Aerial and detritus production of the cordgrass *Spartina densiflora* in a southwestern Atlantic salt marsh

Federico Vera, Jorge L. Gutiérrez, and Pablo D. Ribeiro

Abstract: We used a nondestructive method to estimate aerial and detritus productivity of the cordgrass *Spartina densiflora* Brongn. and evaluated the relative contribution of newly emerged and preexisting tillers to net aerial biomass and detritus production, the relative contribution of tiller detachment and leaf shedding to detritus production, and the incidence of crab (*Neohelice* (*Chasmagnathus*) *granulata* (Dana, 1851)), herbivory in relation to tiller age and its implications for tiller survival. Estimates of aerial and detritus productivity varied between 706.72 (SD = 153.38) and 786.15 (SD = 162.75) g·m^{-2}·year^{-1} and between 1054.23 (SD = 224.49) and 1223.17 (SD = 246.84) g·m^{-2}·year^{-1}, respectively. These estimates of aerial production are far below the higher productivity estimates known for species of the genus *Spartina* but within the range of values obtained with nondestructive methods (i.e., 300–1500 g·m^{-2}·year^{-1}). Detachment of standing-dead tillers and leaf shedding contributed virtually in equal quantities to detritus production (i.e., 52% and 48% of the total detritus biomass, respectively). On the other hand, net aerial biomass production was highly dependent on tiller recruitment, with 67% of total biomass production contributed by the growth of tillers that emerged during the course of the study. However, crabs seem to graze on tillers irrespective of their age. Such nonselective crab grazing on tillers of different age together with the long tiller survival after crab grazing (often more than a year) suggests that crabs do not ostensibly affect *S. densiflora* production.

Key words: Spartina densiflora, primary production, detritus production, nondestructive method, tiller dynamics, *Neohelice (Chasmagnathus) granulata*.

Résumé : Les auteurs ont utilisé une méthode non destructive pour estimer la productivité aérienne et en résidus de la spartine à fleurs denses (*Spartina densiflora* Brongn.). Ils ont évalué: (*i*) la contribution relative des talles préexistants et nouvellement émergés à la production nette de biomasse aérienne et de détritus; (*ii*) la contribution relative du détachement des talles et de la chute de feuilles à la production en détritus, et (*iii*) l'incidence d'herbivorie par les crabes (*Neohelice* (*Chasmagnathus*) *granulata* (Dana, 1851)) en relation avec l'âge des talles et ses implications pour leur survie. Les estimations de la productivité aérienne et en détritus varient entre 706,72 (DS = 153,38) et 786,15 (DS = 162,75) g·m^{-2}·an^{-1}, et 1054,23 (DS = 224,49) et 1233,17 (DS = 246,84) g·m^{-2}·an^{-1}, respectivement. Ces estimations de la productivité aérienne s'avèrent beaucoup plus faibles que les estimés de productivité beaucoup plus élevée pour les espèces du genre *Spartina*, mais à l'intérieur de l'amplitude des valeurs obtenues avec des méthodes non-destructives (i.e. 300 à 1500 g·m^{-2}·an^{-1}). Le détachement de talles sur pied et la chute de feuilles contribuent virtuellement en quantités égales à la productivité en détritus (i.e, 52 et 48 % de la biomasse totale des détritus, respectivement). D'autre part, la production de biomasse aérienne nette dépend fortement du recrutement de nouveaux talles, avec 67 % de la production totale de la biomasse provenant de la croissance des talles qui ont émergé au cours de l'étude. Cependant, les crabes semblent brouter les talles indépendamment de leur âge. Un tel broutage non sélectif des crabes sur les talles de différents âges, avec la longue durée de vie des talles après le broutage des crabes (souvent plus d'une année) suggère que les crabes n'affectent pas beaucoup la productivité du *S. densiflora*.

Mots-clés : Spartina densiflora, production primaire, production de détritus, méthode non destructive, dynamique des talles, *Neohelice (Chasmagnathus) granulata*.

F. Vera.[1] Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, CC 1245, Mar del Plata (7600), Argentina.
J.L. Gutiérrez. Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina; Grupo de Investigación y Educación en Temas Ambientales (GrIETA), Mar del Plata, Argentina; Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina; Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA.
P.D. Ribeiro. Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina; Grupo de Investigación y Educación en Temas Ambientales (GrIETA), Mar del Plata, Argentina; and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

[1]Corresponding author (e-mail: fvera@mdp.edu.ar).

Introduction

Spartina is the most widespread genus of salt marsh macrophytes with representatives on all five continents (Adam 1993; Mitsch and Gosselink 2000). Since *Spartina* frequently develops into nearly monocultures that cover extensive areas (e.g., Bertness 1991; Adam 1993), estimating its productivity is critical to understand energy and material cycling and the overall functioning of marsh ecosystems. Available estimates of net aerial *Spartina* productivity range from 200 to more than 6000 g·m^{-2}·year^{-1} (Fig. 1). Variation in aerial *Spartina* productivity estimates is seemingly associated with latitude (i.e., the higher productivity estimates are observed at low latitudes), plant species (i.e., the higher productivity estimates are observed for *Spartina patens* (Ait.) Muhl., *Spartina cynosuroides* (L.) Roth, and, to a lesser degree, *Spartina alterniflora* Loisel.), and estimation methods (i.e., the higher productivity estimates are based on destructive harvesting methods rather than nondestructive census techniques; see Fig. 1). Nevertheless, there may also be location-specific sources of variation in *Spartina* productivity. The aerial productivity of *Spartina* during a given period of time can be viewed as the sum of the biomass contributed by newly emerged tillers plus the biomass contributed by the growth of preexisting tillers (Dai and Wiegert 1996). In the same vein, detritus production by *Spartina* can be viewed as the sum of the biomass of senescent tissues detached during that period. Since newly emerged tillers have the potential to produce more live biomass and a lower amount of senescent tissues than preexisting ones, spatial variations in tiller age-class distribution are likely to result in concomitant variations in the net annual production of aerial biomass and detritus by *Spartina*. In addition, local factors affecting tiller growth and survival, such as herbivory, can introduce further variation in *Spartina* productivity, particularly if their effect is biased toward the younger tillers (i.e., those having the larger potential for subsequent biomass production). Thus, studying the dynamics of tiller populations may allow a more comprehensive understanding of the demographic processes that underlie *Spartina* productivity.

