PRIMARY PRODUCTION AND METABOLISM OF AN AMMOPHILA BREVILIGULATA (AMERICAN BEACHGRASS) COMMUNITY

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ABSTRACT

PRIMARY PRODUCTION AND METABOLISM OF AN AMMOPHILA BREVILIGULATA (AMERICAN BEACHGRASS) COMMUNITY

By

Eric N. Hansen

Estimates of the net primary production of an American beachgrass community located on a foredune on the east shore of Lake Michigan were determined by harvesting. Gross photosynthetic assimilation, plant respiration, soil respiration and community respiration were estimated from measurements of rates of CO_2 exchange in light, dark and soil chambers. CO_2 flux was measured with an infrared gas analysis system. Laboratory measurements of beachgrass photosynthesis were used in the interpretation of annual metabolic variation observed in the field. Interactions of rodents and insects with the beachgrass were also studied.

Net primary production of the community was 347 g/m^2. This figure was a total of aboveground biomass increase (183 g/m^2), belowground biomass increase (91 g/m^2), and aboveground biomass mortality (73 g/m^2). The maximum production possible was estimated to be 555 g/m^2 and minimum production possible was estimated to be 218 g/m^2. At the time of peak aboveground living biomass, the ratio of aboveground living to total belowground biomass was 4.1. The mean caloric values for aboveground living, dead, and total belowground biomass were 4.70 ± 0.02, 4.80 ± 0.02 and 4.62 ± 0.03 Kcal/g dry weight respectively. The efficiency of beachgrass during the growing season was 0.23% and 0.14% annually.

Maximum rates of gross photosynthetic assimilation occurred in late June and early July, whereas maximum rates of aboveground plant respiration occurred in August. Mean daily rates of gross photosynthetic assimilation, aboveground plant respiration and soil respiration during the growing season were 2.64, 1.27 and 1.41 g C/m^2/day respectively.

Staining aggregations of sand found on the study site revealed a possible vesicular-arbuscular mycorrhizal association of beachgrass with a fungus closely resembling Glomus macrocarpus.

The large proportion of juvenile males and the absence of burrows and aboveground nests and runways indicated that the two prevalent rodent species trapped, Peromyscus maniculatus bairdi and Microtus pennsylvanicus were not residents on the study site. The absence of beachgrass in the digestive tracts of these rodents revealed that beachgrass does not contribute to their diets. Only Phyllophaga rugosa larvae appeared to be utilizing beachgrass as their main food source.

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INTRODUCTION

Primary Production In Terrestrial Ecosystems

Primary production refers to the new organic material created by photosynthesis in plants and often is expressed as weight or energy (Westlake, 1969). A not-so-obvious component of primary production is the energy required to maintain the living biomass (respiration). The total primary production of a plant (gross primary production) consists of the accumulated organic material (net primary production) plus that used in respiration. For a more complete estimate of gross primary production, plant material which disappears during the growing season should also be included.

Net primary production in terrestrial communities has been measured primarily by harvesting plant biomass (Woodwell and Whittaker, 1968). Improved techniques have been developed for the evaluation and comparison of different methods of assessing grassland aerial net primary production and biomass dynamics (Kelley et al., 1974; Singh et al., 1975). However, reliable estimates of grassland root production for inclusion with aerial production for complete plant net primary production are difficult to obtain and frequently are not included in productivity estimates (Kucera et al., 1967). The separation of roots and rhizomes from the soil is so laborious and time consuming that often it is not practical to get enough replications to insure statistical reliability (Redmann, 1975). Another problem in estimating root production is that the period for root growth corresponds with that of greatest root decomposition rates so that net observable changes may be negligible.

The determination of gross production is done by gas exchange (CO_2) measurements (Bordeau and Woodwell, 1965) taken from enclosed portions of a plant or entire plants (Kanemasu and Hiebsch, 1975). By enclosing entire portions of an ecosystem (Odum and Pigeon, 1970) or by indirect estimates of CO_2 flux (Lemon *et al*., 1970) estimates of ecosystem metabolism can be obtained. Estimates of gas exchange of grassland plants have been mainly limited to crop plants (Milthorpe and Moorby, 1974).

Ammophila breviligulata Fern. (American beachgrass) (Figure 1) grows as a pure community on sand and has only one seasonal peak. The rate of organic matter decomposition in areas where beachgrass grows is slow (Olson, 1958a). These factors alleviate many of the problems of estimating net primary production encountered in more diverse grassland communities.

The Ecology of Ammophila Breviligulata

A taxonomic description of American beachgrass is given by Fernald (1920) and Hitchcock (1950). Morphologically, beachgrass is adapted to the foredune area where sand accumulation occurs. It has tough but flexible pointed leaves which are 0.6-0.9 m long and are able to survive the force of the wind with little harm. Its vertical growth form, unlike many other early successional dune species (Salisbury, 1938), enables it to withstand up to 1 m of burial in a year, provided that more than half of the leaf is not buried at a time (Laing, 1954; Ranwell, 1958; Woodhouse and Hanes, 1966).

Figure 1. *Ammophila breviligulata* on a Lake Michigan sand dune near Saugatuck, Michigan.

The rhizomes are able to penetrate sand and withstand the sand's abrasive action since the apices are enclosed by a hard, spine-like sheathing leaf (Salisbury, 1952). The rhizomes possess potentially unlimited horizontal growth (Cowles, 1899; Ranwell, 1972). Roots do not penetrate significantly deeper than about 1 m (Ranwell, 1972), although individual roots or vertical rhizomes can be much longer (Laing, 1954).

American beachgrass is found on sand dunes along the Atlantic coast from Newfoundland to North Carolina and on the shores of all the Great Lakes (Hitchcock, 1950; Voss, 1972). The Great Lakes beachgrass is thought to have spread from the Atlantic coast since the retreat of the Wisconsin ice sheet (McLaughlin, 1933; Peattie, 1922). The Great Lakes and Atlantic coast beachgrass populations are ecotypes of the same species (Seneca and Cooper, 1971). Beachgrass communities are established, by seeds or through regeneration from rhizome fragments carried by water from eroded dunes, on dunes with active sand deposition. The flowering heads begin to emerge in late July and the seeds are usually mature by late August to mid-September (Laing, 1958). However, in a study on the Baltic coast, Kubien (1970) found that only 4% of the seeds that could develop did. This was due to either abnormal development in the anthers and ovules or a breakdown in the later stages of endosperm development. Of the florets from the Indiana dunes, studied by Laing (1958) 95% had little or no seed development, 4% had shrunken seeds (possibly an endosperm deficiency) and 1% had developed seeds. Seedling establishment is sporadic because of death caused primarily by heat, dessication and sand burial (Gemmell _et al_., 1953; Jagschitz and Bell, 1966; Laing, 1958; Waterman, 1919; Woodhouse and Hanes, 1966). Establishment of seedlings is generally confined to leeward slopes of eroding dunes, moist hollows and occasionally beaches (Laing, 1958).

Rhizome fragments from eroded foredunes are transported laterally along the shore by currents and are eventually cast up on shore where new plants may be established. Laing (1958) feels that this may be more important than seed dispersal in the establishment of new communities.

An established beachgrass community increases its area primarily vegetatively by horizontal rhizomes which, in Michigan, are only produced under long day conditions (Seneca and Cooper, 1971). To remain vigorous, beachgrass needs continual sand accumulation. Once the dune surface becomes stabilized there is a decline in vigor.

Because of its sand binding ability, beachgrass (American and European) has been introduced into a number of temperate areas for sand stabilization (Anon., 1957, Barbour _et al_., 1975; Breckton and Barbour, 1974; Keet, 1936; Michell, 1966; and others). Most of the previous literature on beachgrass is concerned with planting and fertilizing it for this use (Brown and Hafenrichter, 1948a,b,c; Coaldrake _et al_., 1973; Coaldrake and Beattie, 1974; Lehotsky, 1939; Jagschitz and Bell, 1966; Stoesz and Brown, 1957; Westgate, 1904; Woodhouse and Hanes, 1966; and others). Although many grasses have been tried, none has proven as effective in binding sand as beachgrass. Both the above and below ground portions of beachgrass contribute to its sand binding ability. Its aerial portions reduce the wind speed below that needed to move sand (about 4 m/sec or 9 mph) (Olson, 1958b) and its extensive roots and rhizomes provide some protection to the slopes of eroded windward foredunes (Patton, 1934). However there have been no studies of the annual productivity of beachgrass.

There are a variety of insects, spiders, etc. associated with the succession of higher plants progressing inland from the front dune (Shelford, 1913). The succession of tiger beetles (Cicindelidae) is an example of this (Shelford, 1907). Most studies of invertebrates in association with beachgrass foredune communities have been limited to classification of individuals deposited on the beach by wave action during and after storms, or life cycles of the insects living on the shore (Herms, 1907; Needam, 1900, 1904; Shelford, 1909, Snow, 1902). Whether beachgrass is utilized by any of these insects has not been determined.

Few animals are found on or associated with the shore and early successional plants. Toads, skunks and birds may inspect material that has washed ashore (Shelford, 1913) and Laing (1958) found some rodent consumption of young flowering heads. The amount of beachgrass that makes up the diet of rodents in the study area is not known.

The general objectives of this study were to estimate the productivity of beachgrass, and to determine the relationship of animals to beachgrass. The specific study objectives were:

1. to follow the seasonal change in above and belowground biomass;
2. to estimate net and gross primary production and community respiration;
3. to determine the extent of seasonal changes in the photosynthesis of beachgrass leaves; and
4. to evaluate the extent of interactions of rodents and insects with beachgrass.

