PROC. N.S. INST. SCI. (1980)
Volume 30, pp. 109-118

ANGIOSPERM PRODUCTIVITY IN TWO SALTMARSHES OF MINAS BASIN*

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Above-ground angiosperm productivity in 2 saltmarshes of Minas Basin (Bay of Fundy) was estimated at about 500 g dry wt m^{-2} yr^{-1}, a low value compared with marshes on the Atlantic coast of Nova Scotia. Below-ground production may provide an additional 900 g dry wt m^{-2} yr^{-1}. The percentage carbon in the plants was low, about 34% of the dry weight. The addition of NH_4NO_3 to marsh soils increased the above-ground productivity by about 90% despite the high levels of NO^-_3 and NO^-_2 previously reported for these marshes. Three species of angiosperms, *Juncus gerardii, Spartina patens,* and *Spartina alterniflora,* were dominant. All of the standing crop of *S. alterniflora* was transported from the marshes to the surrounding estuarine waters early in the autumn. Standing crop of the other 2 species, as well as below-ground production of all 3 species, remained on the marshes. Shading by the angiosperm canopy had a significant effect on the soil temperature.

Introduction

Saltmarshes in temperate latitudes along the Atlantic coast of North America are highly productive (Odum 1971; Seneca 1974), with much of this production being transported into surrounding waters (Teal 1962) where it forms an important source of nutrients (Teal 1962; Reed & Moisan 1971; Mann 1975). It has been demonstrated (Turner 1976) that energy incident on a saltmarsh area and angiosperm productivity are generally correlated, with productivity decreasing as latitude increases. On the Atlantic coast of Nova Scotia, relatively high levels of productivity were recorded in saltmarshes dominated by the grass *Spartina alterniflora* (Martin 1974; Hatcher & Mann 1975; Livingstone 1978; Patriquin & McClung 1978).

The Bay of Fundy, between Nova Scotia and New Brunswick, is characterized by very large-amplitude tides, rapid tidal currents and high levels of suspended matter (Bousfield & Leim 1960; Dalrymple et al. 1975; Pelletier & McMullen 1972). At the head of the bay, on the soft sediments of Chignecto Bay and Minas Basin, extensive saltmarshes occur. Apart from the study of Morantz (1976) in Cumberland Basin, the productivity of these marshes, which exist under unique physical conditions, has not been examined. The present paper reports on productivity of 2 saltmarsh systems in Minas Basin.

Materials and Methods

Study Areas and Transects

Transects were established on 2 saltmarshes in Kings County, Nova Scotia. One marsh, near Grand Pré, has existed only 15 years, because of recent dyking, and consists almost entirely of a single species, *Spartina alterniflora;* the other marsh, near Kingsport, is an older community with several distinct vegetational zones. Along each transect, 4 floristic zones were recognized, as determined by species dominance at Kingsport, and by growth forms of the single dominant at Grand Pré; one

*Issued as NRCC No. 18239.

sampling station was established near the middle of each zone. Fertilization experiments were conducted in 1979. All other data were collected biweekly during the summer of 1978.

Angiosperm Productivity

Above-ground angiosperm production was measured by quantifying standing crop. Aerial portions of plants were clipped from 0.0625-m^2 quadrats (0.25 m x 0.25 m) randomly positioned near the sampling stations. Three quadrats were harvested at each sampling station on each sampling day. Samples were washed, sorted into living and dead material, dried for 48 h at 105°C, and weighed. Peak above-ground biomass was used to estimate annual production, subject to correction for minor losses of lower leaves in the case of *Spartina alterniflora* (Morantz 1976). Average height of plants was approximated for correlation with biomass.

Fertilization Experiments

Early in June, 2 plots 9 m^2 (3 m x 3 m), experimental and control, were established in each floristic zone. The experimental plot of each pair was fertilized with 500 g NH_4NO_3 (165 kg N ha^{-1}); premeasured amounts of the fertilizer were poured into 100 evenly spaced holes, 1 dm deep, made with a steel rod of 1 cm diameter.

