thus, *Spartina alterniflora* can be a successful primary producer in a broad range of environments.

It has long been known that *Spartina* exhibited seasonal cycles in growth and mortality both above and belowground. These seasonal cycles seem to be a response to temperature and light. The inter-annual variations in Creekside *S. alterniflora* biomass in North Inlet are thought to be the first report of such a temporal event. In North Inlet estuary, this inter-annual variation in biomass seems to be correlated with rainfall and the concurrent depression of salinity. The implications of grass biomass varying in wet years compared to dry years is striking. Most modeling efforts on marshes have assumed a constancy of plant biomass and productivity which must now be re-examined in view of the present findings. Finally, the amount of plant biomass available to the system for processing and exchange varies from year to year depending on environmental conditions. This variability may induce other changes in the system, particularly in the detritus food chain, which are not immediately obvious during a particularly wet or dry year.

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