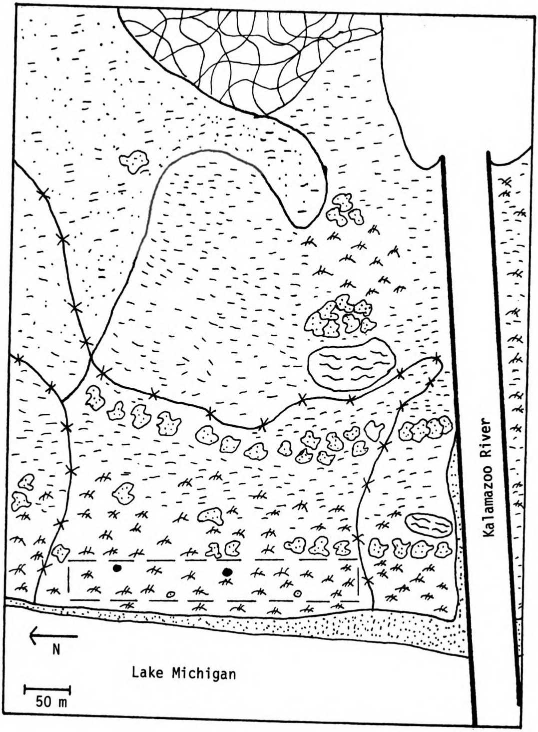
DESCRIPTION OF THE STUDY SITE

The study site was located on the foredune north of the Kalamazoo River near Saugatuck, Allegan County, Michigan (Figure 2). Prior to the selection of this study site in 1973 the east shore of Lake Michigan from Charlevoix to Michigan City was surveyed by boat and through the use of aerial photographs for areas with sufficient beachgrass for a study of this type. Besides the study site, stands of beachgrass were also found on Warren dunes, the dunes around Silver Lake, Sleeping Bear dunes, and South Manitou Island dunes. These four areas were either State or Federal parks. Suitable stands of beachgrass did not exist along the rest of the coast due to erosion or housing developments. From talks with people who have spent their lives near the shore of Lake Michigan, from descriptions by earlier writers (Cowles, 1899; Waterman, 1922) and from the way the beachgrass was growing in the parks, I feel the area chosen was similar to beachgrass communities which existed along the Lake Michigan shore prior to the 1940's.

The study site foredune was approximately 370 m long (N-S) and 50 to 60 m wide (E-W) but only 300 m by 40 m was used for the study. Because of the high lake level during recent years, a cliff 2-3 m high formed the front edge of the foredune. The foredune was bordered to the north, south and partially to the west by bare sand caused by prior dune buggy use; the bare sand to the south had started to form a blowout. All traveling from one sampling area to another was confined

Figure 2. Diagram of the study site.

— —	encloses study site
⋕ ⋕	*Ammophila breviligulata*
○	young *Populus deltoides*
●	young *Salix glaucophylloides*
☁	mature *Populus deltoides*
⊠	early successional forest
▤	early successional vegetation (denser vegetation than in following category)
⬚	early successional vegetation colonizing sand
▒	beach (sand)
≋	dune pond
✳~✳	dune buggy road
━━━	breakwall


Kalamazoo River
N
Lake Michigan
50 m

to paths outside the study site or to a path which penetrated the center of the study site.

The site contained predominately Ammophila breviligulata plus four small areas of low woody vegetation, two of Salix glaucophylloides (blue willow) and two of Populus deltoides (cottonwood). The areas of shrubs consisted of only young vegetation and averaged 1-1.5 m in height and 2-3 m in diameter. Just to the west of the study site was a row of Populus deltoides 8-10 m tall. The area behind the study site graded from pure Ammophila breviligulata to mixed vegetation dominated by either Populus deltoides, Prunus pumila (sand cherry) or Calamovilfa longifolia (reedgrass).

From aerial photographs and discussions with Mr. John Uhl and Mr. John Luther (owners of a portion of the land where the study was conducted), it was learned that there was little vegetation present on the study site prior to 1956. During Lake Michigan's low water level of the late 1950's and early 1960's sand was deposited on the area and the existing beachgrass developed into the community now present. During the current high water level the foredune has lost approximately 20 m from its lakeward side. The vegetation on the foredune was burned in 1972. However Jaschitz and Bell (1966) in Rhode Island found several sections of their beachgrass study area had been burned over with little effect on subsequent growth. Based on their findings, the 1972 burn was not considered a deterrent in the selection of this area as a study site.

Weather data collected by the United States Weather Bureau located at the South Haven Agricultural Experimental Station were used to characterize the study area. The station monitors temperature and precipitation (United States Weather Bureau, 1973-1975a) and is located

28 Km SSW of the study site and within several meters of the lake shore. The cloud cover and wind speed were measured at the United States Weather Bureau in Grand Rapids located 61 Km ENE of the study site (United States Weather Bureau, 1973-1975b). Monthly climatological data from both of these stations are summarized in Table 1.

The mean annual temperatures during this study differed by no more than 0.3° C from the 78 year mean annual temperature of 9.8° C. The climate during the 1973-1975 period was fairly uniform except for precipitation. Precipitation during the growing season in 1973 was 7.7 cm above the 29 year norm. In 1974 it was 14.8 cm below the norm. Precipitation during the 1975 growing season was 21.7 cm above the norm. The wind during the growing season was predominately from the SW.

Table 1. Summary of 1973-1975 climatological data, South Haven and Grand Rapids, Michigan

	1973	1974	1975
Mean annual temperature	10.4°C	9.2°C	10.8°C
Mean growing season(1) temperature	17.0°C	19.9°C	17.0°C
Mean of the coldest month	Feb -2.1°C	Feb -3.4°C	Feb -2.4°C
Mean of the warmest month	Aug 21.8°C	July 21.8°C	July 21.1°C
Total annual precipitation	89.6 cm	78.0 cm	101.3 cm
Total precipitation during growing season	55.2 cm	36.9 cm	67.4 cm
Total evaporation during growing season	81.5 cm	81.3 cm	74.6 cm
Growing season evaporation as % of total annual precipitation	90%	104%	74%
Growing season evaporation as % of growing season precipitation	148%	220%	111%
Mean % possible sunshine during growing season	52%	58%	54%
Mean annual wind speed	4.5 m/sec	4.2 m/sec	4.0 m/sec

(1) April - September

METHODS AND MATERIALS

Productivity And Community Metabolism

Biomass Relations. Seasonal changes in beachgrass biomass and productivity were estimated by periodic harvesting. Of the two principal methods of estimating productivity by harvesting, the less complex method is to measure the total weight of standing vegetation at the end of the growing season (Hadley and Kieckhefer, 1963; Kucera *et al*., 1967). However, this method underestimates total biomass production due to turnover during the growing season. A second method is to harvest the standing vegetation more frequently and equate the season's peak value with above ground net production as done by Bray *et al*., (1959) and Malone (1968). This method also underestimates total biomass production unless estimates of living material which senesced and dead material which decomposed were included (Wiegert and Evans, 1964). Kelley *et al*. (1974) and Singh *et al*. (1975) have reviewed earlier solutions to this problem and present results of different techniques applied to the same data sets in order to more completely resolve the problem. The second harvesting method was chosen for this study along with estimates of senescence and decomposition.

To facilitate the harvesting of beachgrass, the study site was divided into 20 x 20 m squares with stakes prior to the beginning of the study. Since beachgrass vigor appears to be directly related to sand accumulation (Hope-Simpson and Jefferies, 1966; Lain, 1954; Marshall, 1965), five graduated stakes were placed at various positions in the study site during this time, and were checked periodically for any change in sand level.

The number and size of samples to be collected was determined at the beginning of the study in July 1973. From the literature review of grassland primary production measurement techniques, by Milner and Hughes (1970), two sample sizes were selected (0.5 and 1 m^2) and used as nested quadrats. The study site was mapped and five points were chosen at 60 m intervals along the lake side edge of the site. Five more points were placed at 9 m intervals back from each point on the lake side edge (total 25 plots). Greig-Smith's (1964) graphical method of deciding when an acceptable number of samples has been obtained was followed. Ten 1 m^2 samples were determined to be adequate for this study site. The dry weight of the living harvested beachgrass from the front, back, and sides of the study site (Appendix Table 1) were compared using the Student's t test and found not to be significantly different (α = .05).

The study site was mapped and plots to be harvested were selected using a random numbers table. Plots were not harvested adjacent to a previously harvested plot or to the trail which penetrated the center of the study site to insure a lack of recent disturbance of study plots. The plots to be sampled were located in the field by reference to the permanent stakes.

Above ground biomass was harvested at three week intervals from July 1973 through July 1975 except during the winter months (December through February). Each plot was clipped as close to the ground as possible and all biomass and litter were removed and placed in plastic bags. The biomass was later separated into living and dead fractions, and the living fraction was inspected for evidence of insect damage.

To follow more completely the changes in beachgrass biomass, estimates of belowground biomass were also made. In order to determine the best depth for sampling belowground biomass, all roots and rhizomes in three 1 m^2 plots were harvested to a depth of 1 m. The greatest concentration of root and rhizome biomass (85%) occurred in the top 40 cm. Similar results have been found for roots of a tall grass prairie and Tennessee old fields (Dahlman and Kucera, 1965; Kelly, 1975). Each additional 20 cm from 40 to 100 cm added only 5% more beachgrass root biomass. Because of these findings, belowground biomass (living and dead or total belowground) was sampled by removing all sand and plant biomass to a depth of 40 cm.

During each sampling period in 1973 one of the ten plots to be harvested was randomly chosen for belowground sampling. Since this single sample did not produce any recognizable trends, the belowground biomass of three plots, rather than one, was harvested at each sampling period during the rest of the study. The belowground biomass was separated from the sand by shaking through a screen with a mesh of 6 x 6 mm in the field. It was then placed in plastic bags and later the biomass and residual sand were further separated by drying completely, shaking, washing and floating in water, and drying again.

To obtain dry weight estimates, the above and belowground samples were dried for 48 hours in a forced air oven at 100°C and weighed on a triple beam balance. These samples were then ground in a Wiley Mill to pass a 0.5 mm mesh. The belowground samples were again separated from any imbedded sand using a South Dakota Seed Blower. All samples were then subsampled and combusted in a muffle furnace at 550°C and reweighed on a torsion balance to obtain ash free dry weight estimates. The caloric content of living and dead aboveground and belowground biomass harvested during the 1974 sampling period (March through November) was determined using a Parr adiabatic oxygen bomb calorimeter. All samples were run in at least triplicate and on only one occasion did sample replicates differ by more than 0.5%. This variation is within the level of acceptance established by Golley (1961).

Since this community had only one plant species which had no annual living aboveground carry over, only one living biomass peak during the growing season, and negligible herbivory (see results), the peak standing crop determined by sampling throughout the growing season was a valid estimation of the aboveground net primary production (Wiegert and Evans, 1964; Odum, 1960). Also, since all belowground biomass belonged to the one species present, unlike most other grassland studies where multiple root systems exist (Malone, 1968), the measured belowground biomass gave a valid approximation of net belowground primary production. However the estimate of total net primary production was still low until corrected for mortality and disappearance of dead material.

Many of the studies of grassland productivity have neglected the death and disapperance of plant material during the growing season (Singh et al., 1975). Golley's (1965) procedure of estimating the transfer of live to dead biomass and adding this to the estimated net production for a broom sedge community was adopted. However the disappearance of dead material from the plots must also be included for a complete estimate. This disappearance of dead material was measured according to the method of Weigert and Evans (1964) which used paired plots and litter bags. Their formulas were used to estimate both the disappearance of dead material and green material mortality.