Light Extinction

The relative intensity of light reaching the soil surface was determined in all productivity quadrats prior to harvesting. The light intensity above the angiosperm canopy was also measured. These values were applied to the expression

$$\text{Fractional light extinction} = (h\nu_a - h\nu_b)/h\nu_a$$

where $h\nu_a$ = light intensity above the angiosperm canopy and $h\nu_b$ = light intensity at the mud surface beneath the canopy. Light intensity was measured with a Li-Cor LI-185 meter equipped with a quantum sensor.

Temperature

Air, soil surface, and subsoil (-10 cm) temperatures were taken at each sampling station on each sampling day. Temperature determinations were made with a YSI Model 44 electric telethermometer.

Carbon Determination

Carbon was determined, in 18 randomly selected angiosperm samples, by C, H, N analysis, and is expressed as percent of the dry weight.

Results

Flora

The plants observed in each transect are indicated in Table I and Figures 1 and 2. The total dominance of *S. alterniflora* at Grand Pré results from the high frequency of tidal inundation, the marsh being completely flooded on all but the lowest high tides. This, in turn, is because of the relative youth of the Grand Pré marsh, and possibly this marsh is still accreting.

Angiosperm Productivity

Above-ground productivity at Kingsport by *J. gerardii* (zone 1) and *S. patens* (zones 2 and 3) was similar (Table II). Production by *S. alterniflora* (zone 4 of Kingsport and all zones of Grand Pré; Table II) was about 20% higher than that of *J. gerardii* and *S. patens*. Substantial variation in the productivity of the growth forms of *S. alterniflora* was observed. Stands at the edges of channels (zones 1 and 4 at Grand Pré

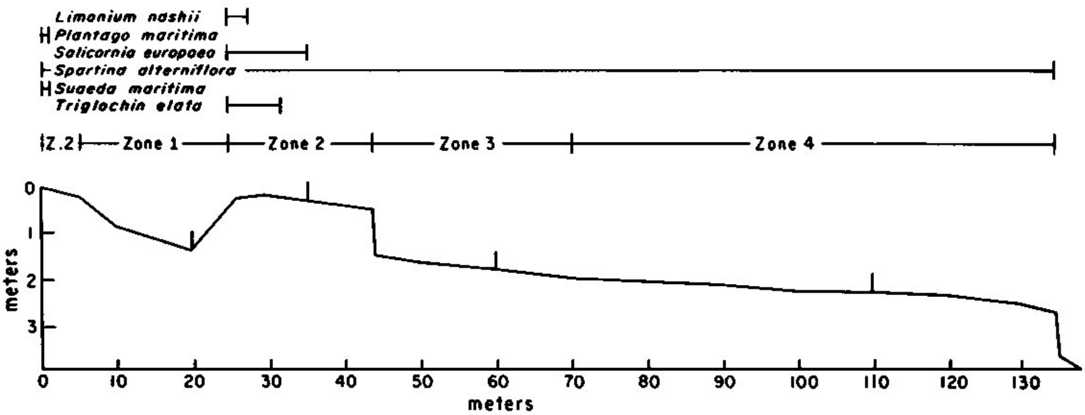

Fig 1. Profile of the Grand Pré transect. The 4 floristic zones and the distribution of the various angiosperm species are indicated by the horizontal bars above the profile. The 4 vertical bars on the marsh surface indicate the location of the sampling stations.

and zone 4 at Kingsport) were taller and exhibited much higher productivity than adjacent shorter growth; at Grand Pré production in zone 1 was more than twice that of zone 2 or 3 (Table II). In fact, there was close correlation between height and biomass throughout the 2 marshes (Table III). The lowermost zones, bordering the estuary (zone 4), showed similar productivity at both marsh sites (Table II). Overall production was slightly greater at Grand Pré, reflecting the higher productivity of *S. alterniflora* (Table II).

