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A 5-YR RECORD OF AERIAL PRIMARY PRODUCTION AND STAND CHARACTERISTICS OF *SPARTINA ALTERNIFLORA*¹

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Abstract. The purpose of this paper is to document and explain the interannual variability in aboveground primary productivity from salt marshes at North Inlet, South Carolina. A census method of measuring production was applied to salt marsh sites vegetated by the grass *Spartina alterniflora*, and a statistically significant relationship between stem age and cumulative leaf loss was used to estimate leaf turnover. Aboveground productivity was 2.3 times as large as the positive increment in standing biomass density due to the turnover of stems and leaves, with stem turnover accounting for 33% and leaf turnover 23% of total aboveground productivity. A numerical simulation demonstrated the sensitivity of destructive harvest methods to sampling errors that are propagated by spatial variability.

Monthly measurements, made at one site for >5 yr, document a twofold variation in annual aboveground production, which has important implications for the biogeochemistry and trophic dynamics of estuaries. Positive correlations indicate that mean sea level and/or rainfall are important determinants of annual production, and their effect on sediment salinity is postulated to be the proximate determinant of interannual variation in production. Monthly growth rates and standing biomass densities from two different marshes, both situated at the mean high tide elevation, have been equivalent for 3 yr despite a consistent twofold difference in stem density. Thus, equivalent aboveground productivity was maintained in populations differing in their allocation of photosynthate between stem growth and asexual reproduction.

Key words: biomass density; census technique; growth; long-term data; LTER (long-term ecological research) site; population density; primary production; salt marsh; South Carolina; *Spartina alterniflora*.

INTRODUCTION

A large literature exists on the productivity of the salt marsh grass *Spartina alterniflora* due to its importance in the trophic structure of estuaries, although the great majority of studies of primary production and of related biogeochemical phenomena are based on limited time series of measurements. The aim of this paper is to document and explain the interannual variability in aboveground productivity that we have witnessed during the past five years at the North Inlet Long Term Ecological Research (LTER) site. The magnitude of this interannual variability has important implications for studies of estuarine carbon budgets and related investigations.

We use a nondestructive method of monitoring plant growth, which, like that described by Dickerman et al. (1986), relies on a periodic census of stem populations on permanent quadrats. This method accounts for stem turnover and, with modifications, leaf turnover. Numerical simulations allowed us to compare results of

this method with those of a commonly used harvest technique. Harvest methods have been reviewed by Kirby and Gosselink (1976), Turner (1976), Shew et al. (1981), Dickerman et al. (1986) and others. Singh et al. (1984) have discussed harvest-based estimates of root production and the positive bias generated by spatial variability. Productivity estimates by these methods can differ fourfold, depending on the method of calculation (Dickerman et al. 1986); their sensitivity to spatial variability (Turner 1976) makes harvest methods particularly unsuited to studies where temporal variability is a primary focus, as it is in our investigations of long-term ecosystem dynamics in the North Inlet estuary, South Carolina.

METHODS

Net aboveground production was measured by censusing the heights of all stems on a monthly basis from permanent quadrats, and estimating the masses of the individually tagged stems from allometric equations that had been derived from earlier destructive harvests. This method is most like that described by Dickerman et al. (1986), with the major difference being our

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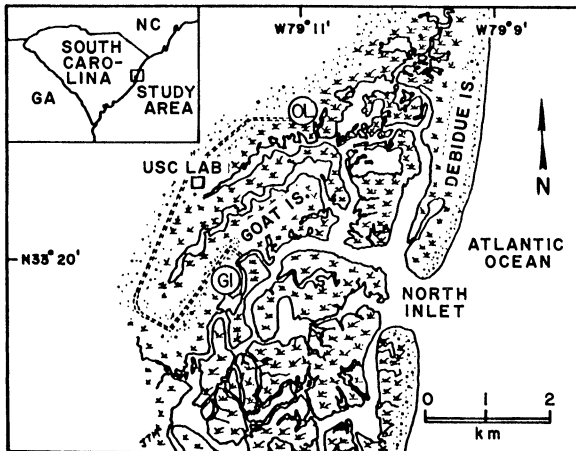


FIG. 1. Locations of the Goat Island (GI) and Oyster Landing (OL) study sites.

monthly calculations of individual stem growth, summed to give monthly total stand growth, as opposed to a summation of annual maximum shoot masses.