Five pairs of paired plots were established at the beginning of each of the following periods: 17 November 1973 - 6 April 1974, 6 April 1974 - 28 June 1974, 28 June 1974 - 1 September 1974 and 1 September 1974 - 2 November 1974. Because of the clumped growth habit of beachgrass, the second plot of each pair was chosen from an area in the immediate vicinity which was most similar to the first plot. The second plot of each pair was harvested at the end of each period. These sampling periods corresponded to the overwinter and pregrowth period, early rapid vegetative growth period, slower growth period associated with the rest of the growing season, and the post growing season period respectively. Thus there were 25 two plot pairs, with the change in five pairs studied during each interval.

The nylon litter bags used for sampling litter loss were 38 by 38 cm, with a mesh of 7 by 5 mm, and were filled with approximately 20 g (oven dry weight) of beachgrass leaves. On 24 November 1973, 16 bags were placed on the sand surface and 16 were buried a few cm below the surface. Four aboveground and four belowground litter bags were randomly chosen and removed after 140 days, 235 days, 281 days and 344 days in the field, corresponding to the dates at the end of each period when the paired plots were harvested.

The dynamics of the aerial shoots were further followed by counting the number of living stems and determining the living leaf area for each plot that was harvested. Laing (1958) estimated there were 50 vegetative shoots/m^2 present on his site in the Indiana dune region. However it is not known if the number increased during the growing season. To help determine this, a 1 m^2 quadrat, divided into 25 sections, was placed over each clipped plot and the living stems in each section were counted during 1974 and 1975.

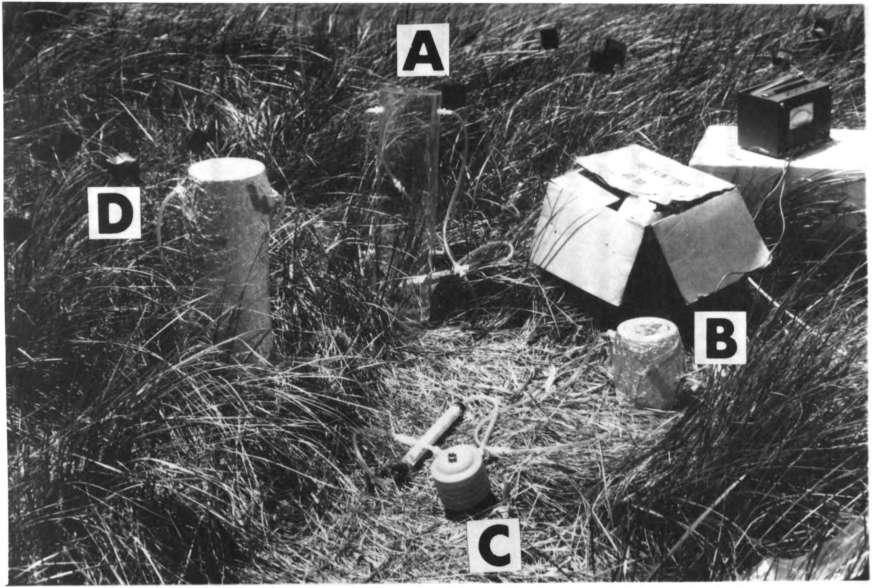
The total leaf area of all living leaves in a 1 m^2 plot harvested in July 1974 was determined. The plot was divided into 25 sections and each was harvested separately. The living and dead leaves were separated and the living leaves were stored moist at 3°C until fully expanded, at which time they were traced on paper and their areas computed. The living leaves and stems were then oven dried and weighed. The dry weights of the leaves (Appendix Table 2) were regressed on their respective leaf areas (r = .98) to develop a linear prediction equation ($y = mx + b$) that was used to calculate the leaf areas of all harvested plots:

Leaf area (cm^2) = 0.6178 x (living dry weight in grams) + 0.1889

Community Metabolism. Daily rates of gross photosynthesis, community respiration, plant respiration and soil respiration were estimated from CO_2 samples collected in the field and measured with an infrared gas analyzer (Beckman, Model 215 A) in the laboratory, using a method adapted from that developed by Barko (1975).

Three portable chambers were used to enclose portions of the beachgrass community for analysis of CO_2 exchange (Figure 3). Two of the chambers were constructed from 0.32 cm thick clear plexiglass, and were 61 cm tall and 16 cm in diameter. Both had 0.64 cm inlet and outlet ports at 55.6 and 17.5 cm from the base respectively. One chamber (dark chamber) was covered with several layers of extra heavy aluminum foil excluding all light, and the other chamber (light chamber) was transparent. The third chamber (soil chamber) was 20 cm tall and 16 cm in

Figure 3. Portable metabolism chambers used in gas exchange study. In a clockwise direction starting in upper center: Light chamber (A), soil chamber (B), hand operated pressure-vacuum pump (C) and dark chamber (D).


A
D
B
C

diameter and had 0.64 cm inlet and outlet ports at 15 and 7.3 cm from the base respectively. This chamber was also covered with aluminum foil to exclude light.

Determinations of community metabolism were made at three week intervals from June 1974 to July 1975 except during December 1974 through March 1975 when the intervals were extended. Community metabolism was measured using six areas with approximately equal numbers of beachgrass plants between 0900 and 2400 hr during a sampling day. The same six areas were used at each sampling time. Measurements usually started at approximately 900, 1230, 1545 and 2330 hr and were completed after 60 to 90 minutes. The light chamber was placed over three of these areas one at a time and the dark chamber over the other three in a similar manner. The soil chamber was placed on three different patches of bare sand close to the plants being monitored. The chambers were pushed into the sand and sand was poured around each base to close large holes. Each chamber was left in place for 15 minutes and then moved to its next site. During this time three samples of ambient air were taken 1.5 m above the ground upwind of the sample area. Gas exchange of the plants used with the light chamber was not measured at night.

The biomass beneath and between clumps of beachgrass was sampled to provide an indication of whether the carbon flux between clumps was a valide estimate for that under a clump. A minimum of 20 biomass samples was removed at two different times with a soil core that removed a core 25.3 cm deep by 16.3 cm in diameter. Roots and rhizomes sampled between the clumps and under the clumps were not significantly different (α = .05) from each other and averaged 8.6 and 10.3 g/core sample respectively.

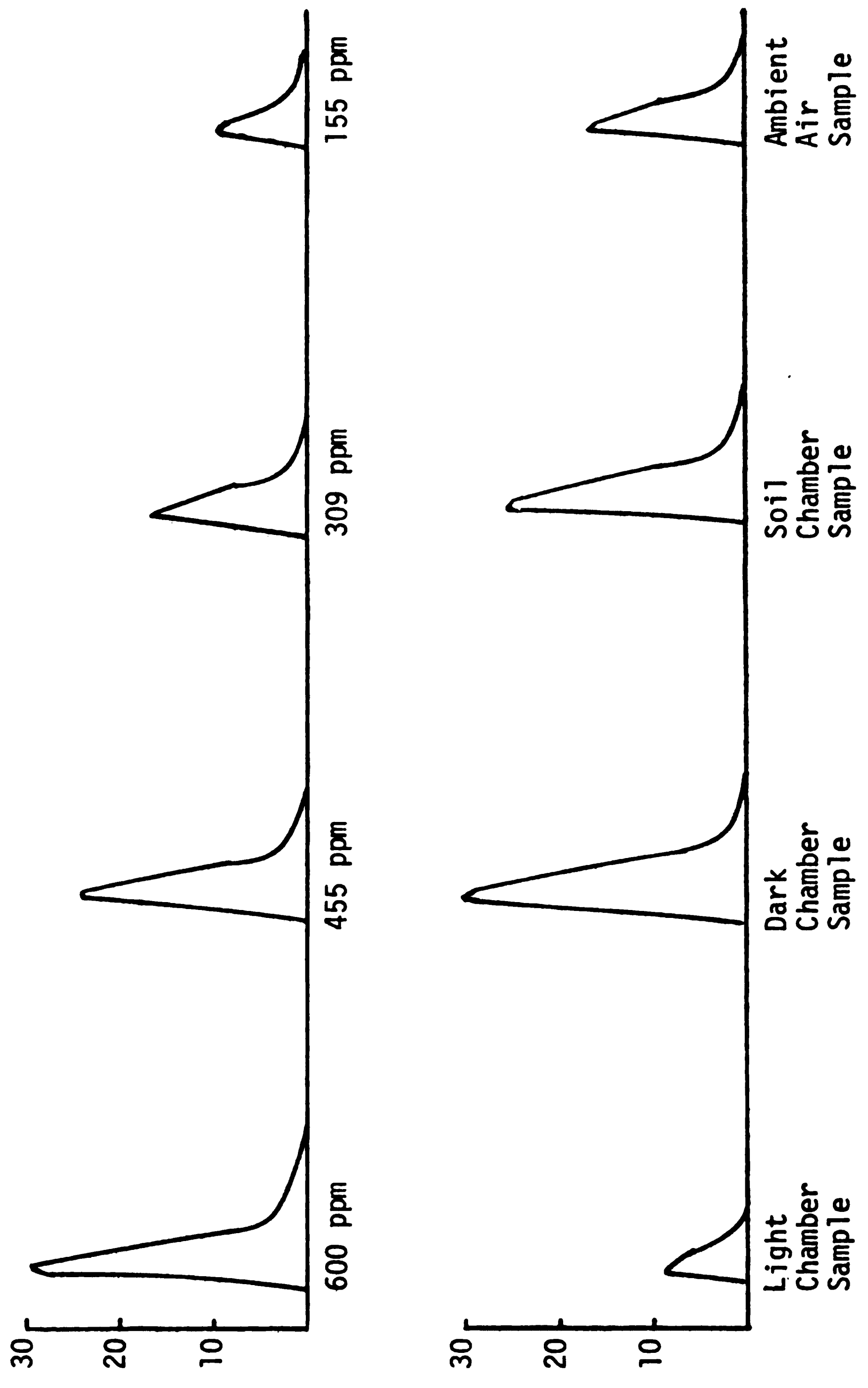
The duration of the incubation period did not inhibit the rate of apparent photosynthesis. Gas samples were removed after 5, 10 and 15 minutes of incubation. Between 5 and 10 minutes and between 10 and 15 minutes there was a mean change of 30.64 ppm CO_2 and 30.92 ppm CO_2 respectively, on 11 July 1975 based on three replications.