Lower leaves of *S. alterniflora* began to die before peak biomass had been reached (Fig 3c), although dead leaves with intact leaf bases persisted on the culms to soil surface level throughout the sampling period. Most of the above-ground production of *S. alterniflora* was, however, swept off the marshes by early December, before the occurrence of any ice-scouring. For these reasons the annual above-ground production in zones dominated by *S. alterniflora* was estimated from the highest total mass sum of live and dead material during the season. In contrast, dead material from previous growing seasons persisted, in large quantities, in areas dominated by *S. patens* and *J. gerardii* (Fig 3a, b), and current growth did not begin to die until maximum biomass was attained. Thus, annual production of *S. patens* and *J. gerardii*

Table III. Correlation between plant biomass and height on the Grand Pré and Kingsport saltmarshes

Zone	Slope	Y intercept	R	R^2
Grand Pré				
1	2.05	4.99	0.91	0.82
2	1.92	6.65	0.87	0.75
3	2.79	3.86	0.99	0.97
4	2.06	1.00	0.99	0.97
Kingsport				
1	1.29	7.91	0.88	0.80
2	0.89	15.63	0.98	0.96
3	0.91	13.96	0.96	0.91
4	1.80	15.04	0.89	0.80

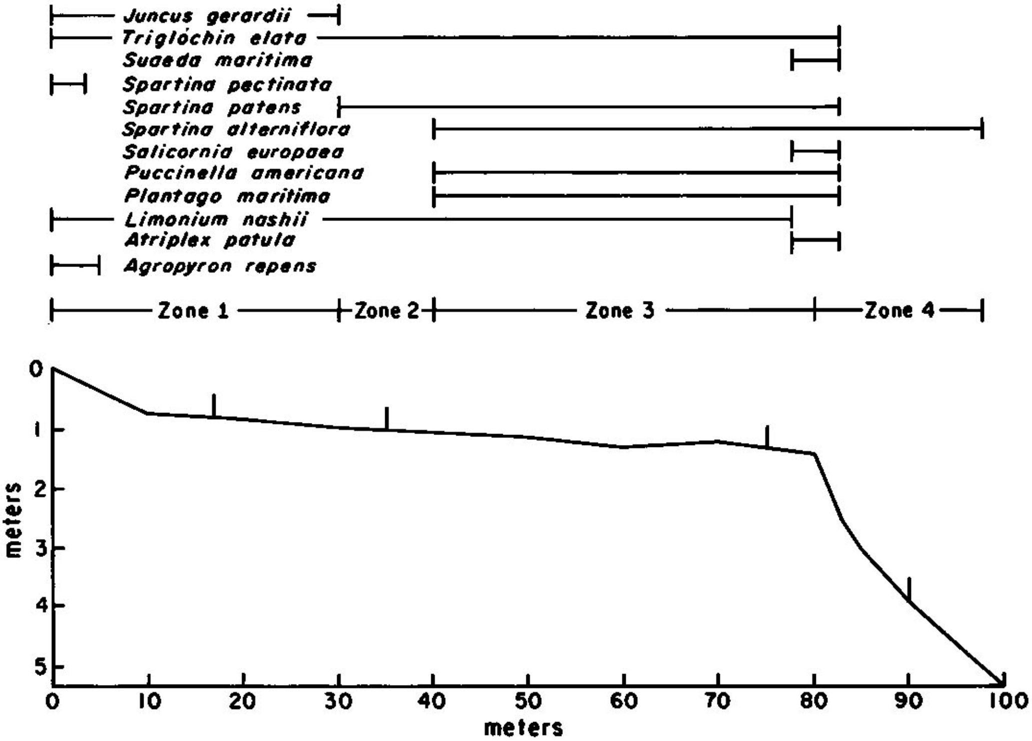

Fig 2. Profile of the Kingsport transect. The 4 floristic zones, the distribution of the various angiosperm species, and the sampling stations are indicated as in Fig 1.

was estimated from the weight of living material only. Below-ground production (Table II) was estimated by multiplying above-ground values by 1.75 (Patriquin & McClung 1978).

Addition of NH_4NO_3 to saltmarsh soils increased the above-ground production of angiosperms by an average of 88%. The increase was large and statistically significant in all zones except zone 2 of the Kingsport marsh (Table IV). Fertilization did, however, have a positive effect on *S. alterniflora* which is scattered on the order of several shoots per m^2 in this *S. patens* community. These plants normally are small and fail to flower, but inside the fertilized plot they were robust and completed the normal reproductive cycle.