The aerial productivity of the cordgrass *Spartina densiflora* Brongn., a species native to southern South America, has received little attention to date. The few available estimates (3 out of the 99 estimates in Fig. 1) are variable and were obtained by means of destructive or nondestructive methods from marshes located at different latitudes and characterized by different local conditions (Table 1). From these estimates, only that of Peixoto and Costa (2004) was obtained from temperate southwestern Atlantic salt marshes (31°S–43°S, southern Brazil to southern Argentina). Nevertheless, these authors used a destructive approach, which is cost-effective but precludes any estimate of the magnitude of detritus production in these marshes and the assessment of potential influences of herbivory by the southwestern Atlantic burrowing crab (*Neohelice* (*Chasmagnathus*) *granulata* (Dana, 1851)) (see Iribarne et al. 1997). That kind of estimate also precludes evaluating the relative contribution of newly emerged and preexisting tillers to aerial plant productivity and the relative importance of tiller detachment and leaf shedding to detritus production (both rarely, if ever, addressed in *Spartina* productivity studies). Here, we report the results of a nondestructive estimate of aerial

Fig. 1. Reported values of net aerial primary productivity (NAPP) for species of the genus *Spartina* (*n* = 99) plotted in relation to latitude. Filled symbols indicate estimations based on nondestructive methods (i.e., those that require periodic harvests of plant material to obtain biomass and productivity estimates), while open symbols correspond to destructive estimations (i.e., those that involve repeated measurements of morphologic and phenologic parameters in tagged plants, which are then used to estimate changes in biomass by means of regression equations). The long dashes indicate the nondestructive estimations of *S. densiflora* productivity obtained in this study and by Vicari et al. (2002), while the short dash corresponds to a destructive productivity estimation for this species. The data were taken from Udell et al. (1969), Kirby and Gosselink (1976), Hopkinson et al. (1978), Linthurst and Reimold (1978), White et al. (1978), Gallagher et al. (1980), Cramer et al. (1981), Reidenbaugh (1983), Roman and Daiber (1984), Schubauer and Hopkinson (1984), Jackson et al. (1986), Cranford et al. (1989), Morris and Haskin (1990), Benito and Onaindia (1991), Lana et al. (1991), Pezeshki and DeLaune (1991), Vicari et al. (2002), Peixoto and Costa (2004), and Edwards and Mills (2005).
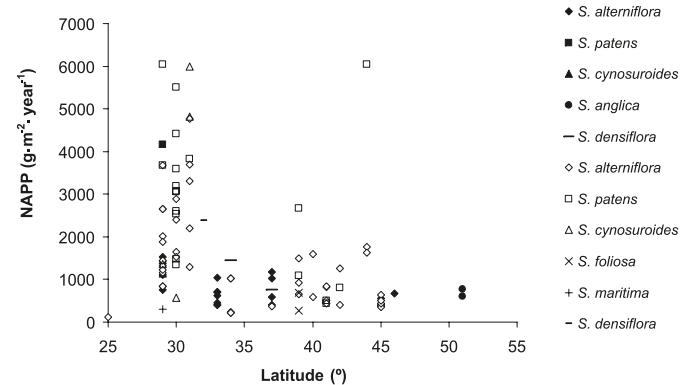
S. densiflora productivity in a southwestern Atlantic salt marsh aimed at filling the abovementioned knowledge gaps with regard to detritus production, the dynamics of tiller emergence and growth, and the incidence and patterns of crab herbivory. The specific goals of this study were to evaluate (*i*) the production of aerial biomass and detritus by *S. densiflora*, (*ii*) the relative contribution of newly emerged and preexisting tillers to net aerial biomass and detritus production as well as their temporal variations, (*iii*) the relative contribution of tiller detachment and leaf shedding to detritus production, and (*iv*) the incidence of crab herbivory in relation to tiller age and its implications for tiller survival.

Materials and methods

Study site and organisms

This study was conducted at Mar Chiquita coastal lagoon, Argentina, (37°45′S). This is a 46 km^2 body of brackish water affected by semidiurnal low-amplitude (≤1 m) tides (Perillo et al. 1999) and characterized by mud flats surrounded by large *S. densiflora* marshes. Field samplings were carried out in a salt marsh located at the eastern margin of Cangrejito creek, a small tidally influenced creek that drains a small basin (approximately 1500 ha) and flows into the lagoon at about 1000 m from the lagoon inlet. In the absence of events of rainwater discharge that may flood the marsh for several weeks, marsh inundation is restricted to

spring tide periods (authors' personal observation). Sampling units were deployed in the lower part of the marsh (between aproximately 0 and 30 cm above the mean high tide level). In this area, *S. densiflora* intercalates with bare sediment patches not larger than 5 m in diameter (F. Vera, personal observation). The burrowing crab *N. granulata*, a facultative herbivorous species (Iribarne et al. 1997), is present in the area at densities of up to 70 burrows·m^{-2} (Gutiérrez et al. 2006).

