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Production and Standing Crop Patterns of Giant Cutgrass (*Zizaniopsis miliacea*) in a Freshwater Tidal Marsh

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Summary. Growth cycles and production of aboveground and belowground giant cutgrass (*Zizaniopsis miliacea* (Michx.) Doell and Asch.) were studied in a freshwater tidal marsh along the lower Savannah River near Savannah, Georgia, USA. Minimum aboveground live standing crop (142 g/m^2) occurred in March with a steady increase thereafter to an October maximum (1,039 g/m^2) followed by a rapid decline. Giant cutgrass aboveground net primary production was approximately 1,530 $g/m^2/yr$. Rhizomes (358 $g/m^2/yr$) and roots (160 $g/m^2/yr$) yielded an annual belowground production of 518 $g/m^2/yr$. Total above and belowground annual net production was estimated at 2,048 $g/m^2/yr$.

Introduction

Interest in wetlands has increased as pressures for their utilization have demanded a more solid understanding of their biology and interaction with surrounding ecosystems. Freshwater tidal wetlands have not received the attention nor the protection accorded other wetlands despite reports of high productivity (Whigham et al. 1978). The role these unique wetlands play in their riverine environment needs to be better understood before they are irretrievably changed.

This study is part of a program examining standing crop structure and production in freshwater wetlands – both tidal and nontidal – in the lower Savannah River Valley. These studies are being undertaken to provide basic information on potential waste asümilative capacity of riverine wetlands and to determine if tides function as subsidies or stresses to these populations.

Study Area

The study was conducted in a freshwater tidal marsh along Augustine Creek near its confluence with the Savannah River slightly north of Savannah, Georgia. The marsh soil is overlaid by an organic mat, 0.5–1 m deep, which is the substrate for most of the marsh plants. The mat is composed of living and dead roots and rhizomes along with some soil from inundation water and the atmosphere. The dead organic matter is in various stages of decomposition, primarily through anaerobic activity, with decomposition being more advanced at the greater depths. Flow of the Savannah River usually prevents salt water intrusion into this area; however, salt water ($<1‰$) entered the site a few times during this study. The mat is covered by approximately 1 m of water during spring tides, barely covered during neap tides, and always uncovered during low tides.

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Dominant plant species in this marsh are giant cutgrass or southern wild rice (*Zizaniopsis miliacea*), northern wild rice (*Zizania aquatica*), arrow arum (*Peltandra virginica*), and pickerelweed (*Pontederia cordata*). These dominants exhibit a patchy distribution with cutgrass occurring in virtual monocultures in large areas. This study was conducted in one of the large monoculture stands of giant cutgrass.

Giant cutgrass (*Zizaniopsis miliacea* (Michx.) Doell and Asch.) is the dominant vegetation in much of the freshwater tidal marshes in the abandoned tidewater rice fields of South Carolina and Georgia and is the focus of this study. Very little is known about cutgrass populations except that they occur in brackish and freshwater marshes along the Atlantic and Gulf coasts from Maryland to Texas and inland to Kentucky, Arkansas, and Oklahoma (Correll and Correll 1972). Giant cutgrass is a robust perennial grass that forms dense colonies through creeping rhizomes. The grass has culms up to 3 meters tall and leaves with very sharp edges that readily cut, hence its name. Most previous interest in this grass has been in its control (Goodrum 1958; Stennis 1950; Stennis and Cottam 1945) because giant cutgrass colonies are often virtual monocultures that are poor waterfowl habitat.

Climate of the area is mild with a definite yearly growth cycle. The first winter of the study (1976–77) was especially cold for the area with sheets of water freezing around the marsh vegetation at high tides.

Methods

Estimating Aboveground Standing Crop and Production

Giant cutgrass standing crops and production was estimated using sixtyfive paired plots established along a transect. The plot size (1 m^2) was determined prior to the study to ensure a manageable variance (Wiegert 1962). Aboveground samples were collected monthly (January 1977 through February 1978) from 5 replicate paired plots, dried at 100° C for five days, and weighed.