The average percentage of carbon in plants on the 2 marshes (1978, unfertilized) was 34.4 3.6% (n = 18). There was little variation among species or throughout the season. This percentage of carbon is considerably lower than the 40.77% for *S. alterniflora* reported by Burkholder and Bornside (1957).

Light

Generally, a good correlation existed between the height of angiosperms and the fractional light extinction by the plant canopy (Table V), except in zones dominated by *S. patens* (Kingsport zones 2 & 3). These zones retained a dense canopy of dead plants from the previous growing season, resulting in high light extinction throughout the summer. As angiosperm height and biomass correlated very well (Table III), light extinction therefore may be viewed as a function of either factor.

A strong negative correlation existed between fractional light extinction and soil temperature (Table VI). Although there was no significant difference in air temperatures over the 2 marshes, the average soil surface and subsoil temperatures were both slightly lower at Kingsport (Table VII). This is probably due to the greater light extinction by canopy of *J. gerardii* and *S. patens* (Kingsport zones 1-3, Table VI).

Table IV. Effects of application of NH_4NO_3 on angiosperm above-ground production in the Grand Pré and Kingsport saltmarshes

Zone	N[1]	Mean[2] g Dry Wt m^{-2}	2 Standard Error Units	% Increase
Grand Pré				
1	+	761.6	57.8	45.1
	-	524.8	62.2	
2	+	620.8	53.2	41.6
	-	438.4	99.6	
3	+	372.8	62.2	137.7
	-	156.8	38.4	
4	+	710.4	106.4	48.5
	-	478.4	34.0	
Kingsport				
1	+	846.4	184.4	128.0
	-	371.2	43.0	
2	+	519.2	207.0	9.8
	-	472.8	141.4	
3	+	809.1	138.0	173.8
	-	295.5	41.8	
4	+	675.2	167.4	117.5
	-	310.4	49.8	

[1] + values are from fertilized (NH_4NO_3) plots; - values are from control plots
[2] n = 8

Table V. Correlation between plant height and light extinction on the Grand Pré and Kingsport saltmarshes

Zone	Slope	Y intercept	R	R^2
Grand Pré				
1	0.025	0.63	0.87	0.76
2	0.006	0.05	0.71	0.50
3	0.006	0.43	0.74	0.58
4	0.005	0.53	0.86	0.73
Kingsport				
1	0.009	0.47	0.85	0.73
2	0.005	0.68	0.50	0.25
3	0.003	0.80	0.50	0.25
4	0.011	0.10	0.91	0.84