General sampling design

Tillers were censused monthly in 20 permanent squared sampling units (10 cm side) from July 2004 to November 2005. The sampling units were systematically deployed in two rows parallel to the shore and located in patches covered by *S. densiflora*. The plots were demarcated with wire stakes and all of the tillers within the plots were tagged with a numbered piece of adhesive tape that permitted their subsequent identification. Every month, tillers were measured from the base to the tip of the longest leaf and their phenological condition recorded as green (for completely or partially green tillers) or standing dead (for entirely brown tillers). New tillers emerging between two sampling dates were tagged and measured in the same way. Additionally, from November 2004 to November 2005, we also recorded grazing on green tillers by *N. granulata*. Grazed tillers can be easily distinguished owing to the presence of irregular and typically yellow cuts in the tops or borders of the leaves (Alberti et al. 2007). When a tagged tiller was no longer found, it was considered as dead and detached from the ramet.

Estimation of tiller biomass

Tiller biomass was estimated by means of height–mass regressions that were constructed from tillers harvested nearby the experimental units in each sampling date (see Morris and Haskin 1990). Green and standing-dead tillers ($n = 50$ each) were taken to the laboratory, measured to the nearest millimetre, dried (72 h at 60 °C), and weighed. The regression analyses were performed independently for each month and phenological condition. Tiller weight and mass data were log transformed to meet the assumptions of the linear regression model (Zar 1984).

Biomass and production at the sampling units

Biomass of green and dead tillers at each sampling unit and date was calculated by summing the dry mass of the individual tillers. Aerial production at each sampling unit and date was calculated by summing the biomass increases of all of the green tillers present within the unit. Detritus production at each sampling unit and each sampling date was calculated by summing the biomass loss by standing-dead tillers. The detritus produced by tagged tillers that were no longer found and assumed to have detached from the ramet (see General sampling design section) was computed as the last estimation of their aerial biomass. To express biomass and production data per square metre of marsh, measurements of tiller biomass (green, standing dead, and total) and production (of both aerial and detritus biomass) obtained from the 10 cm × 10 cm permanent field plots were cor-

rected for the percent marsh area covered by *S. densiflora* using the following equation:

$$[1] \qquad N_{m_i} = \frac{\sum_{j=1}^{20}[N_{u_{ij}} \times 100 \times A_{c_i} + (1 - A_{c_i})N_{d_i}]}{20}$$

where N_{m_i} is the mean value of biomass, aerial, or detritus production per square metre of marsh during month i, $N_{u_{ij}}$ is the biomass, aerial, or detritus production in sampling unit j during month i, A_{c_i} is the proportion of initially covered area that remains covered during month i, and N_{d_i} represents the mean values of biomass, aerial, or detritus production per square metre of initially uncovered area for month i; N_{d_i} was calculated as $N_{d_i} = (n \times 100)/40$, where n is biomass, aerial, or detritus production in month i within 40 square (10 cm side) units deployed in places initially lacking vegetal cover (for a detailed explanation of how A_{c_i} and N_{d_i} were estimated, see Estimation of *S. densiflora* cover and the contribution of initially uncovered areas to tiller dynamics and production). The 100 multiplier was used to convert the density data from the sampling unit to the 1 m^2 scale. Net aerial primary production (NAPP) and detritus productivity were calculated by adding the monthly mean values of aerial and detritus productivity, respectively. This was done for the five different 12-month periods that can be identified throughout the 17 months of study (i.e., August 2004 to July 2005, September 2004 to August 2005, and so on). The SE of the NAPP and detritus production was estimated using bootstrap (Manly 1997) as follows. For each sampling month, 1 of the 20 possible productivity values obtained from the sampling units was randomly chosen. These values were summed giving an estimate of annual production. The previous two steps were performed 1000 times to obtain an equal number of production values and the SD of these values gave an estimation of the SE of the NAPP or detritus production.

Tiller dynamics

The mean values of tiller densities (green, standing dead, and total) per square metre of marsh were calculated using eq. 1 but considering N_{m_i} as the mean number of tillers per square metre of marsh during month i, $N_{u_{ij}}$ as the number of tillers in unit j during month i, and N_{d_i} as the mean number of tillers per square metre of initially uncovered area; N_{d_i} was calculated as $N_{d_i} = (n \times 100)/40$ where n is the number of tillers (green, standing dead, or total) present during month i within the 40 units located in initially uncovered areas (see Estimation of *S. densiflora* cover and the contribution of initially uncovered areas to tiller dynamics and production).

Recruitment, mortality, and detachment of tillers were also calculated using eq. 1 but considering N_{m_i} as the number of tillers per square metre that emerged, died, or detached from the ramets during month i, $N_{u_{ij}}$ as the number of tillers that emerged, died, or detached from the ramets within unit j during month i, and N_{d_i} as the mean number of tillers that emerged, died, or detached in month i per square metre of initially uncovered area (calculated as described above).

Table 1. Published estimates of net aerial primary production in *Spartina densiflora*.

Location	Site characteristics	Estimation method	Productivity estimate	Reference
Paranaguá Bay, Brazil (25°S, 48°W)	Subtropical, microtidal salt marsh	Destructive harvesting method	100–180 g·m^{-2}·year^{-1}	da Cunha Lana et al. 1991
Los Patos Lagoon, Brazil (32°S, 52°W)	Temperate, microtidal salt marsh	Destructive harvesting method	2360 g·m^{-2}·year^{-1}	Peixoto and Costa 2004
Lower Paraná Delta, Argentina (34°S, 58°W)	Temperate, nontidal riverine floodplain	Nondestructive tagging technique	1450 g·m^{-2}·year^{-1}	Vicari et al. 2002

Finally, we constructed survivorship curves to evaluate the survival of the tiller cohorts that emerged during the study period.