Litter is in constant flux due to tides (Linthurst and Reimold 1978) and litter export is poorly estimated using litter bag losses. Both Wiegert and Evans (1964) and Lomnicki et al. (1968) use ground litter in their calculations. Leaf growth and death occur in each plant during most of the year so both live and attached dead plant material are present throughout the year. The Lom-

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nicki et al. (1968) method, with modifications to eliminate the litter component, was used to determine aboveground biomass production. This method requires establishment of single plot replicates at the start of each sampling interval. The dead material is removed from the plot at time t_0, then both the live (L_n) and new dead (a_n) produced within the interval are collected at time t_1. A second plot was set up at the start of the study to obtain a beginning estimate of the live standing crop (L_{n-1}). After the first interval, the L_n of the plots of one interval becomes the L_{n-1} of the plots of the next interval. Production during each interval is then estimated using the equation $p_n = L_n - L_{n-1} + a_n$. Yearly production (P) is the sum of the monthly estimates ($P = \sum_1^{12} p_n$).

The aboveground live biomass removed from one of the plots at the end of each interval (L_{n-1}) was used as the estimate of the monthly live standing crop. Likewise, the aboveground standing dead removed from both companion plots at the beginning of each interval (D_{n-1}) was used as the estimate of the monthly dead standing crop. The sum of monthly live and dead standing crops provided an approximation of the total monthly cutgrass standing crop throughout the year. Monthly mortality (a_n) was estimated by removing the new dead produced within the sampling interval from the live that had been trimmed of dead at the start of the interval. This modification of the method of Lomnicki et al. (1968) for estimating productivity is referred to as the mortality method through-out this paper.

Litter production (c_n) is defined here as the rate at which attached dead plant material leaves the plant. It was derived by assuming that the standing crop of attached dead giant cutgrass (D_{n-1}) at the start of one sampling interval must either remain attached dead giant cutgrass (D_n) or break from the plant and become litter. Not all of the attached dead at the end of the interval, however, would have been attached dead at the start of the interval (D_n); some of it would have been live material which died during the interval (a_n). The dead attached cutgrass that becomes litter during the sampling interval, therefore, is equal to the difference in attached dead cutgrass at the beginning and end of the month plus the interval mortality ($c_n = D_{n-1} - D_n + a_n$). This formulation does not take into account any leaching of material from the dead attached plant material, which may be appreciable but is unknown. Yearly litter production is the sum of the monthly estimates, and, because of unknown losses noted above, it is a minimum estimate.

Estimating Belowground Standing Crop and Production

The standing crops of roots and rhizomes were collected monthly from 0.25 m^2 of each plot pair from March 1977 through March 1978. Collections were accomplished by sawing vertically through the organic mat and removing the mat plug down to the soil substrate (50 to 80 cm below mat surface). The portion of roots in the soil substrate was insignificant. The resulting pit in the mat provided a convenient pool that aided in the immediate separation of live and dead roots and rhizomes. All samples were dried at 100° C for five days and weighed. Since only one belowground growth cycle occurs during the year, annual rhizome and root production were estimated by subtracting the minimum from the subsequent maximum standing crop. Underground production is underestimated to the extent that mortality occurs during the growing season.

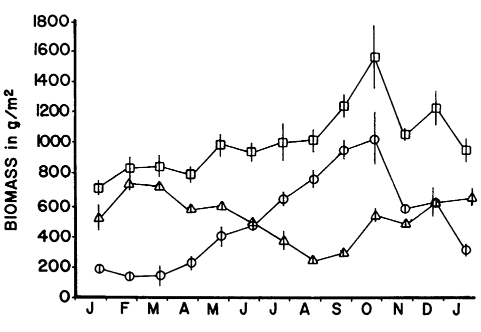

Fig. 1. Monthly estimates of aboveground cutgrass biomass (□) in g/m^2 with live (○) and standing dead (△) components ($\bar{Y} \pm$S.E.)

Results

Aboveground Standing Crops

Live aboveground standing crop (Fig. 1) was approximately 191 g/m^2 in late January 1977 and declined to a minimum of approximately 142 g/m^2 in February and March. Standing crop biomass increased steadily thereafter at a rate of approximately 4.3 g/m^2/day until early November when it reached 1,039 g/m^2. Standing crop biomass dropped to 307 g/m^2 by the end of January 1978 – approximately 100 g/m^2 higher than the previous year. Thus, the annual cycle of live aboveground standing crop appears to reach a minimum in February and March with a steady increase to an October maximum followed by a nearly steady decrease through January.