Stem populations were censused monthly in six permanent 1-dm² quadrats that were established in May 1984 in a mid-marsh habitat. The site is characterized by a dense population of *Spartina alterniflora* with stem heights generally <30 cm. The plots were located on the east side of Goat Island (Fig. 1) at the North Inlet LTER site near Georgetown, South Carolina (79°12' W, 33°20' N). The site is 70 cm above mean sea level (MSL) at the elevation of mean high tide (MHT). The plots were delineated with plastic stakes, and all stems within plots were tagged with plastic, number-coded bird bands (National Band and Tag Company). Every month the stem heights were recorded, new stems were tagged, and dead stems were noted. An additional site with 6 quadrats was added in 1986, also at MHT, at Oyster Landing (Fig. 1); the size of the quadrats there was increased to 2 dm² to accommodate the same number of stems per quadrat (15) as the Goat Island site.

Polynomial regressions of individual stem mass as functions of stem height were derived from harvests of 5013 *Spartina* stems that were made during March, June, September, and December. Samples were collected annually during these months for several years by harvesting all of the stems within quadrats of 625 cm² size that were located along creek banks, mid- and high-marsh habitats, and in different marshes within the North Inlet system. The harvested plants were returned to the lab, the height of each individual stem from the base to the tip of the longest leaf or inflorescence was recorded, and then the stems were dried (60°C) and weighed. These data were analyzed independently by site and then pooled, with the exception of collections made in September (Table 1), when we determined that no significant differences existed. Fur-

thermore, plants harvested in June were segregated into two classes by height (≤ 50 and > 50 cm, Table 1) to improve the overall fit. Polynomial regressions and analyses of variance were performed using the SAS statistical package (SAS Institute 1982).

Monthly and annual rates of net aboveground production were calculated for each quadrat by summing the positive growth rates of all individual stems, and averaging by site. Computer software was written to transform stem height to mass using precalibrated polynomial regressions (Table 1), and to calculate individual stem growth rates from time series of individual stem heights. Linear interpolation was applied to the coefficients in the polynomial equations to smooth the seasonal changes in the mass–height relationships.

Leaf turnover

Leaves on 20 stems from the censused population at the Goat Island marsh site were tagged with string during May, and were later censused during July, November, and March. The masses of tagged leaves were estimated from harvests of leaves of equal size from adjacent plants. At each leaf census the number of leaves lost since the last census, the age of the stem, and the height of the stem were recorded.

RESULTS

Height and mass relationships

An analysis of covariance performed on the heights and long-transformed stem masses indicated that the mass–height relationship of *Spartina* varied seasonally ($P < .0001$) even when stems > 60 cm height were excluded from the analysis. Stems of a given height that were harvested in June weighed more than stems of equal height that were harvested at other times of year (Fig. 2). Stems harvested in September generally weighed less than stems of the same height that were harvested at other times of year. Thus, it appears that stems either gain mass before elongating or they lose mass, probably as leaves are lost, later in the growing season.

We found no significant differences in the mass–height relationship of plant populations from different locations of the marsh during the months of March, June, and December. However, during September there was a significant difference between the mass–height relationship of low-marsh (creek bank) and mid- and high-marsh plants, and different polynomial equations were used to describe these populations (Table 1). Therefore, allometric relationships derived from one population or location may not adequately describe plants from other physiographic locations. In all groups except June plants > 50 cm, plant height explained $\geq 82\%$ of the variability in plant mass (Table 1).

Spatial heterogeneity

The size of the area of marsh that must be sampled in order to obtain a representative estimate of the

TABLE 1. Least-squares estimates of the coefficients used in the allometric formula $M = c_0 + c_1H + c_2H^2 + c_3H^3 + c_4H^4$, where M is dry plant mass (g) and H is plant height (cm), by month of harvest and area of marsh. The sample size (N) and r^2 for each regression are also given.

Month*	Zone	c_0	c_1	c_2	c_3	c_4	N	r^2
March	All	0	3.10×10^{-3}	-2.40×10^{-5}	1.46×10^{-5}	-6.25×10^{-8}	999	0.88
June: 0–50 cm	All	0	1.20×10^{-2}	-6.74×10^{-4}	2.81×10^{-5}	0	743	0.82
June: >50 cm	All	10.76	-3.27×10^{-1}	3.20×10^{-3}	0	0	154	0.65
September	Low	0	4.59×10^{-2}	2.79×10^{-4}	1.10×10^{-6}	0	243	0.95
September	Mid-high	0	-1.46×10^{-5}	8.60×10^{-4}	9.00×10^{-7}	0	1627	0.95
December	All	0	8.75×10^{-4}	5.17×10^{-4}	1.00×10^{-5}	-9.55×10^{-8}	1247	0.94

* June plant populations were segregated into two height classes, and the coefficients for September data are given for both low marsh (creekbank) and mid-high marsh zones. Plants harvested during other months from all areas of the marsh were pooled.

standing biomass density depends on the spatial heterogeneity of the site. At the Goat Island site we characterized the small-scale (square decimetres) spatial heterogeneity by successively harvesting the standing biomass on 1-dm² plots and computing a mean biomass density each time a new pair of quadrats was analyzed. These results indicated that the actual standing biomass density within a 1-m² area at this site (367 g, Fig. 3) was rapidly approached when 6 of the 1-dm²

quadrats had been harvested, although the asymptote was not reached until the sample size reached 14 quadrats. However, estimates of mean monthly biomass density from the six quadrats at Goat Island (Fig. 5A) and biomass harvests made by Dame and Kenny (1986) at an adjacent marsh site at North Inlet in 1984 gave equivalent results, which indicates that our choice of sample size was a reasonable compromise between accuracy and work load.