Estimation of *Spartina densiflora* cover and the contribution of initially uncovered areas to tiller dynamics and production

Percent *S. densiflora* cover was estimated monthly to express biomass and production data per square metre of marsh. To estimate the cover percentage at the beginning of the study, a quadrangular grid (0.5 m sides, divided 0.1 m side square subunits) was placed at 3 m intervals along three transects (60 m length) demarcated parallel to the shoreline (i.e., a total of 60 grids and 1500 subunits). *Spartina densiflora* coverage was measured as the percentage of subunits where at least one tiller was present. Changes in percent *S. densiflora* cover during the study period were estimated as follows. The proportion of initially covered area that lost its coverage was estimated by randomly placing 40 square sampling units (10 cm sides) in covered patches and monitoring the presence or absence of tillers in each sampling date. Similarly, the proportion of initially bare area that acquired coverage during the study period was estimated by monitoring the presence or absence of tillers in 40 square sampling units (10 cm sides) initially deployed in bare patches. The tillers that emerged in the sampling units initially placed in bare patches were tagged and measured as previously described to evaluate the contribution of such areas to biomass production and tiller dynamics and to incorporate them into the calculations (as can be seen in eq. 1).

The proportion of bare area in each sampling date was calculated using the following equation:

$$[2] \quad \text{ANC}_{(i)} = \text{ANC} - \text{ANC}\left(\frac{D_{\text{veg}}}{D_t} - \frac{C_{\text{bare}}}{C_t}\right)$$

where $\text{ANC}_{(i)}$ is the proportion of uncovered area in month i, ANC is the proportion of uncovered area at the beginning of the study (obtained from the grid sampling along transects), D_{veg} is the number of sampling units placed in initially uncovered areas showing vegetal cover in month i, D_t is the total number of sampling units placed in uncovered areas at the beginning of the study (i.e., 40), C_{bare} is the number of sampling units placed in initially covered areas showing no vegetal cover during month i, and C_t is the total number of sampling units placed in areas with vegetal cover at the beginning of the study (i.e., 40).

Herbivory patterns

Monthly variations in the intensity of crab herbivory were evaluated by considering only the percentage of newly emerged tillers (i.e., tillers not observed in the previous sampling date) that were affected by herbivory at each sampling date. We focused only on newly emerged tillers because the marks left by crabs in grazed leaves may remain for more than a month (F. Vera, personal observation) and, thus, herbivory marks observed in older tillers at a given time cannot be unequivocally attributed to herbivory occurring during the preceding month. While focusing only on newly emerged tillers precludes measurement of the actual incidence of crab herbivory on *S. densiflora*, it provides a useful relative measure of temporal variation in the intensity of crab herbivory.

We evaluated the relationship between tiller age and the probability of suffering herbivory for the first time using data from the tillers that emerged in the sampling units during the study period. Assuming a constant probability of first herbivory for all tiller ages, we calculated the probability of observing tillers that have never undergone herbivory using the following equation (Model 1) (see Appendix A for more details):

$$[3] \quad P_{\text{nh}_{(t)}} = (1 - P_{\text{h}})^t$$

where $P_{\text{nh}_{(t)}}$ is the probability of observing tillers of age t (in months) without signs of herbivory until age t and P_{h} is the probability of first herbivory.

We explored whether the probability of first herbivory P_{h} can be assumed constant for all tiller ages by calculating the expected probability of observing tillers of different ages that have undergone herbivory for the first time. Given that the probability of receiving herbivory for the first time at age t implies that the tiller has not been consumed by crabs until age $t - 1$, the probability of observing tillers of different ages with signs of first herbivory will be given by the following expression (Model 2) (see Appendix A for more details):

$$[4] \quad P_{\text{ph}_{(t)}} = (1 - P_{\text{h}})^{t-1} P_{\text{h}}$$

where $P_{\text{ph}_{(t)}}$ is the probability of observing tillers of age t with signs of first herbivory and P_{h} is the probability of first herbivory.

These equations allowed us to obtain for each tiller age the expected number of tillers that have never undergone herbivory (Model 1) and that have undergone herbivory for the first time (Model 2), assuming that P_{h} is constant for all ages. We calculated r^2 between the observed and the expected values to evaluate the models' fit and the best estimate for P_{h} was obtained by minimizing the sums of squares. Confidence intervals (5%) for P_{h} estimates were constructed using a likelihood profile (Hilborn and Mangel 1997).

The age t at which it would be expected that half of the tillers from a given cohort have undergone herbivory in at least one opportunity ($t_{0.5}$) is calculated with the following equation (see Appendix A for more details):

$$[5] \qquad t_{(0.5)} = \frac{\ln (0.5)}{\ln (1 - P_h)}$$

The confidence interval for $t_{0.5}$ was obtained by replacing the values for the confidence interval for P_h obtained in Model 1.

Results and discussion

Production of aerial biomass and detritus by *Spartina densiflora*

The values of total *S. densiflora* biomass reported in this study are similar to those reported by Vicari et al. (2002). Total aerial biomass progressively decreased from 1744 g·m^{-2} (SE = 89) at the beginning of the study period (July 2004) to 1040 g·m^{-2} (SE = 78) at its end (October 2005). This occurred concurrently with an overall decreasing trend in tiller densities during the study period (Fig. 2). Maximum total tiller density was recorded in December 2004 (mean = 2286 tillers·m^{-2}, SE = 107) and January 2005 (mean = 2286 tillers·m^{-2}, SE = 111), while the lowest value was observed in October 2005 (mean = 1809 tillers·m^{-2}, SE = 137). The biomass of green tillers tended to be higher than the biomass of standing-dead tillers during all months with the exception of October 2005 (Fig. 2). Although dead tiller densities tended to exceed green tiller densities in some months (November 2004 to January 2005) (Fig. 2), green tiller biomass tended to remain higher than dead tiller biomass. The lower biomass of standing-dead tillers relative to green tillers is probably due to microbial degradation (Newell et al. 1989) and (or) leaf shedding.