Temperature in all chambers and ambient air were monitored at 4 to 5 minute intervals with a six channel YSI telethermometer. The temperature of the light chamber was maintained close to the ambient air temperature by circulating the chamber air 2.3 times per minute with a Millipore pressure-vacuum pump powered by a portable generator through 42.19 m of copper tubing (0.31 cm inside diamter) surrounded by ice in a styrofoam ice chest. The dark and soil chambers remained at their respective ambient air temperatures and therefore were not cooled.

Gas samples were removed from the dark and soil chambers and the ambient air with a hand operated pressure-vacuum pump (910 ml capacity) causing a sight positive pressure in the chambers. The Millipore pressure-vacuum pump removed the gas samples from the light chamber. The gas samples passed through a column containing filters and drierite to prevent contamination due to microbial activity under humid conditions before entering the 500 ml glass collecting flasks.

An infrared gas analyzer, coupled to a strip chart recorder (Honeywell, Model 193), was calibrated with known gases in 20 cc samples injected into a stream of nitrogen flowing through the analyzer. This produced a series of normal curves on the recorder (Figure 4). The areas under the curves of the calibration gases, determined by planimetry, were regressed on their respective CO_2 concentrations to develop linear prediction equations ($y = mx + b$). These equations were used to

Figure 4. Infrared gas analysis determination of carbon dioxide concentrations. The top curves are from calibrated gases while the bottom curves are from field samples.


30
20
10
600 ppm
455 ppm
309 ppm
155 ppm
30
20
10
Light Chamber Sample
Dark Chamber Sample
Soil Chamber Sample
Ambient Air Sample

calculate the CO_2 concentration (in ppm) of the sample gases.

The three ambient air samples from each 60 - 90 minute sample period were averaged and subtracted from the CO_2 concentration in each dark and soil chamber sample and added to each light chamber sample. All samples were then converted to mg C evolved in one hour:

mg C/hr =

$$\left(\frac{\left(\frac{\text{ppm } CO_2}{15 \text{ min}}\right) \times \left(\frac{60 \text{ min}}{\text{hr}}\right) \times \left(\frac{273°K}{CT}\right) \times \left(\frac{12 \times 10^3 \text{ mg/mole}}{22.4 \text{ liter/mole}}\right)}{10^6 \text{ ppm/liter}}\right) X \left(\begin{array}{c}\text{vol of system}\\ \text{in liters}\end{array}\right)$$

where: CT = chamber temperature in $^\circ$K

The carbon flux in the soil chamber was expanded to a square meter basis. The three estimates for soil respiration were averaged and subtracted from the carbon flux estimated for each dark chamber and added to each light chamber estimation.

The extimation of the carbon flux in the light and dark chamber was then expressed on a square meter basis:

$$\text{mg C/m}^2\text{/hr} = \left(\frac{\text{mgC/hr}}{CL}\right) \times \left(\frac{FL}{m^2}\right)$$

where: CL = the weight of living beachgrass in each chamber.

FL = the average weight of living beachgrass per square meter harvested during the same sampling period.

The three flux estimations from the light chamber were averaged as were the estimates from the dark chamber.

Gross photosynthesis was calculated as an hourly rate by summing the carbon flux from the average values estimated in the light and dark chambers. The mean hourly rates were expanded to daily rates by multiplying by the number of hours between sunrise and sunset. Aboveground plant respiration was taken as the carbon flux in the dark chamber minus the soil respiration (including root and microbial respiration) as the carbon flux in the soil chamber. The carbon flux through the sand was determined by placing the soil chamber over sand from which the belowground biomass had been removed 24 days earlier. This was compared with the carbon flux measured by placing the soil chamber between undisturbed beachgrass clumps. The carbon flux from the disturbed areas was 45% of that measured on the undisturbed site.

Community respiration was taken as the sum of aboveground plant respiration and soil respiration. Daily rates of plant respiration, soil respiration and community respiration were plotted on curves. The growing season rates, sampling period rates and annual mean rates of respiration were determined by integrating the areas under their respective curves with respect to time. Plant respiration plus net primary production (from biomass estimates) were combined to give estimates of gross production.

The daily pattern of solar radiation at the study site during each 24 hr sampling period was determined with a Belfort recording pyrheliograph. During the entire study period, solar radiation was determined with a recording Eppley pyrheliometer, located at the Kellogg Biological station, approximately 65 Km from the study site. It was assumed that 50% of the total solar radiation (wavelengths between 390 and 760 nannometers) could be used in photosynthesis (Bray, 1961; Talling, 1961).

Factors Controlling Photosynthesis. The effects of varied light intensities and the influence of different CO_2 concentrations on net photosynthesis of beachgrass were investigated in the laboratory using single leaf chambers. This apparatus is in the laboratory of Dr. Klaus Raschke and has been described (Raschke *et al.*, 1975).

Measurements of young leaves were taken on 16 May 1975 and of mature leaves on 29 July 1975. Several clumps of beachgrass with roots and rhizomes attached were taken from the field the evening before testing. They were placed in containers with sand, watered, taken to the laboratory and placed in a 3°C cold room over night. The following morning, assimilation chambers were clamped to the upper and lower surfaces of fully expanded detached leaves. Light intensities were maintained with neutral density filters. Leaf chamber temperatures were not controlled and closely approximated temperatures recorded in the field under similar light intensities: leaf chamber temperatures averaged 25°C under lower light intensities and up to 30°C under full light intensity.

Rates of net photosynthesis were measured with four replications at varied light intensities of 62.5, 135.0, 252.5, and 500.0 W/m^2 (151, 264, 479 and 947 x 10^2 lux respectively) at a constant CO_2 level of 300 ppm. Another measure of photosynthesis, also with four replications, was made at varied CO_2 levels 0, 100, 200, 300, 400 and 600 ppm at a constant light intensity of 252.5 W/m^2. Finally, chambers were covered with a dark cloth to give an estimation of dark respiration.

Since the only measurable gas exchange occurred on the lower surface of beachgrass leaves, the location of stomates on leaves was determined by making leaf skeletons (Dilcher, 1974). Leaf pieces were heated in 20% potassium hydroxide for 48 hours and bleached with a 5% solution of hydrogen peroxide. The location of stomates was noted and the number per unit area counted.

Estimation of Animal Activity

Although tracks of rodents were seen around the study site, the species present were unknown. It was also unknown whether they were feeding on the beachgrass. In order to clarify these points, rodents were trapped and the contents of their stomachs inspected. Whether the invertebrates present in the study site were likely to be feeding on beachgrass was also investigated by identification of the most numerous kinds present.

Vertebrates. Rodents were trapped with groups of three Victor snap traps placed at 20 meter intervals along two lines 5 and 35 m in from the lake side border of the study site (total, 96 traps). The traps were baited with peanut butter. During July 1973, it was found that trapping more than one night brought in fewer rodents on later nights as compared to the trapping results on the first night. This has also been found by Gentry and Odum (1957) under similar conditions. Trapping was conducted on the study site for one night at three week intervals corresponding to beachgrass harvesting dates from July 1973 to August 1974 except for the period of November 1973 through March 1974. Rodents were identified according to Burt (1957) and verified by John Fitch (Michigan State University), sexed, and divided into age groups (Blair, 1940a,b,c).

To determine if beachgrass contributed to the rodents' diet, their stomachs were opened, the contents removed and placed in a fine mesh net, and then washed in water, separating the particles as much as possible. The staining technique was modified from one developed by J. Hall (University of Georgia, personal communication).

1.	50% ethanol	30 seconds
2.	1% Cholozol Black E in 70% ethanol	35 seconds

3.	95% ethanol	60 seconds
4.	95% ethanol (rinse)	30 seconds
5.	95% ethanol (rinse)	30 seconds
6.	Absolute ethyl alcohol	30 seconds

Sections were brought from absolute ethyl alcohol to xylene and permatized with a 60% Harleco resin solution in xylene. Two slides were made from each stomach. Since the stomach contents were homogenously mixed, ten locations were randomly located under low microscopic power and the contents were classified as plant, invertebrate or unknown (Baumgartner and Martin, 1939; Brusven and Mulkern, 1960; Williams, 1962).

The specific identification of beachgrass leaf cells was accomplished by making permanent reference slides. Beachgrass leaf pieces were macerated by hand or separated by Jeffrey's Method (Sass, 1951), and stained and mounted as described previously. Epidermal characteristics present in these reference slides were used for possible identification of beachgrass plant cells present in the rodent stomachs (Baumgartner and Martin, 1939).

Invertebrates. Insects were collected in the sample area by sweeping the study site during the growing seasons from July 1973 to August 1974. A De Vac was also used during this time. Pitfall traps 8 cm deep by 10 cm in diameter were placed in the sand with the tops at ground level, and filled with 2 to 3 cm of ethylene glycol and a small amount of detergent. Using these different collecting methods, the most numerous kinds of insects present in the study site could be determined (Delong, 1932; Gray and Treloar, 1933; Smalley, 1960). Once the kinds of insects were known their potential for beachgrass herbivory was evaluated.