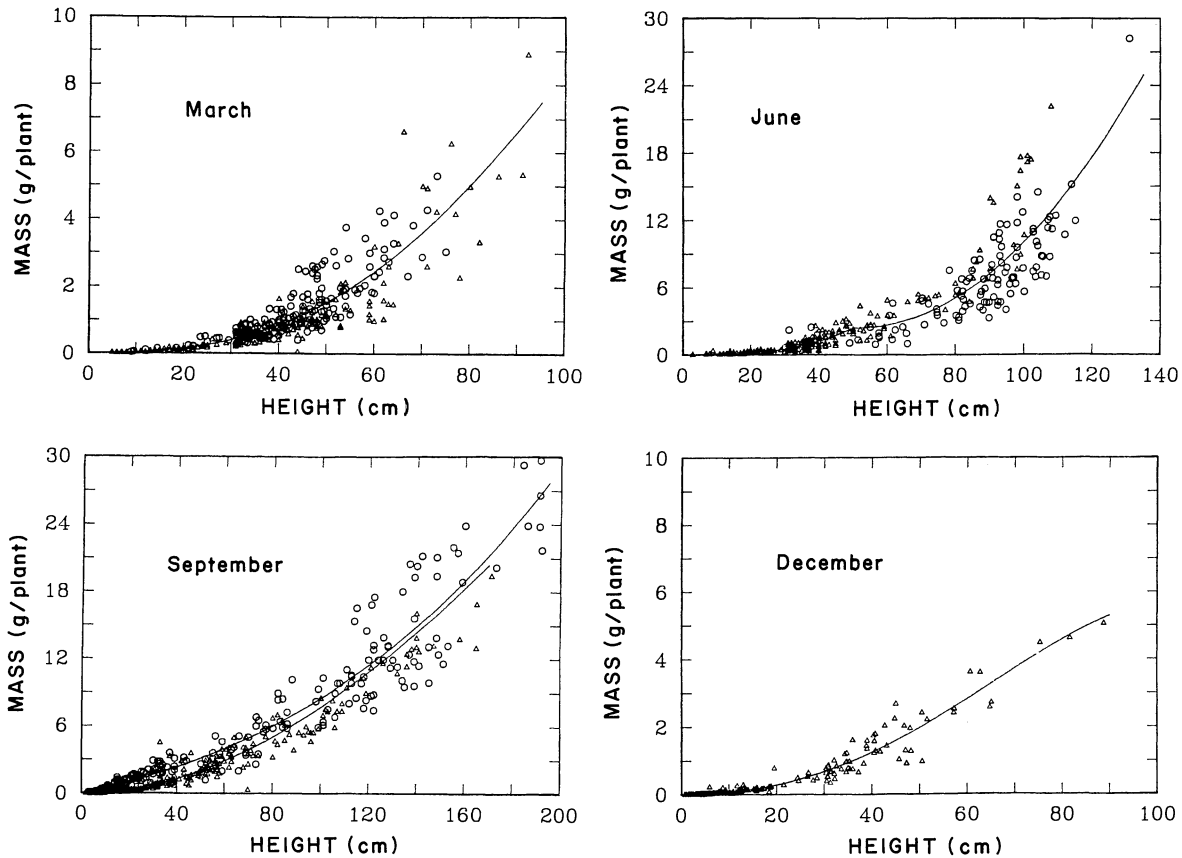


FIG. 2. Total stem dry mass vs. stem height in *Spartina alterniflora* from harvests made at different times of year. Data for plants taken from mid- and high-marsh sites (Δ) and from low-marsh (creek bank) sites (\circ) are plotted, as well as the best-fit polynomial equations.

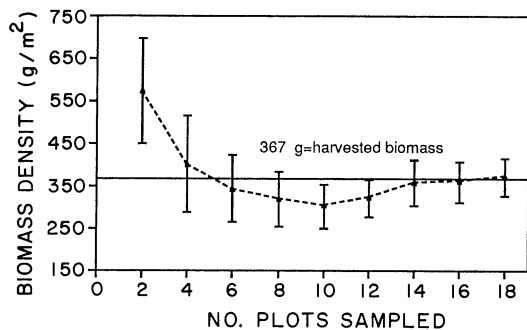


FIG. 3. The standing biomass density (mean ± 1 SE) from successive harvests of pairs of 1-dm² plots within a larger 1-m² plot with standing biomass density of 367 g/m².