Mean NAPP varied between 706 (SE = 153) and 786 (SE = 162) g·m^{-2}·year^{-1} depending on the annual period under consideration (Table 2). These estimates are markedly lower than many of the values reported for the genus *Spartina* (e.g., >6000 g·m^{-2}·year^{-1}: Hopkinson et al. 1978; Linthurst and Reimold 1978) (see Fig. 1). However, it is worth mentioning that nondestructive estimations of *Spartina* productivity generally lie between 400 and 1500 g·m^{-2}·year^{-1}, showing much less variation than destructive estimates (Fig. 1). This suggests that some of the high productivity values frequently reported for the genus *Spartina* could be overestimations owing to limitations inherent to the destructive methods (Morris and Haskin 1990; Dai and Wiegert 1996). Monthly rates of aerial production tended to be lower in winter (Fig. 2), which is in agreement with a variety of studies showing decreased winter production in temperate *Spartina* salt marshes (e.g., Kaswadji et al. 1990; Morris and Haskin 1990; Vicari et al. 2002).

The contribution of the initially bare patches to total tiller recruitment, mortality, and aerial production during the whole study period (August 2004 to November 2005) was negligible (0.30%, 0.27%, and 0.32%, respectively). Indeed, NAPP estimates would be virtually identical without considering the contribution of these patches (Table 2). Tiller recruitment was observed in only 8 out of the 40 sampling units initially placed in areas without *S. densiflora* cover, while only 2 out of the 40 units initially placed in areas with *S. densiflora* cover turned into bare sediments. In contrast, correcting productivity measurements by percent *S. densiflora* cover when extrapolating from the plot (100 cm^2) to the square metre scale proved to be important, since NAPP would otherwise be overestimated by more than 100 g·m^{-2} (Table 2). It is worth considering here that percent *S. densiflora* cover remained high and relatively constant throughout the study period (between 87% and 89%). However, this kind of overestimation would proportionally increase in marshes with a higher proportion of bare sediment areas.
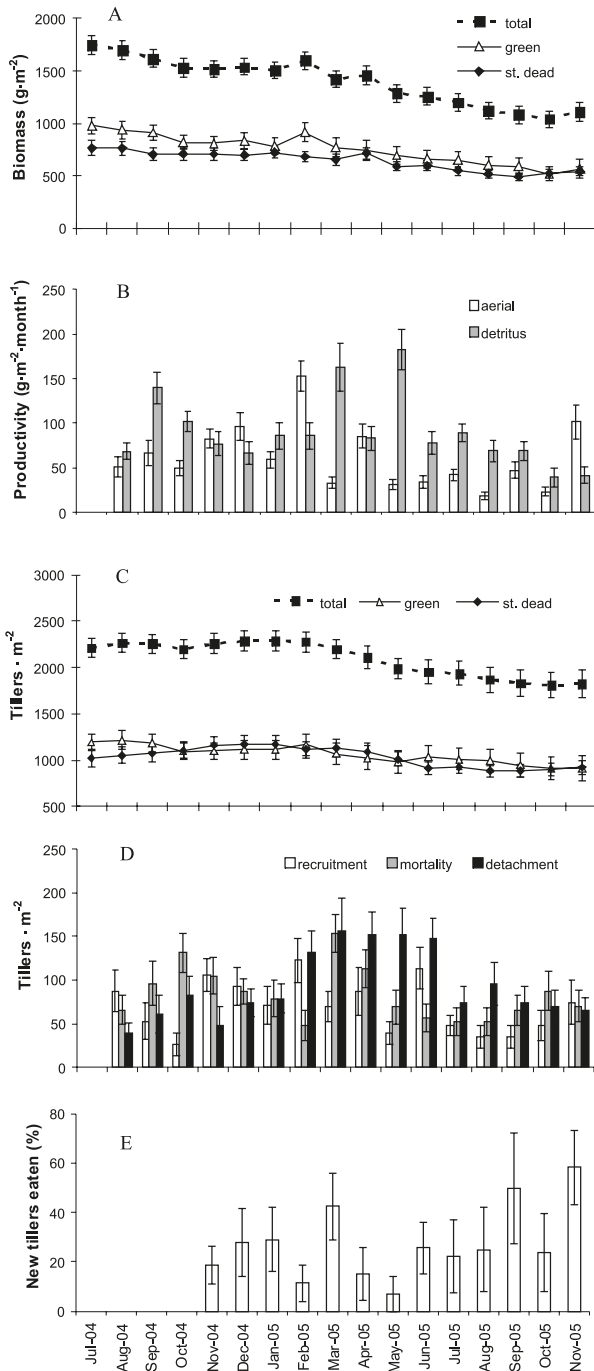
Detritus production ranged between 1054 (SE = 224) and 1223 (SE = 246) g·m^{-2}·year^{-1} depending on the annual period considered (Table 2). The maximum monthly rate of detritus production (mean = 182 g·m^{-2}, SE = 22) was observed in May 2005, while the minimum rate (mean = 39 g·m^{-2}, SE = 10) was registered in October 2005 (Fig. 2). The fact that detritus production estimates were higher than NAPP estimates is in agreement with the net loss of plant biomass observed during the study period (see above). This suggests the occurrence of interannual variations in *S. densiflora* productivity and biomass (presumably linked to climatic variability).