RESULTS

Productivity and Community Metabolism

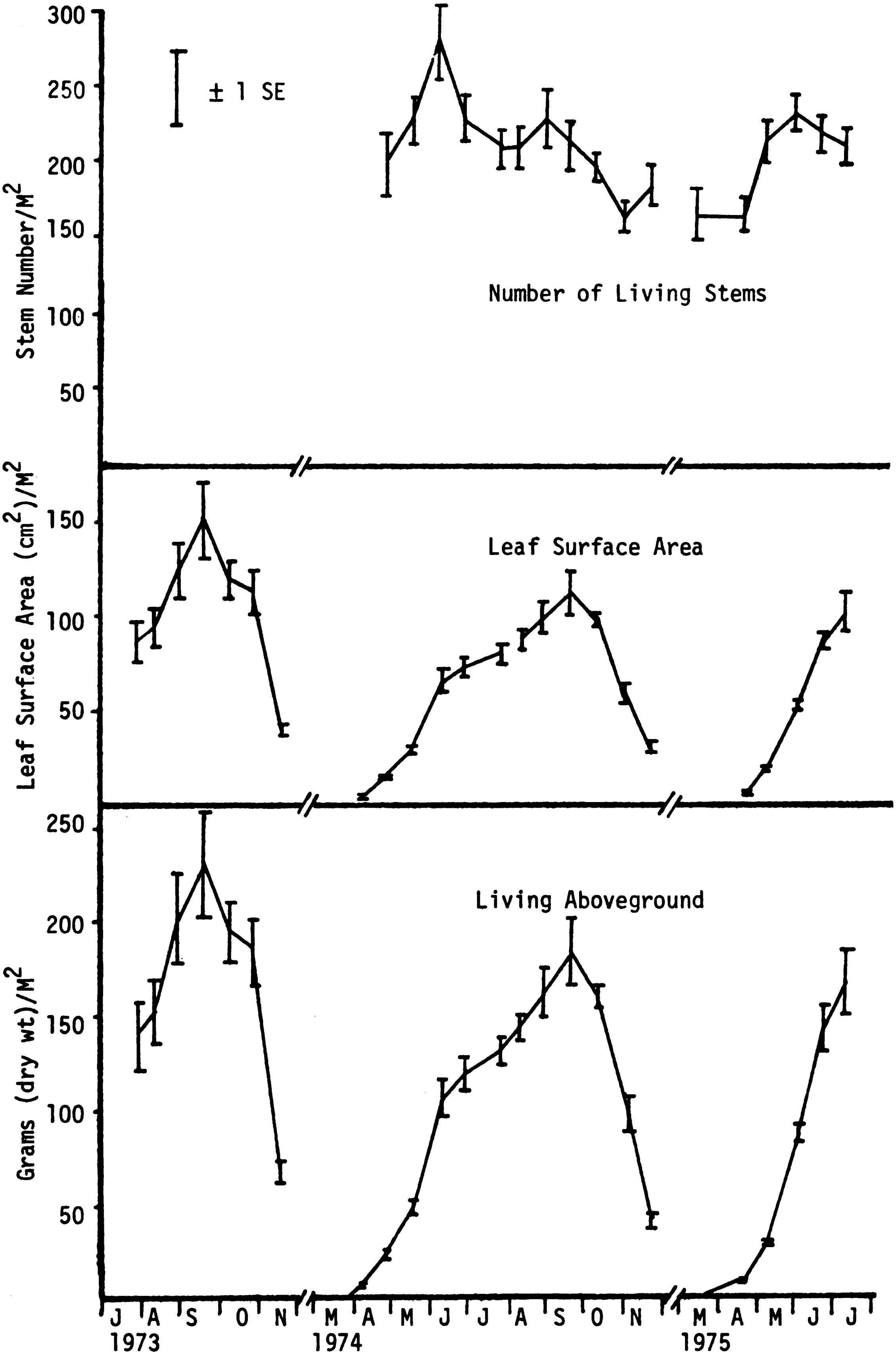
Biomass Relations and Community Structure:

Aboveground. Beachgrass began growth in late March, living biomass peaked in mid September, and then commenced to die back (Figure 5). From late March to early June living biomass increased by an average of 1.6 $g/m^2/day$. This rate declined to an average of 1.3 $g/m^2/day$ for the period of June through late September. Maximum aboveground living biomass production was 230 g/m^2 in 1973 and 183 g/m^2 in 1974 (Appendix Table 3). Based on the 1973 through 1975 growth rates it was estimated that over 250 g/m^2 would have been produced by September 1975. Beachgrass died back at an average of 2.3 $g/m^2/day$ from late September into November, although as late as mid November an average of 58 g/m^2 of living beachgrass was still present on the study site (28% of the total living biomass).

The number of living stems increased annually from April to early June and then decreased through November (Figure 5). Although the trends in 1974 and 1975 were similar, the number of living stems present was not. The maximum mean number of living stems present per m^2 was 280 in 1974 and 233 in 1975.

The photosynthetic leaf surface area increased during each growing season until mid September and then declined (Figure 5). The trends were similar to those of the aboveground living biomass. The maximum

Figure 5. Seasonal changes in aboveground living biomass, leaf surface area and the number of living stems of *A. breviligulata*, 1973-1975.


300
250
200
150
100
50
Stem Number/M^2
± 1 SE
Number of Living Stems
150
100
50
Leaf Surface Area (cm^2)/M^2
Leaf Surface Area
250
200
150
100
50
Grams (dry wt)/M^2
Living Aboveground
J
A
S
O
N
M
A
M
J
J
A
S
O
N
M
A
M
J
J
1973
1974
1975

1974 living leaf surface area of 113 cm^2/m^2 was a 25% decrease from the 1973 maximum of 151 cm^2/m^2.

The aboveground dead biomass has increased by 373 g/m^2 from 261 g/m^2 to 634 g/m^2 over the course of the study (Figure 6, Appendix Table 3). During the growing season in 1974 (April through mid September), dead biomass increased by an average of 0.3 g/m^2/day, (total 56 g/m^2). From mid September through November in 1973 and 1974, when the living beachgrass was dying back, the dead biomass increased at an average rate of 2.0 g/m^2/day. During the entire study, excluding the periods between December through February, the dead biomass increased by an average of 0.8 g/m^2/day. Also during this period the number of dead stems increased 70% from a mean of 60 stems/m^2 in April 1974 to a mean of 197 stems/m^2 in late June and July of 1975. Comparing the change in dead biomass during the winter months (December through February) for 1973-1974 and 1974-1975, it appeared that no measurable amounts were lost.

Belowground. Total belowground biomass exhibited seasonal changes, but the overall trend was toward increased belowground biomass (Figure 7, Appendix Table 3). The biomass decreased 209 g/m^2 (2.9 g/m^2/day) from a high of 795 g/m^2 during the spring of 1975 to 586 g/m^2 (March-May 1974) and then increased 191 g/m^2 (8.3 g/m^2/day) to a mean of 777 g/m^2 (June - July 1974). The initial spring decrease in biomass in 1975 occurred later in the season than during 1974, although it decreased by a similar amount (208 g/m^2). This spring decrease corresponded to an increase in living aboveground biomass and living stem numbers. In August 1974, there was a second biomass decrease of 154 g/m^2 followed by an increase to 921 g/m^2. From March to mid September 1974, there was a net increase

Figure 6. Seasonal changes in aboveground dead biomass of *A. breviligulata*, 1973-1975.

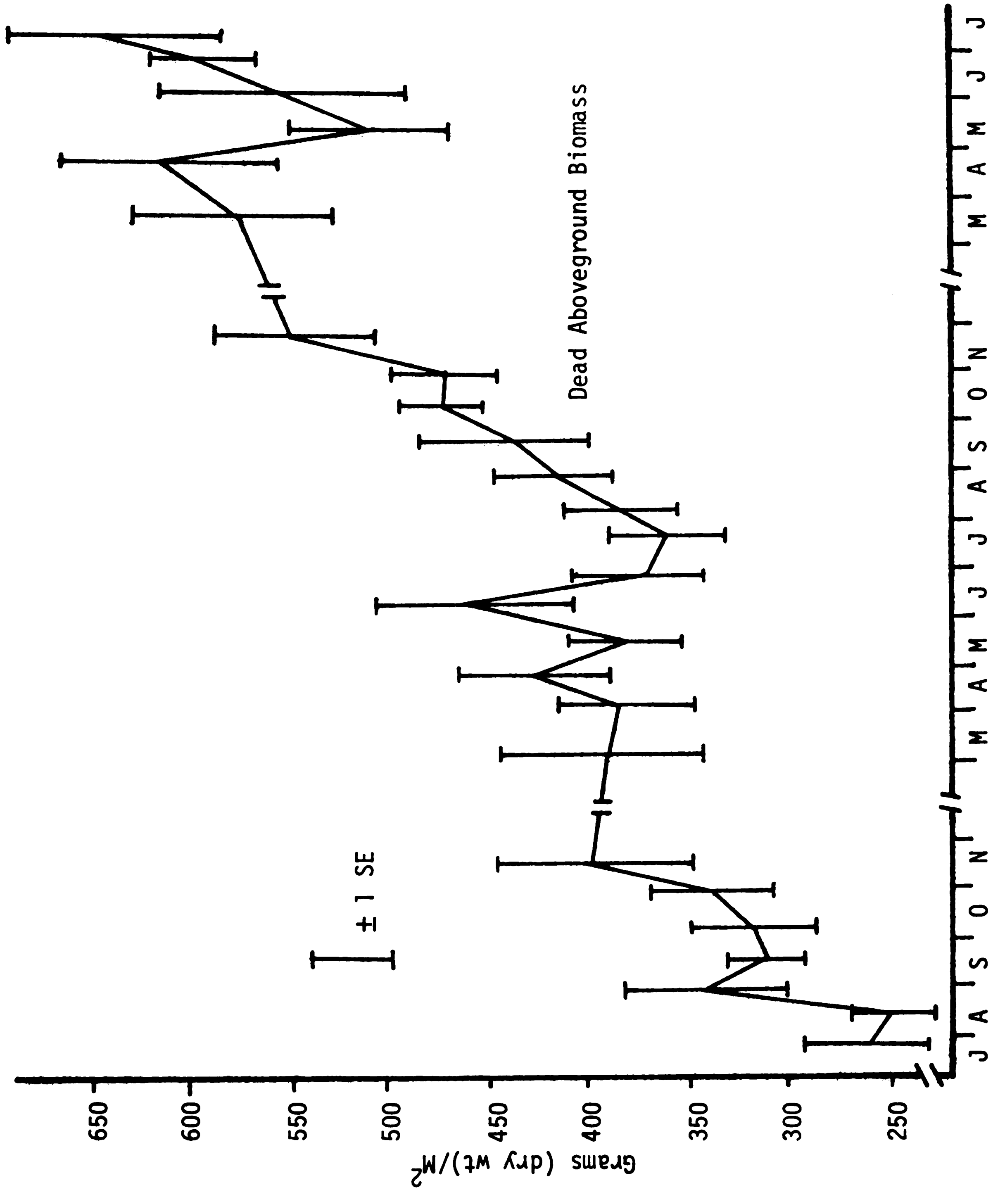
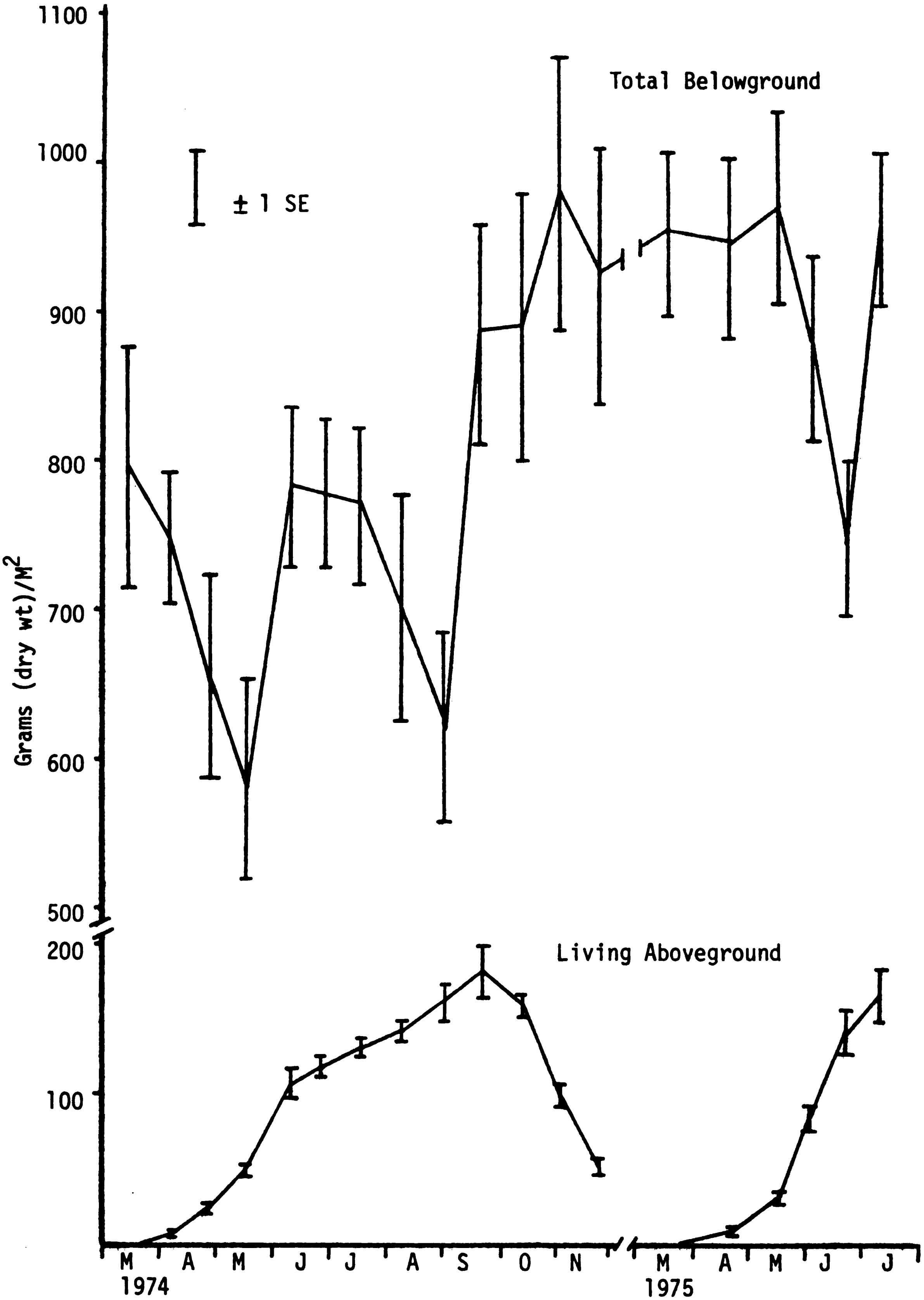