Leaf turnover

Analyses of several possible relationships between leaf turnover and stem characteristics revealed that stem age was the best predictor of leaf turnover. Significant relationships ($P < .0001$) were found between stem age and leaf loss when expressed either as a percentage of current stem mass (Fig. 4A), total cumulative mass of leaves lost (Fig. 4B), or total cumulative number of leaves lost (Fig. 4C). This analysis indicates that leaf loss is an important component of net production for stems > 10 mo of age. Stems that live for 18 mo, which is about the maximum life span in the North Inlet marshes, will have lost 160% of their current mass (Fig. 4A).

We calculated net aboveground production with and without corrections for leaf turnover. Without leaf turnover, production was calculated as the sum of the positive monthly differences in individual stem masses as calculated by the allometric equations (Table 1). (Note: The census method automatically accounts for stem turnover provided that stem turnover is less frequent than the census.) When leaf turnover was included, each individual stem mass (M_t) calculated from the allometric equations was modified using an empirical relationship between leaf loss and stem age (Fig. 4A). A "phantom" mass (M_t^*) was calculated that included the cumulative lost leaf-mass:

$$M_t^* = M_t(1 + 0.00002A_t^{3.91337})$$

where A_t is the age (months) of the stem at time t , M_t is the current stem dry mass in grams as calculated from the polynomial equations (Table 1), and the constants in the equation were derived empirically (Fig. 4A). Production was then calculated as the sum of the positive monthly differences in individual "phantom" masses.

Biomass density and production

Patterns of biomass density (Fig. 5A) and growth (Fig. 5B) varied seasonally and annually. For the Goat Island site where we have the longest record, aboveground production (Table 2) and aboveground biomass

density (Fig. 5A) were lowest during 1984 and 1988 and greatest in 1985. Annual production and maximum aboveground biomass density have varied by a factor of two. Biomass density and production characteristics at Oyster Landing and Goat Island (Table 2) were similar, and the growth trends parallel (Fig. 5B), despite large differences in stem density (Fig. 5C) and soil characteristics (Morris 1988). Peak biomass density occurred consistently during September. The quotient of annual production (corrected for leaf turnover)/peak biomass density has varied annually between 1.5 and 2.0, with the lowest ratio occurring during the year of greatest production. The correction for leaf turnover added 20–38% to the estimated productivity depending on the year (Table 2), excluding the 1st yr of the census which had an anomalously low leaf turnover because stem ages in the first cohort could not be determined. Maximum monthly growth rate occurred most commonly during July or August, and

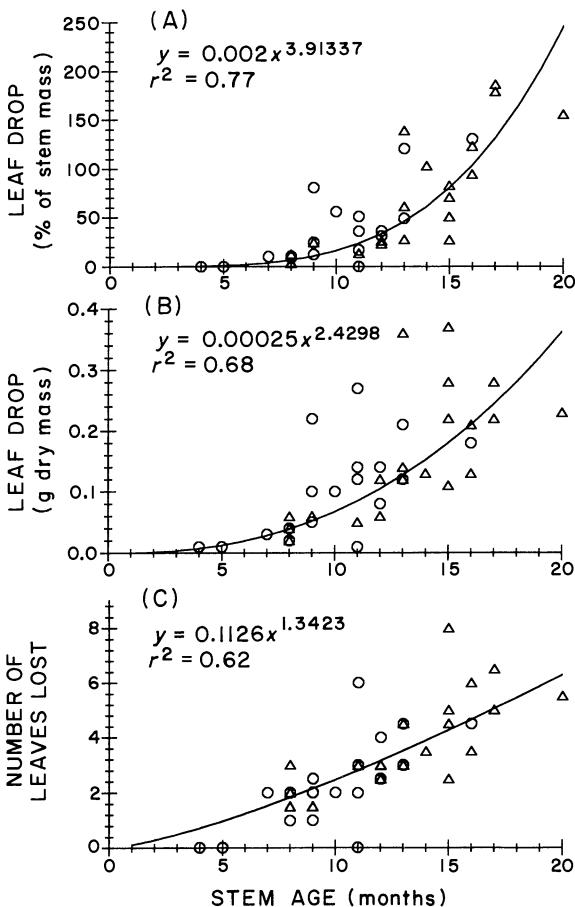


FIG. 4. Cumulative leaf drop as a function of stem age expressed as (A) percentage of current stem mass, (B) total cumulative mass loss in the form of leaves, and (C) total cumulative number of leaves lost. Curves were fitted to data from the final census of tagged stems (Δ). Data from earlier censuses of the same stem population, which should move along the same trajectory, are also plotted (O).