Maximum standing crop of attached dead cutgrass (Fig. 1) occurred in March at 723 g/m^2, concurrent with the minimum standing crop of live aboveground giant cutgrass. Standing dead giant cutgrass biomass decreased steadily from the March high to 247 g/m^2 in August followed by an increase through the fall and early winter to 653 g/m^2 – 70 g/m^2 less than the previous winter.

Standing dead giant cutgrass biomass exceeded live cutgrass by about five times in March. By May, the increase in live and the concurrent decrease in standing dead caused a sharp increase in the live/dead ratio of cutgrass. This condition persisted until September when there was three times as much aboveground live as standing dead giant cutgrass. The cycle changed in October with this ratio falling to the levels of the previous year by January.

Total aboveground standing crop (live plus standing dead) (uppermost curve, Fig. 1) reached a minimum of approximately 712 g/m^2 in the latter part of January and then increased slowly and steadily at a rate of about 1.5 g/m^2/day until the first of September. This very slow gain occurred because the increase in live standing crop was slightly greater than the decrease in standing dead. During the next two months, September and October, (total aboveground standing crop reached a high of 1,577 g/m^2) the increase was greater than previous gains (9.3 g/m^2/day) since both the live and standing dead cutgrass increased at the same time. The standing crop decreased thereafter to the level of the previous winter and spring.

Belowground Standing Crops

Rhizome standing crop estimates (Fig. 2) fluctuated more throughout the year than the aboveground live standing crop. Rhizome biomass reached a minimum (439 g/m^2) at the end of June and a maximum (782 g/m^2) at the end of December with an average growth rate during this period of about 2 g/m^2/day.

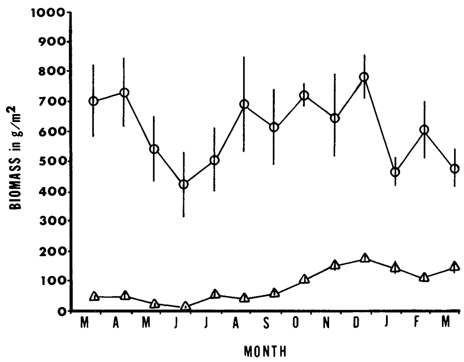

Fig. 2. Monthly estimates of cutgrass rhizome (○) and root (△) biomass in g/m² ($\bar{Y} \pm$S.E.)

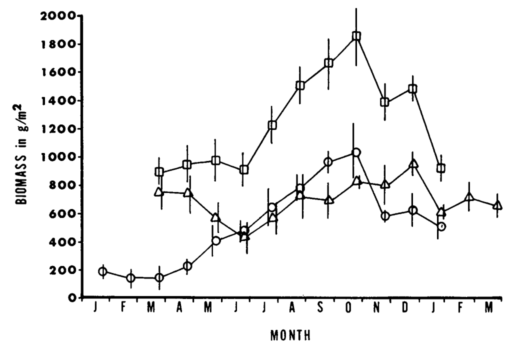

Fig. 3. Monthly estimates of total live cutgrass biomass (□) in g/m² with aboveground (○) and belowground (△) components ($\bar{Y} \pm$S.E.)

Root standing crop (Fig. 2) followed a growth cycle similar to that of the rhizomes but with less fluctuations. The minimum root standing crop occurred in the middle of the summer (15 g/m²) and the maximum in the middle of the winter (175 g/m²) ith an increase during this period of 1.1 g/m²/day in root dry weight.

Total belowground standing crop (Fig. 4) reached a minimum in the latter part of June at 439 g/m² and a maximum between December and January at 957 g/m². This maximum is approximately the same as the peak aboveground biomass (1,039 g/m²).

Total Live Standing Crop

Total live standing crop (Fig. 3) consists of the sum of the standing crops of the live aboveground giant cutgrass and the rhizomes and roots. This standing crop was at a minimum of approximately 950 g/m² from the end of January through the end of June, increased through October to 1,865 g/m², and then decreased to about 920 g/m² by the end of January.