Dead Aboveground Biomass
± 1 SE
Grams (dry wt)/M²
650
600
550
500
450
400
350
300
250
J
A
S
O
N
1973
M
A
M
J
J
A
S
O
N
1974
M
A
M
J
J
1975

Figure 7. Seasonal changes in living aboveground and total belowground (0-40 cm) biomass of *A. breviligulata*, 1974-1975.


1100
1000
900
800
700
600
500
200
100
Grams (dry wt)/M^2
± 1 SE
Total Belowground
Living Aboveground
M
A
M
J
J
A
S
O
N
M
A
M
J
J
1974
1975

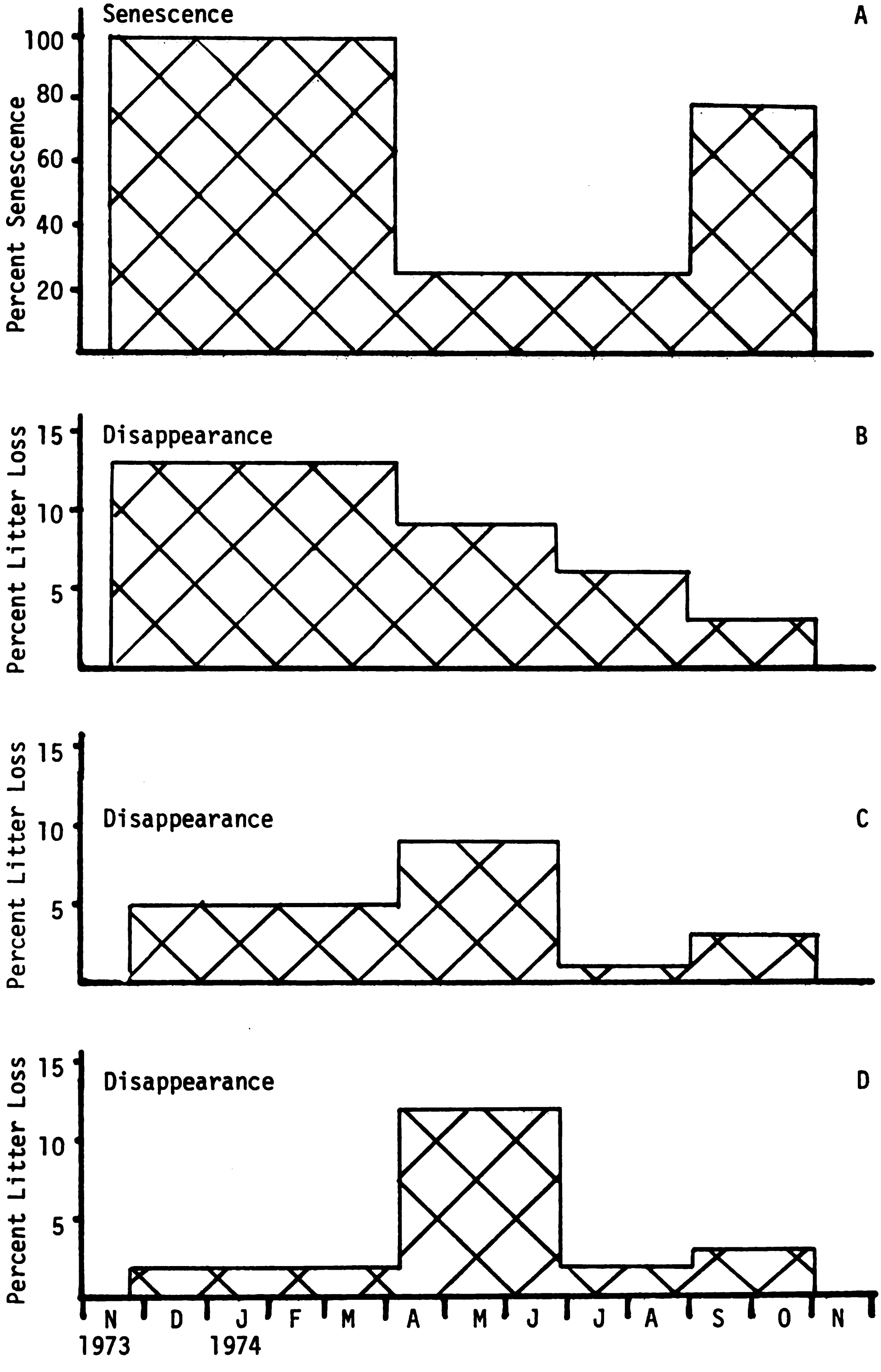
of 91 g/m^2. Between September and November there was a further increase of 40 g/m^2 which occurred while the aboveground living biomass was dying back.

Decomposition and mortality. Litter decomposition was about the same above and belowground as indicated by the litter bags (Figure 8c,d). The rate of decomposition was greatest during the period between April and July. However, this represented only a 9 and 12% loss for litter above and belowground respectively. It would appear that although some sand accumulation does not change the rates of litter decomposition for an entire year, it does so seasonally. It was estimated during April through September that aboveground litter lost was 51 g/m^2 and buried litter lost was 57 g/m^2.

Litter decomposition estimated for the entire year by paired plots (Figure 8b) was greater than that estimated by litter bags. This difference was due in most part to estimated loss during the winter months and partially due to loss during June through September. It was estimated that during April through September 60 g/m^2 of litter disappeared from the paired plots.

All measurable green biomass died back during the winter and was beginning to die back in the fall on the paired plots (Figure 8a). This was similar to results obtained by harvesting the aboveground living biomass at three week intervals (Figure 6). It was estimated from the paired plots that during the period of April through September, 73 g/m^2 senesced. This was 17 g/m^2 or 23% greater than the 56 g/m^2 estimated by the increased in dead biomass during the same period from the plots harvested every three weeks.