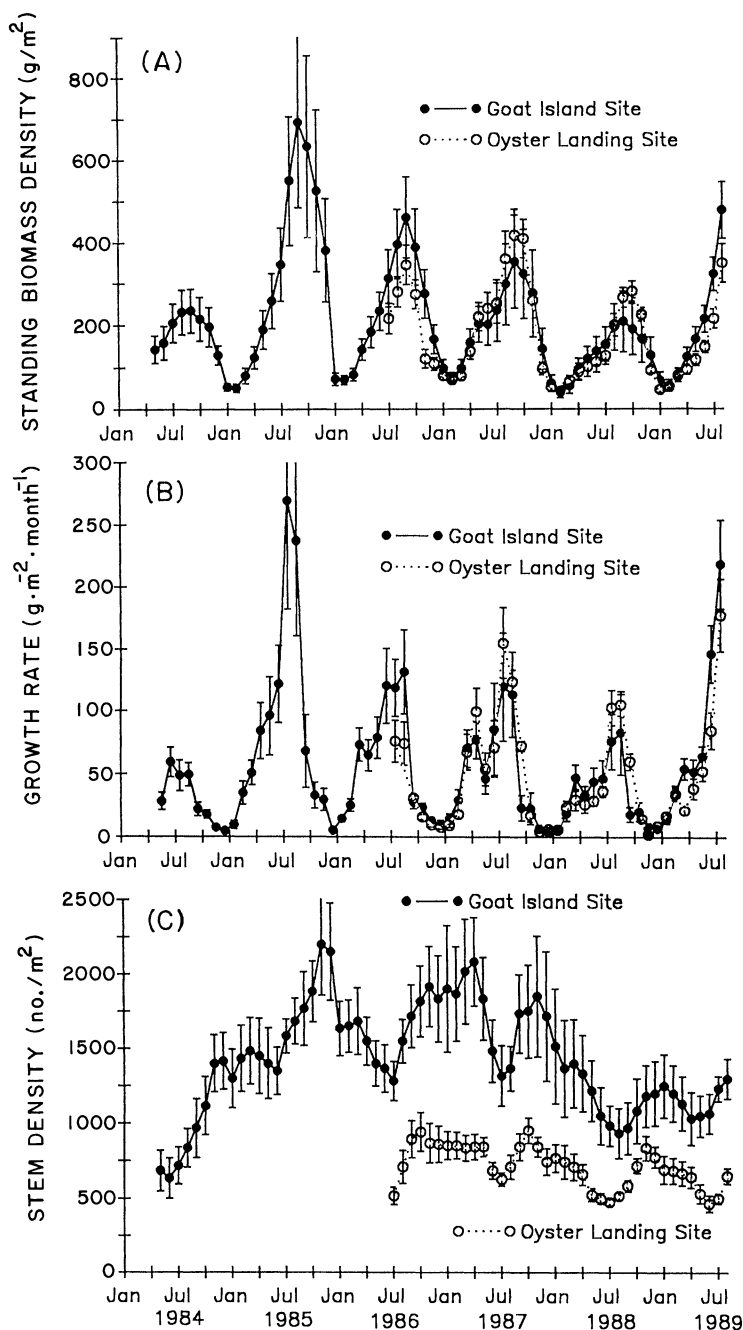


FIG. 5. (A) Standing density of dry biomass by month at the Goat Island and Oyster Landing sites (mean ± 1 SE, $n=6$). (B) Monthly, aboveground dry mass productivity at the Goat Island and Oyster Landing sites (mean ± 1 SE, $n=6$). Growth rates plotted here include a correction for leaf turnover. Growth rates calculated without the turnover correction have an identical pattern, and differ only from the turnover-corrected rates by having a slightly lower amplitude during the peak growth periods. (C) Stem density by month at the Goat Island and Oyster Landing marsh sites (mean ± 1 SE, $n=6$).

was highest, $270 \pm 87 \text{ g} \cdot \text{m}^{-2} \cdot \text{mo}^{-1}$ ($\bar{X} \pm 1$ SE, Fig. 5B), during August of 1985.

Stem density

Stem density also demonstrated considerable variability both seasonally and annually (Fig. 5C). Our

census includes all living stems as small as 1 cm height, and consequently may not be comparable to other published data. Peak density occurred during late autumn or winter, and minimum density occurred during June or July. Maximum stem density occurred several months after peak biomass density, and stem density

TABLE 2. Annual aboveground dry mass productivity ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, $\bar{X} \pm 1 \text{ SE}$) and maximum standing dry biomass density (g/m^2) by year at mid-marsh sites from Goat Island (GI) and Oyster Landing (OL) as calculated by the census method, with and without a correction for leaf turnover. Means with the same letter superscript are not significantly different by Duncan's multiple range test at $\alpha = .05$.