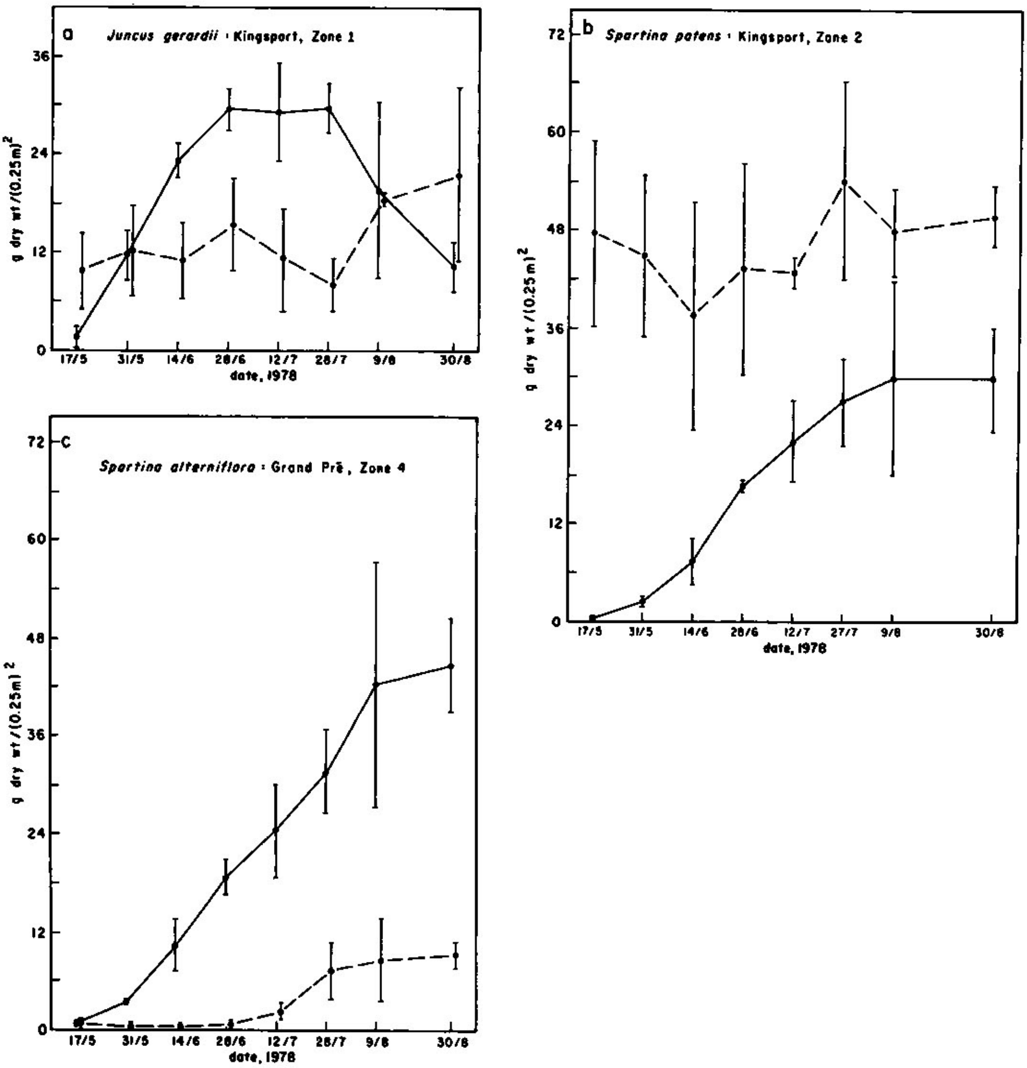

Fig 3. Seasonal distribution of live (—) and dead (--) angiosperm material in marsh communities dominated by (a) *Juncus gerardii*, (b) *Spartina patens*, and (c) *Spartina alterniflora*. Each point is the average of 3 measurements. Vertical bars indicate ± $2S_{\bar{x}}$.

Table VI. Correlations between light extinction and subsurface (-10 cm) soil temperature, based on the averages of each zone over the entire summer[1]

Grand Pré

Zone	Temp. (°C)	Light Extinguished		Slope	Y intercept	
1	16.0 ± 2.6	0.71	0.12	6.59	20.8	-0.84
2	17.1 ± 3.0	0.56	0.12			
3	16.9 ± 3.2	0.66	0.08			
4	16.4 ± 3.4	0.64	0.11			

Kingsport

Zone	Temp. (°C)	Light Extinguished		Slope	Y intercept	
1	14.3 ± 3.1	0.78	0.08	2.15	15.6	0.81
2	13.7 ± 2.9	0.80	0.09			
3	13.6 ± 2.9	0.90	0.05			
4	14.4 ± 3.1	0.53	0.14			

[1]All values given with a ± 2S $\bar{x}$ estimate of sample variation (n = 21)

Table VII. Comparisons of various parameters measured dn the Grand Pré, Kingsport, and other saltmarshes

Parameter	Grand Pré	Kingsport	Other
% light extinction[1]	0.64 ± 0.05	0.79 ± 0.05	
soil surface temperature[1] (°C)	21.9 ± 1.7	18.4 ± 1.3	
subsoil (-10 cm) temperature[1] (°C)	16.6 ± 1.4	13.9 ± 1.1	
above-ground angiosperm biomass[2] (g dry wt m^{-2} yr^{-1})	529.8	492.8	750 (Martin 1974) 710 (Hatcher & Mann 1975 483 (Morantz 1976)