Relative contribution of newly emerged and preexisting tillers to net aerial biomass and detritus production

Net aerial biomass production was highly dependent on tiller recruitment. Overall, 67% of the total biomass produced during the 17 months of the study period was due to the growth of tillers that emerged during the course of the study. In addition, the monthly rate of aerial production was maximum in February 2005 (mean = 152 g·m^{-2}, SE = 17) concurrently with maximum tiller recruitment (Fig. 2). This suggests that factors affecting tiller recruitment and their subsequent growth may have an important effect on marsh productivity. This might be the case for certain herbivores that graze preferentially on young tillers because of their higher nutritional content causing their senescence (e.g., Fenner et al. 2002). Nevertheless, crab grazing in our marsh seems unlikely to cause such an effect on marsh productivity (see Incidence of crab herbivory in relation to tiller age and its implications for tiller survival).

In contrast with aerial production, the production of detritus by tillers emerged during the study period was low (i.e., 9% of the total detritus biomass). This is an ancillary consequence of the long survivorship of tiller cohorts (Fig. 3). All of the tiller cohorts that emerged during the study presented a survival greater than 25% at its end (Fig. 3). In addition, from a total of 273 green tillers tagged at the beginning of the study, 52 remained alive by its end (i.e., after 16 months). Furthermore, *S. densiflora* stands retain an important proportion of standing-dead biomass (Fig. 2), which indicates that there is a time lag between tiller senescence and detritus detachment (Fig. 3). Since tillers must die or at least have an important proportion of dead biomass to significantly contribute to detritus production, it can be concluded that the study period was not long enough to allow important detritus production by new cohorts.

Fig. 2. Temporal variations in (A) aerial biomass of total, green, and standing-dead *Spartina densiflora* tillers, (B) monthly rate of aerial and detritus production, (C) tiller density, (D) tiller recruitment, mortality, and detachment, and (E) percentage of newly-emerged *S. densiflora* tillers affected by crab (*Neohelice granulata*) herbivory (C). Error bars represent ±1 SE; *n* = 20.

60 cm height and smaller fragments of dead leaves in a rather similar mass. The production of large detritus pieces via tiller detachment may have important implications for the retention of organic matter within the marsh. Because of their lower surface to volume ratio (and, thus, smaller surface available for microbial degradation per volume unit), detached tillers are expected to take longer to decompose than shed leaf fragments. In addition, it is important to note that the tidal flushing of detritus from the marsh surface will strongly depend on detritus size. Large detritus pieces, such as detached tillers, will be little susceptible to be transported by tides across the interstices left by the *S. densiflora* canopy, resulting in significant detritus trapping (e.g., Newell et al. 1998). Detritus trapped by the *S. densiflora* canopy could subsequently be subject to fragmentation and subsequent tidal export. Nevertheless, this is unlikely in our marsh, where sediment excavation by crabs virtually buries all of the detritus occurring as litter in the marsh (J.L. Gutiérrez, unpublished data). Therefore, detached tillers could significantly contribute to carbon accretion in the marsh soil and overall organic matter retention within the marsh as a consequence of their physical interaction with cordgrass canopies (detritus trapping) and burrowing crabs (detritus burial).

Incidence of crab herbivory in relation to tiller age and its implications for tiller survival

The percentage of newly emerged tillers affected by herbivory varied between 7.14% (SE = 7.14) in May 2005 and 58.33% (SE = 15.10) in November 2005, showing no seasonal pattern (Fig. 2). This is likely a consequence of crab activity patterns. Crabs leave their burrows and graze on *S. densiflora* primarily during marsh flooding (Alberti et al. 2007). Both the length of flooding periods and the overall number of flooding dates in the marsh are expected to vary between months because of variations in the height of spring tides, upland freshwater runoff, and tidal forcing by winds. Since variation in these hydrological and climatic factors is not necessarily seasonal at our study site (Perillo et al.1999), we could expect coupled, nonseasonal patterns of crab herbivory.

A constant probability of first herbivory for all tiller ages satisfactorily explains both the observed numbers of tillers that were never affected by herbivory at each age class (Model 1: $r^2 = 0.99$, $P_h = 0.26$, upper confidence limit = 0.28, lower confidence limit = 0.24) and the number of tillers that underwent herbivory for the first time at each age class (Model 2: $r^2 = 0.89$, $P_h = 0.27$, upper confidence limit = 0.33, lower confidence limit = 0.21) (Fig. 4). This is in disagreement with the hypothesis of positive selection of young and totally green tillers (see Bortolus and Iribarne 1999). According to this hypothesis, younger tillers would be more nutritive and palatable than mature ones owing to higher nitrogen and lower silica content (Howe and Westley 1988). However, in the case of small herbivores, like *N. granulata*, foraging takes place at a spatial scale that could allow the crabs to select for the younger leaves of mature tillers, which could be as profitable as the younger tillers. Under this last scenario, a similar probability of herbivory for tillers of different ages can reasonably be expected. Since half of the tillers of a given cohort are ex-

Relative contribution of tiller detachment and leaf shedding to detritus production

Detachment of standing-dead tillers and leaf shedding contributed virtually in equal quantities to detritus production (i.e., 52% and 48% of the total detritus biomass, respectively). This implies that the macrodetritus produced by *S. densiflora* includes detached dead tillers of up to 50–

Table 2. Mean (SE) net aerial primary productivity (NAPP) and detritus productivity of *Spartina densiflora* for the different annual periods that can be considered during the 17 sampling months and the contribution to the NAPP of the areas that initially lacking vegetal cover and the NAPP obtained by assuming a 100% vegetal cover.