Year	Without correction		With turnover correction		Max. biomass	
	GI	OL	GI	OL	GI	OL
1984*	384 \pm 64 ^{bc}	...†	402 \pm 68 ^{bc}	...	235 \pm 53 ^g	...
1985	820 \pm 219 ^{ab}	...	1042 \pm 310 ^a	...	694 \pm 208 ^f	...
1986	581 \pm 102 ^{bc}	...	700 \pm 122 ^{abc}	...	461 \pm 98 ^{fg}	346 \pm 48 ^g
1987	496 \pm 128 ^{bc}	514 \pm 78 ^{bc}	621 \pm 173 ^{abc}	701 \pm 98 ^{abc}	354 \pm 113 ^g	418 \pm 63 ^{fg}
1988	295 \pm 70 ^c	325 \pm 25 ^c	408 \pm 115 ^{bc}	447 \pm 48 ^{bc}	209 \pm 73 ^g	281 \pm 24 ^g

* First 5 mo of 1984 growth estimated from the January through May means of the subsequent 5 yr.

† No data.

(Fig. 5C) was generally negatively correlated with monthly growth rate (Fig. 5B). Stem density was consistently greater at the Goat Island site by approximately a factor of two, but the temporal density patterns at the two sites were highly correlated.

Correlations with climatic variables

Parallel growth trends between sites, both annual and seasonal (Fig. 5B), suggest that interannual variation in productivity was a consequence of regional-scale phenomena. Annual productivity was correlated positively with cumulative rainfall during summer months (Fig. 6) and with mean relative sea level during July and August (Fig. 7). As discussed below (see *Discussion*), these correlations suggest that annual primary production responded to changes in sediment salinity brought about by variation in rainfall or tidal flooding during months of maximum potential growth. Maximum potential growth occurs during a 3-mo period, June–August, when 52–60% of annual growth occurred.

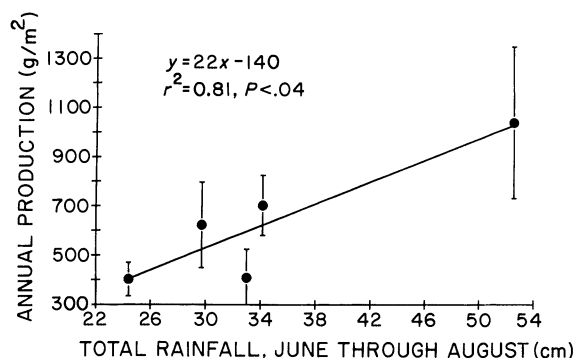


FIG. 6. Correlation between total rainfall during the period June through August and annual, aboveground dry-mass production (mean $\pm 1 \text{ SE}$, $n = 6$ estimates for each mean) at the Goat Island site for years 1984 through 1988. Rainfall data are from a meteorological station at the North Inlet LTER site. The 30-yr mean precipitation (June through August) from gauging station 2E at Georgetown, South Carolina, is 45.9 cm.

Simulations of harvest-based calculations

We calculated productivity using Milner and Hughes' (1969) method by simulating a monthly harvest of the six permanent plots at the Goat Island site. Total biomass density from these individual plots was treated as though it represented sites that were destructively harvested each month, and production was calculated by summing the positive differences in mean biomass density between months: $P = \sum [B(t+1) - B(t)]$ for all $[B(t+1) - B(t)] > 0$. When monthly mean biomass density was computed using data from all six plots, total production integrated over the first 12 mo was calculated by this difference technique to be 230 g/m^2 . We have defined this a priori as the error-free harvest estimate, because the entire six-plot area was sampled, and the resulting calculation was free of sampling error. The first 12 mo of productivity calculated by the census technique (beginning May 1984) was $400 \pm 76 \text{ g}/\text{m}^2$ ($\bar{X} \pm \text{SE}$) without correction for leaf turnover. The 74% greater production value obtained by the census technique compared to the error-free harvest method represents the contribution to productivity made by stem turnover during the first 12 mo. And, since leaf turnover contributes an additional 30% (Table 2), the census-based productivity estimate is ≈ 2.3 times as large as that calculated by the error-free summation of positive increments in mean standing biomass density. This is consistent with a common criticism of the Milner and Hughes method, which is that it underestimates production by failing to account for leaf and stem turnover.