Cutgrass Production

Aboveground production estimates were determined monthly for each of the five replicates throughout the year by the mortality method (Table 1). From the end of January until the end of October, monthly production increased at a mean daily production rate of 6.2 g/m²/day. No further net increase occurred from October to January. Total annual aboveground production was estimated at 1,530 g/m²/yr (Table 2), an annual average rate of 4.3 g/m²/day.

Plant production estimates for wetlands seldom include the underground portions of the plants because of the difficulties encountered in sampling, but we determined that at least 25% of yearly cutgrass production occurred underground (Table 2). Peak rhizome standing crop (782 g/m²) was reached in late December, two months after the peak live aboveground standing crop. Rhizome standing crop increased steadily from early summer indicating that some production products were being shunted into rhizome storage and vegetative reproduction. Rhizome production of 359 g/m²/yr was estimated by subtracting the minimum live standing crop of 424 g/m² in June from the maximum of 782 g/m² in December. Root production of 160 g/m²/yr resulted from subtracting the June minimum of 15 g/m² from the December maximum of 175 g/m². Total giant cutgrass production, consisting of the sum of the aboveground and belowground components, was estimated to be 2,048 g/m²/yr (Table 2).

Litter Production

The sum of the accumulated litter production through the year (Table 2) was 1,282 g/m²/yr. A litter production rate of slightly more than 3.33 g/m²/day appeared to be rather constant throughout the year despite negative values for October and December (Table 1). Estimated litter production was approximately 248 g/m² less than the estimated 1,530 g/m²/yr aboveground net production. This resulted from 248 g/m² more standing live and dead giant cutgrass at the end of the year than at the beginning.

Table 1. Monthly estimates ($\bar{Y} \pm$S.E.) of aboveground cutgrass production, litter production and mortality from five replicates (g/m²/day)

Month	Aerial Production Rates		Mortality
	Live	Litter	
Feb	3.58 ± 1.60	−2.13 ± 4.18	5.23 ± 0.56
Mar	2.32 ± 2.59	2.18 ± 1.24	2.30 ± 0.54
Apr	4.86 ± 2.17	6.18 ± 4.96	1.89 ± 0.12
May	6.51 ± 2.89	3.15 ± 2.96	0.65 ± 0.25
Jun	3.75 ± 1.91	4.76 ± 1.00	1.54 ± 0.33
Jul	9.65 ± 1.46	7.24 ± 2.15	3.70 ± 0.59
Aug	7.17 ± 3.74	5.46 ± 3.77	2.89 ± 0.26
Sep	9.75 ± 3.96	1.40 ± 2.33	3.47 ± 0.55
Oct	8.25 ± 7.16	−2.03 ± 2.92	5.91 ± 0.72
Nov	−7.07 ± 5.53	10.42 ± 3.63	8.09 ± 0.74
Dec	5.69 ± 2.14	−2.71 ± 2.80	4.33 ± 0.25
Jan	−3.46 ± 1.52	8.54 ± 2.94	7.22 ± 1.01

Table 2. Annual net production of aboveground (mortality method) and belowground (max.-min. method) cutgrass populations ($\bar{Y} \pm$S.E.) as well as litter annual net production

Aboveground	1,530 ± 103 g/m²/yr
Belowground	518 ± 135 g/m²/yr
Rhizomes	358 ± 136 g/m²/yr
Roots	160 ± 10 g/m²/yr
Total net production	2,048 ± 101 g/m²/yr
Aboveground litter net production	1,282 ± 65 g/m²/yr

Discussion

Giant cutgrass is a perennial with a distinct yearly developmental cycle in temperate marshes. Aboveground standing crop in our study was never less than 700 g/m^2. The minimum standing crop of winter consisted of 191 g/m^2 of live and 521 g/m^2 of dead plant material. Peak standing crop in late October of 1,577 g/m^2 consisted of 1,039 g/m^2 of live and 483 g/m^2 of standing dead, thus the population always consisted of both live and dead. A preliminary study of giant cutgrass growth patterns led us to believe that the peak standing crop (live + standing dead) was probably a biased estimate of production since some aboveground live (142 g/m^2) and considerable standing dead (723 g/m^2) were present at the start of the growing season (late March). Further study revealed that most of this standing dead hold-over from the previous year's growing season had broken from the plant by August and had virtually disappeared by October (at peak standing crop). The aboveground live standing crop present at the start of the growing season was outer leaf bases which were among the first plant parts to die during the growing season. Accordingly, the peak aboveground standing crop in October was all produced within the year and, therefore, appeared to be a good estimate of giant cutgrass aboveground production in this marsh. This same pattern of annual growth and export of the previous year's standing dead also was observed in *Spartina* populations in Georgia salt marshes (Odum and Fanning 1973). Peak live standing crop, however, is not a good estimate of production because of the mortality that occurs between the start of the growing season and peak standing crop (de la Cruz 1978).