Annual period	NAPP ($g·m^{-2}·year^{-1}$)	Detritus productivity ($g·m^{-2}·year^{-1}$)	Contribution of the initially uncovered patches to NAPP (%)	NAPP assuming 100% cover ($g·m^{-2}·year^{-1}$)
August 2004 to July 2005	786.15 (162.75)	1222.70 (257.18)	0.28	898.76 (185.04)
September 2004 to August 2005	753.37 (160.88)	1223.17 (246.84)	0.31	861.24 (182.28)
October 2004 to September 2005	733.08 (157.94)	1152.08 (243.36)	0.25	838.84 (174.47)
November 2004 to October 2005	706.72 (153.38)	1089.55 (232.58)	0.24	808.86 (171.31)
December 2004 to November 2005	724.69 (162.53)	1054.23 (224.49)	0.14	830.61 (191.19)

Fig. 3. (A) Survivorship curves for the tiller cohorts of *Spartina densiflora* that emerged during the study period and (B) percent tillers that senesced in each month during the study period remaining as standing-dead tillers over time.
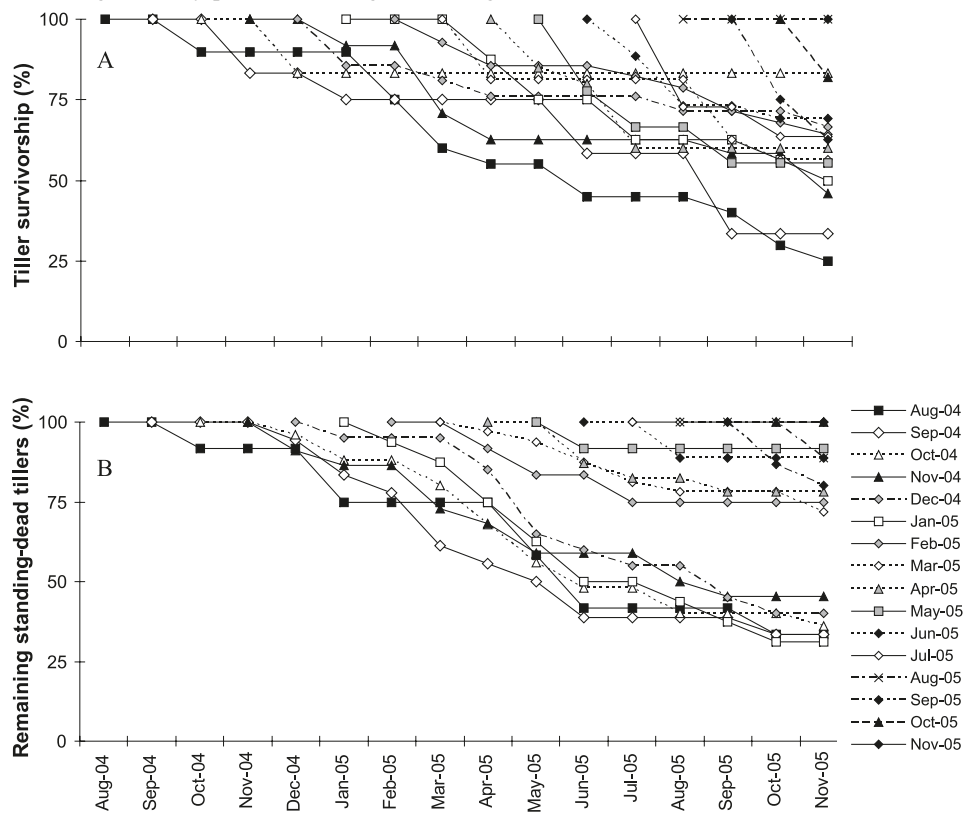

pected to suffer herbivory at the age of 2.2 months (upper confidence limit = 2.9, lower confidence limit = 1.7), it can be stated that crab herbivory does not ostensibly affect tiller survivorship.

Ancillary considerations on the temporal dynamics of tiller emergence, mortality, and detachment

Noteworthy emergence, mortality, and detachment of tillers were observed all year round and in a nonseasonal fashion (Fig. 2). Previous studies showed that the emergence and death of *S. densiflora* tillers can be either seasonal (Vicari et al. 2002) or nonseasonal (Nieva et al. 2005). It seems likely that *S. densiflora* takes advantage of moments with favorable environmental conditions and (or) increased resource availability to achieve clonal expansion and produce new tillers. For instance, it is known that clonal plants may de-

tect spatial variations in the distribution of resources and (or) stressors preferentially expanding into the most favorable microhabitats (e.g., MacDonald and Lieffers 1993). Likewise, clonal plants might exploit temporal heterogeneity increasing their expansion and producing new tillers during favorable periods. It is worth noting that this type of strategy could lead to both seasonal and nonseasonal patterns of recruitment and mortality depending on how resources and environmental conditions distribute in time. In marshes that are periodically affected by tidal action (e.g., Nieva et al. 2005; this study), the interaction of climate and tides may generate short-term variations (i.e., hours to weeks) in environmental conditions (e.g., salinity, temperature, and soil moisture) and resource availability (e.g., variations in nutrient availability because of the effect of environmental conditions on biogeochemical processes) and, as a conse-

Fig. 4. Observed numbers of tillers of different ages that were never consumed by crabs (*Neohelice granulata*) (filled symbols) and that were affected by herbivory for the first time (open symbols). The curves show the expected numbers according to Models 1 and 2 (see text), which assume a constant probability of first herbivory for all tiller ages.
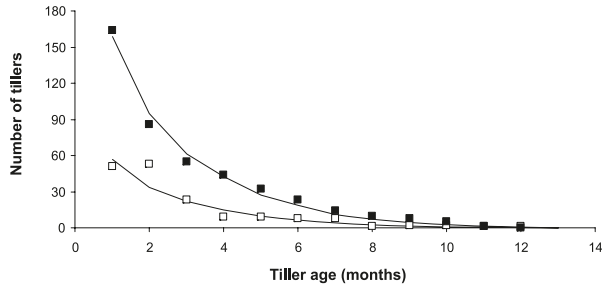
quence, short-term variations in tiller recruitment and mortality. On the other hand, the emergence and mortality of tillers in marshes that are not affected by periodic tidal inundation or other nonseasonal disturbances (e.g., Vicari et al. 2002) are more likely to vary according to seasonal changes in environmental conditions and their consequent controls on resource availability.