A more realistic simulation of a harvest-based method is one in which there is error in the estimate of mean biomass density. In this case, the calculated productivity increases exponentially as the error increases (Fig. 8), because positive errors are additive while negative errors are ignored when summing monthly differences in biomass density. We simulated the effect of spatial variability on calculations of productivity (Milner and Hughes [1969] method), by using the computer to randomly sample each month a subset (from 1 to 5 per simulation) of the six Goat Island quadrats to compute the mean standing biomass density. The degree of error

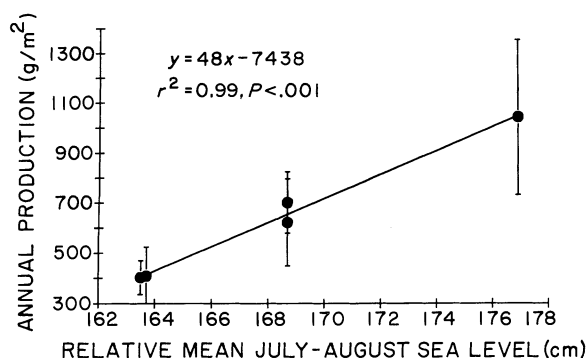


FIG. 7. Correlation between mean sea level during the period July through August and annual aboveground dry mass production (mean \pm 1 SE, $n = 6$) at the Goat Island site for years 1984 through 1988. Sea-level data were calculated as means from readings every 6 min from the National Ocean Survey/NOAA tide gauge in Charleston Harbor, South Carolina, and are relative to the tide gauge.

(defined below as d) was varied by changing the number of quadrats sampled randomly: A monthly random sample of one quadrat deviated an average of $\pm 38\%$ from the actual biomass density (the mean of all six plots), while biomass density estimates improved as the sample size increased (Fig. 8).

The harvest-based production estimate, when corrupted by spatial variability, is inflated above the error-free calculation by an average factor R , which was empirically calculated by fitting an exponential equation to the data in Fig. 8 ($r^2 = 0.64$):

$$R = e^{0.0258d}$$

for

$$d = (100/n) \times (|\mu_1 - \hat{\mu}_1|/\mu_1 + |\mu_2 - \hat{\mu}_2|/\mu_2 + \dots + |\mu_n - \hat{\mu}_n|/\mu_n),$$

where n is the number of estimates made of mean biomass density in the time series, μ is the actual biomass density for each time point, the estimated mean biomass density is $\hat{\mu}$, and d is the error or mean deviation. For example, the equation predicts that for a mean deviation (d) of $\pm 38\%$, the estimate of annual production was increased to $613 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, or by a factor of 2.66. Also note that actual calculations of productivity can be greater than or less than this (Fig. 8), depending on the specific time series of biomass density estimates, and that the calculations are most frequently greater than the error-free productivity calculation, 230 g/m^2 , even when the sampling error is as little as $\pm 10\%$ (Fig. 8).

DISCUSSION

Harvest methods like the one simulated above give questionable estimates of production when spatial variability and turnover are moderate, although the two have opposite effects. The method is positively biased by spatial variability, but underestimates production by an amount equal to the turnover. The problems of spatial variability and turnover make harvest methods unsuitable for investigations where temporal variation in productivity is important. In contrast, the census method provides an unbiased estimate of temporal variability; it is insensitive to spatial variability when permanent quadrats are censused, and accounts for stem turnover provided that the census is more frequent than the turnover of stems.

Our simulated, error-free harvest estimate of the first 12 mo of production, calculated by summing the positive increments in standing biomass density on all six quadrats, was $< 50\%$ of the census-based production estimate due to the combined contribution of leaf and stem turnover, with stem turnover making the greater

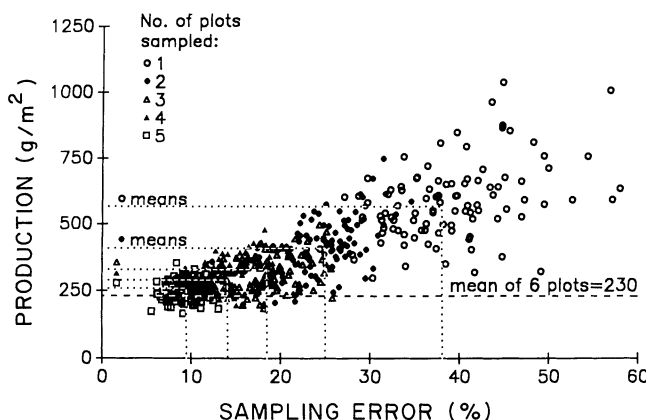


FIG. 8. Simulated calculations of total aboveground production ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) as a function of sampling error (see *Results: Simulations of harvest-based calculations*). The actual biomass density was defined a priori as the monthly mean biomass density from the six permanent plots at the Goat Island site, while an estimate of the biomass density was made by randomly sampling, by computer, a subset of these data. Annual production was calculated by summing the positive differences between these monthly biomass density estimates that were made when 1–5 subsets of biomass data were drawn randomly each month. Also indicated (dotted lines) are the mean error and biomass density obtained for 1000 simulations of each subset.

contribution. This contribution of leaf and stem turnover is greater than that estimated by Houghton (1985), 23–25%, in a Long Island, New York, salt marsh, but turnover may be limited there by freezing winter temperatures. We would expect lower leaf turnover where stem age is limited to <12 mo (Fig. 4).