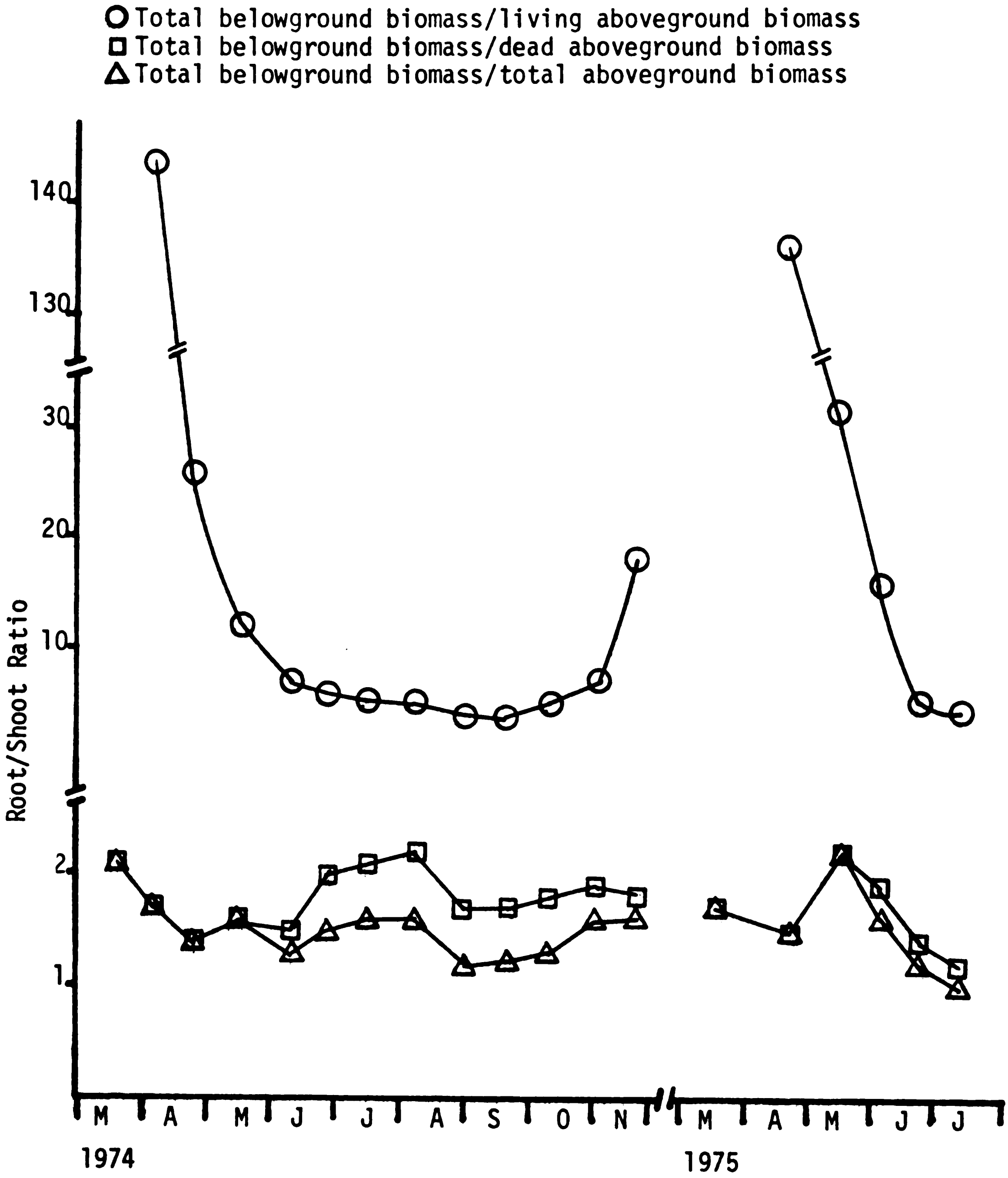
Figure 8. Percent mean living leaf mortality and litter disapperance. A and B were calculated by the paired plot method, and C and D were calculated from above and belowground litter bag results respectively.


Senescence
A
Percent Senescence
100
80
60
40
20
Disappearance
B
Percent Litter Loss
15
10
5
Disappearance
C
Percent Litter Loss
15
10
5
Disappearance
D
Percent Litter Loss
15
10
5
N
D
J
F
M
A
M
J
J
A
S
O
N
1973
1974

Net primary production. During the 1974 growing season the aboveground living biomass increased 183 g/m^2. When this is added to the estimated leaf mortality (73 g/m^2) and belowground biomass increase (91 g/m^2) an estimated net primary production of 347 g/m^2 was given. The maximum net primary productivity was estimated by adding the maximum aboveground living biomass (276 g/m^2) and the maximum belowground biomass increase (206 g/m^2) harvested on 21 September 1974 plus the estimated mortality (73 g/m^2). The minimum net primary production was estimated by adding the minimum aboveground living biomass (128 g/m^2) and the minimum belowground biomass increase (17 g/m^2) harvested on 21 September 1974 plus the estimated mortality (73 g/m^2). Maximum, average and minimum net primary production for 1974 was 555 g/m^2, 347 g/m^2 and 218 g/m^2 respectively.

Root/shoot ratio. The ratio of total belowground biomass to living aboveground biomass decreased steadily in 1974 from a high of 143.5 in April to 4.1 in mid September (Figure 9). This decline in the ratio corresponded to the period of greatest living aboveground biomass production. As the living aboveground biomass began to die back, the ratio once again increased. This pattern began to be repeated in 1975. The ratio of total belowground biomass to dead aboveground biomass remained relatively constant during the entire sampling period with a mean of 1.8. The increase in this ratio during late June through early August 1974 corresponded to an increase in total belowground biomass (Figure 7) and a decrease in the amount of dead belowground biomass to total (living and dead) aboveground biomass also remained fairly constant over the sampling period, at a mean of 1.5.

Figure 9. Ratio of belowground biomass to aboveground biomass.


O Total belowground biomass/living aboveground biomass
□ Total belowground biomass/dead aboveground biomass
△ Total belowground biomass/total aboveground biomass
Root/Shoot Ratio
140
130
30
20
10
2
1
M
A
M
J
J
A
S
O
N
M
A
M
J
J
1974
1975

Annual patterns of carbon and caloric content. The organic content (ash free weight) of the beachgrass remained fairly constant throughout the sampling period. The organic content expressed as a percent of oven dry weight for aboveground living, aboveground dead and total belowground biomass was 96%, 96% and 97%, respectively.

Conversely, caloric content of aboveground living biomass was not constant during the 1974 sampling period (Figure 10). It averaged 4.57 Kcal/g during the first part of April, but by the end of April and through June it had increased by 0.10 Kcal/g to a mean of 4.67 Kcal/g, corresponding to the rapid increase in living biomass at the beginning of the growing season (Figure 5). From late July through September the aboveground living biomass increased steadily and the caloric content also increased by 0.11 Kcal/g to a mean of 4.78 Kcal/g. When the aboveground living biomass began to senesce, the average caloric content dropped 0.10 Kcal/g to a mean of 4.68 Kcal/g. Each of the previously mentioned changes in the caloric content of the living aboveground biomass was statistically significant ($\alpha = 0.05$). The caloric content of aboveground dead biomass increased slightly during the sampling period and averaged 4.80 Kcal/g. Total belowground biomass had a low caloric content of 4.41 Kcal/g in March. The caloric content then increased 0.26 Kcal/g to an average of 4.67 Kcal/g for the major portion of the sampling period and then decreased 0.08 Kcal/g to 4.60 Kcal/g by late November. Mean caloric values for aboveground living, dead, and total belowground biomass during the entire 1974 sampling period are given in Table 2.

Ecological efficiency. Total caloric production was 1,536 Kcal/m^2 based on the caloric content of peak aboveground living biomass present

Figure 10. Seasonal changes in the caloric content of _A. breviligulata_, 1974.

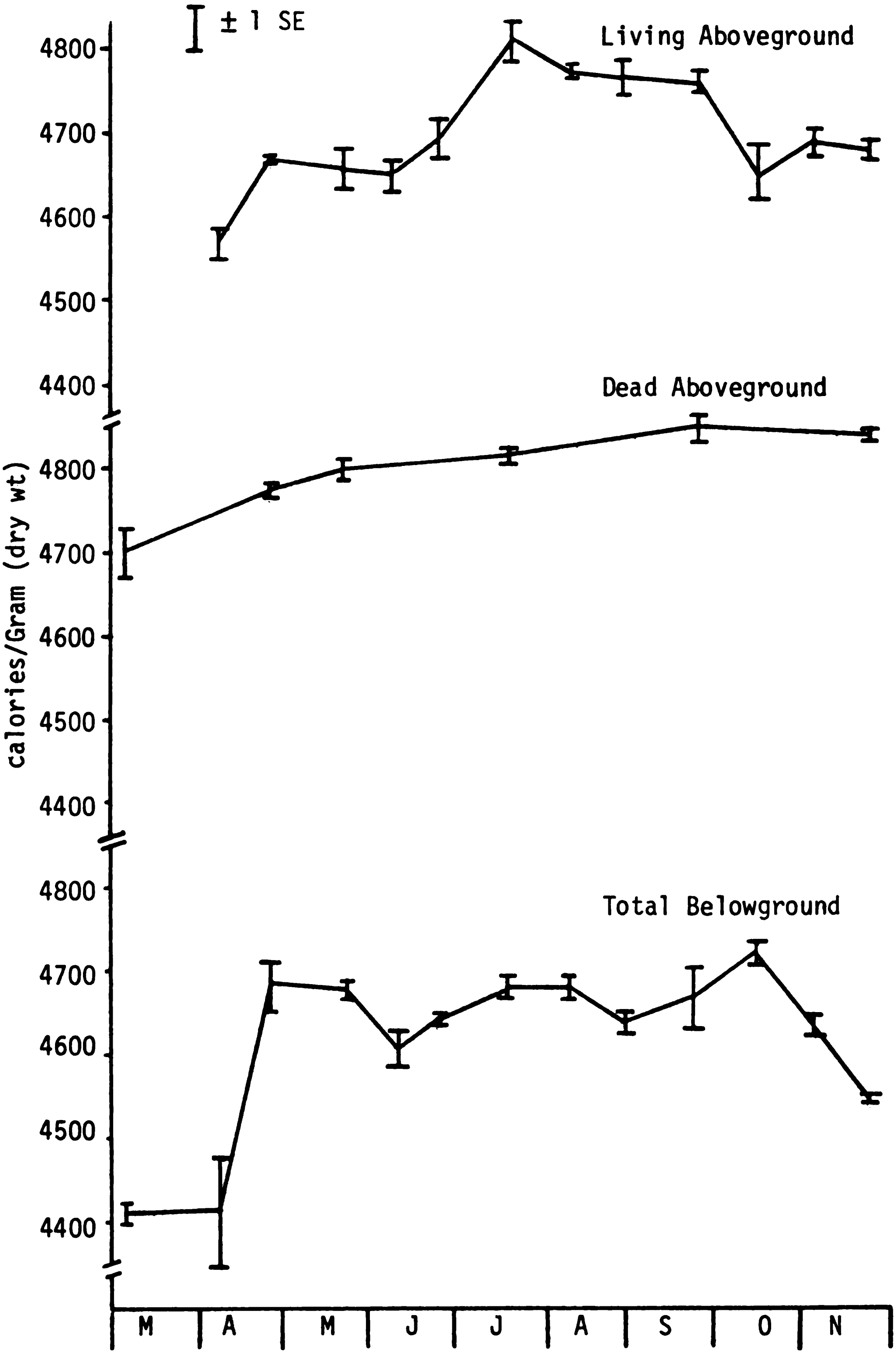

± 1 SE
Living Aboveground
Dead Aboveground
Total Belowground
Calories/Gram (dry wt)
4800
4700
4600
4500
4400
4800
4700
4600
4500
4400
4800
4700
4600
4500
4400
M
A
M
J
J
A
S
O
N
1974

Table 2. Mean caloric values for aboveground living, dead and total belowground biomass during the entire 1974 sampling period.