This giant cutgrass production estimate is in general agreement with wild rice (*Zizania aquatica*) peak standing crops of 1,600 g/m^2 (Good and Good 1975) and 1,475 g/m^2 (Whigham and Simpson 1977), and generally comparable to estimates of *Phragmites communis* at 1,367 g/m^2 (Flemer et al. 1978) and 1,727 g/m^2 (McCormick and Ashbough 1972). Our estimate is higher, however, than most peak aboveground standing crop (live + standing dead) estimates of tidal (both freshwater and brackish) emergents along the middle Atlantic coast. These emergents generally are aboveground annuals in that their tops die back each year. If dead biomass of the year remains attached to the parent plant and translocation from the aerial structures to the underground storage after peak standing crop is not great, then peak standing crop is a good estimate of production, as was the case in our studies.

The Wiegert and Evans (1964) method, which measures the change in the live standing crop and the export of litter, is sometimes used in tidal wetland (predominantly salt marsh) production studies (Hopkinson et al. 1978, Kirby and Gosselink 1976, Linthurst and Reimold 1978, Reimold et al. 1975, White et al. 1978) and appears to be among the most accurate methods of estimating net primary production. This method depends on either (1) there being no difference in net litter movement between plots with and without live plant material present or (2) litter bag loss rates being equivalent to net litter export. Tidal marshes are well known for erratic litter fluctuations and litter import (Linthurst and Reimold 1978) which can alter the result of the Wiegert-Evans method appreciably. We used litter bags to determine the litter decay rate and found that there was still 26% of the dead leaf material remaining after a year, indicating that large accumulations of litter should build up on the marsh surface. This did not happen in these tidal marshes since the surface was devoid of litter at times. Litter in a bag is not carried out by tides as would be the case for unrestrained litter. Linthurst and Reimold (1978) concluded and we concur that the weak point in using the Wiegert-Evans method in tidal wetlands is getting a good measure of litter flux. The mortality method of estimating aerial net production appears to measure the flow of biomass from the living compartment to the dead with a fair degree of accuracy. The removal of the litter compartment from the methodology eliminated the erratic fluctuations in net production estimates due to tidal import and export of litter.

Different estimates of aboveground production ($\bar{Y} \pm SE$ $g/m^2/yr$) were generated using the following methods: peak standing crop (Kucera et al. 1967) ($L = 1{,}039 \pm 167$, $L + SD = 1{,}577 \pm 203$), maximum-minimum (Ovington et al. 1963) where the minimum standing crop is subtracted from its subsequent maximum ($L = 897 \pm 148$, $L + SD = 865 \pm 243$), trough-peak (Singh et al. 1975) where all statistically significant (alpha = 0.10) positive increments of biomass are summed through the year ($L = 897 \pm 148$, $L + SD = 910 \pm 238$) (coincident standing dead refers to that standing dead whose positive increment was coincident with a positive live increment) ($L + CSD = 1{,}208 \pm 215$), and Smalley method (Smalley 1959) ($1{,}595 \pm 276$). These range from minimum estimates of approximately 900 $g/m^2/yr$ by the max-min and trough-peak methods to maximum estimates by the Smalley, peak standing crop, and mortality methods of approximately 1,570 $g/m^2/yr$. The results derived by the methods within each of these two groups are not significantly different from each other whereas there are significant differences between groups.

Estimates based on the mortality method, Smalley method and peak standing crop (live + standing dead) probably can all be used in this marsh with confidence. This confidence would not have been possible, however, without substantial knowledge of the growth processes of the giant cutgrass population and a method of estimating the annual net productivity in which we already had ample confidence.