Our data raise questions about the regulation of stem density and allocation of resources between stem growth and vegetative reproduction. For example, we found equivalent production at our two study sites (Table 2), although the stem density was twice as great at Goat Island as at Oyster Landing (Fig. 5C). Thus Goat Island plants allocate a greater proportion of growth to vegetative reproduction. The high correlation between seasonal density patterns at the two sites (Fig. 5C) indicates that vegetative reproduction is regulated by regional phenomena, such as photoperiod, while the quantitative difference in density between sites suggest that site-specific edaphic or genetic phenomena are also important. Both sites are situated at approximately the same elevation, near mean high tide (MHT), and the edaphic differences between them appear ultimately to relate to the age of the marshes, which differ as a consequence of rising sea level and landward migration of the salt marsh (Morris 1988). Oyster Landing is a younger marsh with less accumulation of sediment organic matter.

The positive correlations between mean sea level (MSL) or rainfall and annual production suggest that sediment salinity is a proximate determinant of interannual variation in primary production. And the months of rainfall and sea level data that proved to be significant (Figs. 6 and 7) suggest that the impact of rainfall and sea level on annual production is greatest during summer months when sediment salinity and growth potential are both maximal. Several studies indicate that the magnitude of sediment pore water salinity at our study sites, 50 ppt during summer, is great enough to inhibit growth. Growth of *Spartina alterniflora* is greatest at salinities of 20 ppt or less (Phleger 1971, Haines and Dunn 1976), and laboratory growth experiments (Phleger 1971, Linthurst 1980) and field measurements (Woodhouse et al. 1972, Webb 1983) indicate that the upper limit for salt tolerance is near 60 ppt. Drake and Gallagher (1984) found *Spartina* biomass density was negatively correlated with salinity, and *Spartina* was absent at salinities >75 ppt.

Sea level anomalies should influence growth because of their effect on sediment salinity. Sediment salinity generally increases with elevation above MSL to a maximum in the high intertidal zone (Webb 1983). Sediment salinity is sensitive to the rate of evapotranspiration, and to the frequency and duration of flooding. The spatial position of the sediment salinity maximum and its magnitude change in response to variation in MSL, because of the change in flood frequency and duration. Thus, the effect of MSL anomalies on salt marsh primary production is potentially large.

Sea level varies over a spectrum of different frequencies. We have observed interannual variations as great as 10–15 cm in mean annual sea level, which is 35 times the long-term rate of sea level rise along the South Carolina coast. Seasonally, mean sea level varies by 30 cm on the Atlantic and Gulf coasts of North America (Pattullo et al. 1955, Hicks and Crosby 1974, Kjerfve et al. 1978), with steric (specific-volume) changes explaining most of the variability (Pattullo et al. 1955). The timing of these oscillations appears to be a critical factor in determining estuarine productivity (Morris et al. 1990).

It is too early to choose between MSL anomalies and rainfall as the major determinant of interannual variability in production. Furthermore, the effect of rainfall and sea level may depend on their relative states. For example, sea level may be particularly important when rainfall is low, as it was during 4 yr of this study (Fig. 6). Preliminary growth data for 1989 (Fig. 5B) indicate that productivity during 1989 will be relatively high. This is consistent with a total precipitation during June through August 1989 of 52.85 cm, which approaches that during 1985, the year of maximum production (Fig. 6). Sea-level data for July and August 1989 were not yet available.

The twofold annual variation in primary production documented here was unexpected, and raises questions about the possibility of a response by secondary producers. Does secondary production covary with primary production, with or without a lag, or are higher trophic levels buffered against variability in primary production by virtue of the importance of the detritus-based food chain in estuarine ecosystems? Positive correlations between sea level anomalies and the commercial landings of shrimp (*Penaeus aztecus* and *P. setiferus*) and menhaden (*Brevoortia patronus* and *B. tyrannus*), species that utilize salt marsh habitats as juveniles, suggest that secondary producers are responding to primary production and/or to habitat availability (Morris et al. 1990). These data and the long-term record of *Spartina* production document large interannual variations in estuarine productivity that are apparently dominated by physical processes.

ACKNOWLEDGMENTS

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