Conclusions

The estimates of *S. densiflora* productivity presented in this study fall within the range of other nondestructive estimates of *Spartina* spp. production (300–1500 $g \cdot m^{-2} \cdot year^{-1}$) as well as the range of other available estimates for this species (300–2400 $g \cdot m^{-2} \cdot year^{-1}$) (Table 1). However, interannual variations and longer-term oscillations in productivity could be expected as suggested by the higher rates of detritus production relative to biomass production as well as the overall decreasing trend in biomass and tiller density observed during the study period. Detritus production is almost equally dependent on tiller detachment and leaf shedding. On the other hand, net annual primary production is largely dependent on tiller recruitment (67% of productivity contributed by newly emerged tillers), which suggests that herbivores that selectively feed on the younger tillers (e.g., because of their higher nutritional content) may have critical effects on productivity. This does not seem to be the case of burrowing crabs in our marsh, since a constant probability of first herbivory for all tiller ages is enough to predict the observed numbers of tillers that were never affected by herbivory at each age class and the number of tillers that underwent herbivory for the first time at each age class. In addition, considering that tillers can survive more than 16 months and that half of the tillers of a given cohort are expected to suffer herbivory at the age of 2 months, it can be stated that crab herbivory does not ostensibly affect tiller survivorship.

Acknowledgments

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Appendix A

Rationale underlying the equation for the calculation of the probability of observing tillers without herbivory

Given an initial number N of tillers within a cohort and the probability of herbivory (P_h) constant for all tiller ages, then the probability of observing tillers of age t that have never undergone herbivory can be calculated as

$$[A1] \quad P_{nh_{(t)}} = \frac{N - \sum_{n=1}^{t} N_{h_{(n)}}}{N}$$

where $N_{h_{(n)}}$ is the number of tillers of age n that have undergone herbivory. Then, to calculate $P_{nh_{(1)}}$, $P_{nh_{(2)}}$, and $P_{nh_{(3)}}$, we have

$$[A2] \quad P_{nh_{(1)}} = \frac{N - N_{h_{(1)}}}{N}$$

$$[A3] \quad P_{nh_{(2)}} = \frac{N - N_{h_{(1)}} - N_{h_{(2)}}}{N}$$

$$[A4] \quad P_{nh_{(3)}} = \frac{N - N_{h_{(1)}} - N_{h_{(2)}} - N_{h_{(3)}}}{N}$$

Given that

$$N_{h_{(1)}} = NP_h$$

$$N_{h_{(2)}} = (N - N_{h_{(1)}})P_h \Rightarrow N_{h_{(2)}} = (N - NP_h)P_h$$

$$N_{h_{(3)}} = (N - N_{h_{(1)}} - N_{h_{(2)}})P_h \Rightarrow$$

$$N_{h_{(3)}} = [N - NP_h - (N - NP_h)P_h]P_h$$

$$N_{h_{(3)}} = (N - 2NP_h + NP_h^2)P_h$$

replacing the above expression in eqs. A2, A3, and A4 results in

$$P_{nh_{(1)}} = \frac{N - NP_h}{N}$$

$$P_{nh_{(2)}} = \frac{N - NP_h - (N - NP_h)P_h}{N}$$

$$P_{\text{nh}_{(3)}} = \frac{N - NP_h - (N - NP_h)P_h - (N - 2NP_h + NP_h^2)P_h}{N}$$

Performing some algebraic changes results in

$$P_{\text{nh}_{(1)}} = (1 - P_h)^1$$

$$P_{\text{nh}_{(2)}} = (1 - P_h)^2$$

$$P_{\text{nh}_{(3)}} = 1 - 3NP_h + 3NP_h^2 + NP_h^3 \Rightarrow P_{\text{nh}_{(3)}}$$
$$= (1 - P_h)^3$$

By extending the reasoning, we can see that these always fit the general expression (Model 1)

[A5] $\quad P_{\text{nh}_{(t)}} = (1 - P_h)^t$

By modifying eq. A1, we can achieve an equation for the number of tillers of age t that have never undergone herbivory:

$$N_{\text{nh}_{(t)}} = N - \sum_{n=1}^{t} N_{\text{h}_{(n)}}$$

From this equation, we can calculate the age at which it would be expected that 50% of the tillers have undergone herbivory:

$$t_{(0.5)} = \frac{\ln{(0.5)}}{\ln{(1 - P_h)}}$$

Rationale underlying the equation for the calculation of the probability of observing tillers that have undergone herbivory for the first time

Given an initial number N of tillers within a cohort and the probability of herbivory (P_h) constant for all tiller ages, then the probability of observing tillers of age t that have undergone herbivory for the first time (P_{ph}) be calculated as

[A6] $\quad P_{\text{ph}_{(t)}} = \dfrac{N_{\text{nh}_{(t)}} P_h}{N}$

where $N_{\text{nh}_{(t)}}$ is the number of tillers of the cohort that have never undergone herbivory up to age t. Given $N_{\text{nh}_{(t)}} = P_{\text{nh}_{(t-1)}} N$, substituting into eq. A6, we obtain

$$P_{\text{ph}_{(t)}} = \frac{P_{\text{nh}_{(t-1)}} N P_h}{N} \Rightarrow P_{\text{ph}_{(t)}} = P_{\text{nh}_{(t-1)}} P_h$$

and by using eq. A5, we obtain that the probability of observing tillers with signs of first herbivory can be calculated as (Model 2)

$$P_{\text{ph}_{(t)}} = (1 - P_h)^{t-1} P_h$$