A clear minimum biomass occurred for both roots and rhizomes during late June; a subsequent steady increase produced a maximum in late December (Fig. 2). The spring rhizome level was lower during the second winter than the first, while the roots appear to have been higher along with the aboveground biomass (Fig. 1). The first winter was much more severe than the second so the temptation exists to speculate that the roots and aboveground portions translocated more materials to the rhizomes in the first winter and that the stored energy and materials were retained longer in the rhizomes the first winter than the second. A subsequent year's data would have been very helpful in determining if the study year's production was normal or if the lower starting point resulted in a lower peak biomass and/or production.

Rhizome biomass continued to increase after October when photosynthesis was clearly on the decrease. Translocation of energy and nutrients are know to occur during senescence before the leaf chlorophyll is broken down (Greulach 1973). Leaves, therefore, that are weighed before senescence translocations begin would tend to be heavier than the same leaves after much of this net outward translocation has taken place and before the leaves turn yellow or brown. Translocation would result in a negative production estimate and we believe this is what was responsible for the negative estimates in the late fall and early winter (Table 1). Therefore, some of the late fall and early winter rhizome production probably was counted earlier as leaf production and counted again as leaf production during the subsequent late winter and early spring. This concept of energy translocations within populations between aboveground and belowground (or leaves and stem-root storage in trees and shrubs) and its effects on production estimation is in need of critical study.

Total annual giant cutgrass production includes the annual net production of both the aboveground and belowground components of the population. These components were estimated separately. Total annual giant cutgrass net production was estimated both by summing the estimates of the separate components and by estimating both separately but simultaneously. The simultaneous estimates were lower than combinations of similar estimates because the peaks (and troughs) did not occur at the same time in the aboveground and belowground portions of the plants.

No method similar to the mortality or Lomnicki method that takes both mortality and biomass balance into account has been developed for working belowground; thus, equivalent estimates may not be made. The more accurate methods used aboveground must be summed with the less accurate belowground production estimate to arrive at a production estimate that is about twice the simultaneously derived max.-min. estimate.

The ratio of aboveground cutgrass production estimated by the mortality method to that estimated by the max.-min. method was 1.7. If an assumption is made that this ratio is the same belowground as it is aboveground, then belowground production, including mortality, would be 881 $g/m^2/yr$. The sum of this belowground estimate and the mortality method aboveground estimate would be 2,411 $g/m^2/yr$. The simultaneous whole plant max.-min. estimate was only 68% of the sum of the separate estimates. If this ratio applies to estimates derived simultaneously by other methods, then the whole plant production estimate would be 1,640 $g/m^2/yr$.

We believe, however, that the whole plant net primary production estimated by the mortality (aboveground) and max.-min. (belowground) methods at 2,049 $g/m^2/yr$ (20,490 Kg/ha/yr, 8,708 $KCal/m^2/yr$) is a fair estimate. This places it among the highest producers of temperate tidal wetlands (Whigham et al. 1978) and communities in general (Whittaker 1975).

Much of the litter production of 1,282 $g/m^2/yr$ is exported from the marsh and contributes to the detrital import base of the estuarine and coastal marine systems. The proportion of this 12,782 Kg/ha/yr that is exported and its contribution to the estuarine and coastal marine ecosystems is unknown.

Conclusions

Giant cutgrass is a robust grass that starts the growing season with a little live and a lot of dead aerial biomass from the previous year's production. When subjected to tidal water movements, it appears to shed its previous years's standing dead biomass while retaining most of the standing dead produced within the year by the time of peak aerial biomass. In this particular situation, aerial net production appears to be quite near the peak aerial live plus dead standing crop.

Root and rhizome production was estimated to be 1/3 that of the aerial portion or 1/4 the total production of the population. This is a minimum estimate that does not account for mortality within the year as did the aerial estimate

Net production in freshwater tidal wetlands range up to 2,100 $g/m^2/yr$ (Whigham et al. 1978). However, most net production estimates of grass in this type of wetland are around 1,600 $g/m^2/yr$ compared to the estimate here of 2,049 $g/m^2/yr$. The longer growing season probably accounts for part of this larger estimate.

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