[1]mean value for the entire summer sampling period (1978)
[2]calculated from seasonal maxima

Discussion

Compared with marshes on the Atlantic coast of Nova Scotia, productivity in Minas Basin marshes was low (Table VII). The reasons for these low values are unclear, but the dramatically different tidal regime—irregular and brief inundation of marshes, especially high marsh—is undoubtedly nutrient-limiting and has been suggested as contributing to lower overall productivity of marshes in the Bay of Fundy (Morantz 1976). Enhancement of above-ground production by addition of nitrogen suggests that this element may be limiting, although previous data (Smith et al. 1979) showed that NO_2^- and NO_3^- nitrogen were present in high concentrations. Indeed, these levels are sufficient to inhibit biological nitrogen fixation. If nitrogen is limiting, the situation is paradoxical: starvation in the midst of plenty. Similar phenomena have been reported for saltmarshes on the Atlantic coast of the United States (Morris 1978; Mendelssohn 1979). Smith et al. (1979) found low levels of NH nitrogen in Minas Basin saltmarshes, and high ammonium concentrations are reported for Massachusetts saltmarshes (Valiela et al. 1975). On the Atlantic coast of Nova Scotia, high concentrations of NH_4^+ nitrogen were observed in a high marsh situation (Patriquin & Keddy 1978), but low concentrations of NH_4^+ and NO_3^- nitrogen in the low marsh (Livingstone 1978). High nitrite levels (Smith et al. 1979) had not been previously reported in saltmarsh soil water, and these levels observed in the study area may indicate some type of blockage in the oxidization or reduction of nitrite. Such a blockage could play a role in the apparent nitrogen limitation. However, the precise cause of nitrogen limitation is uncertain and is the current subject of investigation by various workers (e.g. Mendelssohn 1979). Another factor which may have limited productivity is extreme anaerobiosis of the fine clay substrate, producing an oxygen limitation around plant roots.

Spartina alterniflora in Bay of Fundy marshes differs from that in marshes on the Atlantic coast of Nova Scotia with respect to export of biomass during the growing season. Hatcher and Mann (1975) reported losses of older leaves in Atlantic coast plants to the extent of 23.3 to 35.1% of annual above-ground production. Morantz (1976), however, found that about 12% of plants sampled in mid-summer displayed abscission of lower leaves, and calculated a net loss during the growing season of only 6.8%. Although *S. alterniflora* in the present study had intact lower leaf bases to soil surface level, the decreasing proportion of dead material during August (Fig 3c) suggest that minor attrition of older material, whether as entire leaves or their distal portions, was occurring, and production values for this species are probably slightly underestimated.

The year-round presence of large amounts of dead angiosperm material in zones 1, 2, and 3 of the Kingsport marsh (*S. patens* and *J. gerardii*) indicates that much of the production of these zones was not being exported to the estuarine waters. In contrast, nearly all annual above-ground production of *S. alterniflora* was exported from the marsh during October and November. Presumably all below-ground production remained on the saltmarshes and was slowly mineralized or buried. At Grand Pré, roots of *S. alterniflora* occurred at a depth of at least 1 m, and at the end of the transect was the exposed edge of an old saltmarsh root layer about 2 m below the current layer. This turf is probably the remains of the marsh which existed here prior to construction of the present dyke, and is indicative of the relative youth of the present marsh. Burial may also be related to the increasing tidal amplitude in the Bay of Fundy (Amos 1977).

The shading effect of the angiosperm canopy could exert a significant effect on algal, microbial, and invertebrate populations living on the mud surface. Lower subsoil temperatures under the dense *S. patens* and *J. gerardii* canopies of both living and dead material may have contributed to the lower production by these 2 species.

Acknowledgements

We thank Charles Trick for aid in establishing this program, and Laura Taylor, Emily Fraser and Scott Wilson for their assistance with the field work.

Funds to support this research were provided by the Federal Summer Job Corps grant number 16-01-001.

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