Living aboveground	Dead aboveground	Total belowground
4.7010(1) ± .0195(2)	4.7960 ± .0233	4.6203 ± .0279
4.8777(3) ± .0225	5.0038 ± .0320	4.7735 ± .0329

(1) Kcal/g dry weight

(2) ± 1 SE

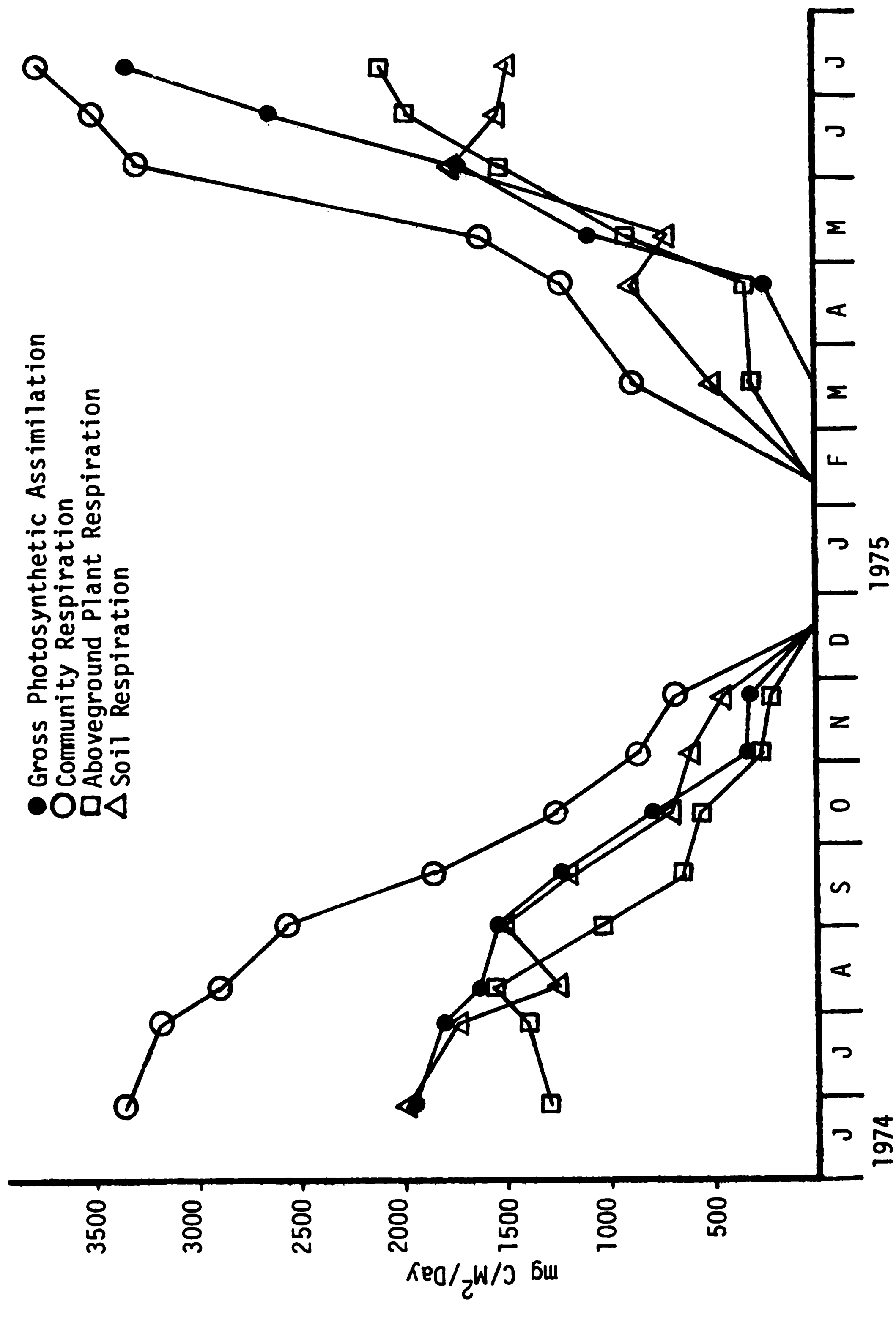
(3) Kcal/g ash free dry weight

in mid September 1974, living biomass that senesced during the growing season, plus total increase in belowground biomass which accumulated since the beginning of the growing season. The total visible radiation during the 1974 growing season was 668,160 Kcal/m^2. The ecological efficiency was 0.23% for the growing period (caloric content/visible radiation) and 0.14% annually. The efficiency between consecutive harvesting periods varied from 0.06% to 0.30%, with the highest efficiency occurring between 18 May and 10 June 1974.

Community Metabolism

Annual patterns. The annual patterns of gross photosynthetic assimilation, community respiration, aboveground plant respiration and soil respiration for the 13 month period from June 1974 through July 1975 are presented in Figure 11. Community respiration (R) exceeded gross photosynthesis (P) throughout the entire sampling period, giving a P/R ratio of less than one. However, the ratio of gross photosynthesis to aboveground plant respiration exceeded one throughout most of the

Figure 11. *A. breviligulata* community metabolism.


● Gross Photosynthetic Assimilation
○ Community Respiration
□ Aboveground Plant Respiration
△ Soil Respiration
mg C/M²/Day
3500
3000
2500
2000
1500
1000
500
J
J
J
A
S
O
N
D
J
F
M
A
M
J
J
1974
1975

sampling period except in early spring.

As stated earlier, it is felt that beachgrass growth during the 1975 growing season would exceed that measured during the 1974 growing season. This was also shown by the estimate of gross photosynthesis on 24 June 1975 which exceeded that on 28 June 1974 by 0.68 g C/m^2/day. Peaks of 1.95 and 3.32 g C/m^2/day in gross photosynthesis occurred in late June 1974 and in early July 1975, respectively. By the time living aboveground biomass reached its peak (22 September 1974), the rate of gross photosynthesis had decreased 0.71 g C/m^2/day from the June high.

The mean daily rates for the respective portions of community metabolism based on the growing season sampling period, and annual means are presented in Table 3. The ratio of the aboveground plant respiration to gross production during the growing season and annually was 48% and 66%, respectively. Gross production when expressed as a percent of community respiration was 98% during the growing season and 71% during the entire year. The ratios of net production to gross production during the growing season and annually were similar (35% and 34%, respectively).

Community respiration followed the general patterns of soil and aboveground plant respiration. It peaked in late June 1974 and early July 1975 at a mean of 3.41 g C/m^2/day (24 hr). The ratio of plant respiration to community respiration averaged 47% during the growing season. During October through November 1974 and March through April 1975 the ratio averaged 30%.

Aboveground plant respiration averaged 0.27 g C/m^2/day (24 hr) during late fall and early spring, increased till August 1974 (1.54 g C/m^2/day) and decreased throughout the fall.

Soil respiration exceeded plant respiration throughout most of the

Table 3. Mean daily rates of _A_. _breviligulata_ community metabolism.

	Growing season mean(1) (g C/m^2/day)	Sampling period mean(2) (g C/m^2/day)	Annual mean(3) (g C/m^2/day)
Gross primary production	2.640	1.724	1.306
Net primary production	0.926	0.622	0.446
Aboveground plant respiration	1.268	1.102	0.860
Soil respiration	1.409	1.220	0.968
Community respiration	2.676	2.343	1.828

(1) Based on 179 days from June to September 1974 and April to June 1975.

(2) Based on 262 days from June to December 1974 and April to June 1975.

(3) Based on 365 days from June 1974 to June 1975.

sampling period. Soil respiration increased from February to June (mean of 1.64 g C/m^2/day) (24 hr) and then decreased during the rest of the sampling period. On 20 March 1975 soil respiration was estimated to be 0.58 g C/m^2/day. At the time of this estimate portions of sand were frozen in the belowground biomass samples. Since the respiration of soil organisms such as fungi, bacteria, and various invertebrates, plus beachgrass roots and rhizomes were included in soil respiration, it was not possible to separate out that portion contributed only by beachgrass.

Daily patterns. Daily interrelationships between gross photosynthesis, solar energy, gross photosynthetic efficiency and day length are given in Table 4 for the sampling periods between 28 June 1974 and 11 July 1975. Gross photosynthetic efficiency generally increased during the growing season, however many of the dates had fairly similar efficiencies. The highest efficiencies occurred during 13 October 1974 and 24 June 1975 when a heavy cloud cover was present most of the day. The estimates of plant metabolism on 11 July 1975 were greater, as computed on a per m^2 or per gram basis, than estimates on prior sampling dates. An analysis of possible correlative factors affecting gross photosynthesis showed little relationship between gross photosynthesis and day length, solar energy or chamber temperature (Table 5). The highest correlation ($r = 0.60$) was with solar energy, as would be expected.

The measuring of CO_2 exchange rates at three to four different periods during each diurnal measurement cycle provided an opportunity to observe any diurnal rate fluctuations. Hourly rates of gross photosynthetic assimilation, plant respiration and soil respiration measured during four days which represent the general trends during spring,

Table 4. Daily relationships between gross photosynthesis of *A. breviligulata* and solar energy, indices of efficiency and daylength.

Sampling	Gross photosynthesis(1) g C/m^2/day	Solar energy g cal/cm^2/day	Efficiency(2) index (x10^{-3})	Day-length(3)
28 June 1974	1.95	434.27	4.49	14.75
28 July	1.80	440.19	4.09	13.33
9 Aug.	1.63	343.26	4.74	12.75
1 Sep.	1.53	304.66	5.01	10.83
22 Sep.	1.24	286.14	4.61	10.33
13 Oct.	0.78	83.07	9.39	8.75
2 Nov.	0.34	182.50	1.85	8.25
23 Nov.	0.32	78.46	4.09	8.00
22 Apr. 1975	0.24	307.12	0.80	11.75
11 May	1.09	261.42	4.16	13.25
3 June	1.72	423.03	4.05	13.75
24 June	2.63	216.95	12.12	14.00
11 July	3.32	427.80	7.76	13.50

(1) Calculated by multiplying mean uptake by hours of daylight.

(2) Gross photosynthesis/solar energy.

(3) Hours between sunrise and sunset.

Table 5. Analysis of factors correlated with gross photosynthesis(1).

	Correlation coefficient (r)
Gross photosynthesis and daylength (2)	0.53
Gross photosynthesis and solar radiation(3)	0.60
Gross photosynthesis and chamber temperature	0.54

(1) Linear regression analysis

(2) Hours between sunrise and sunset

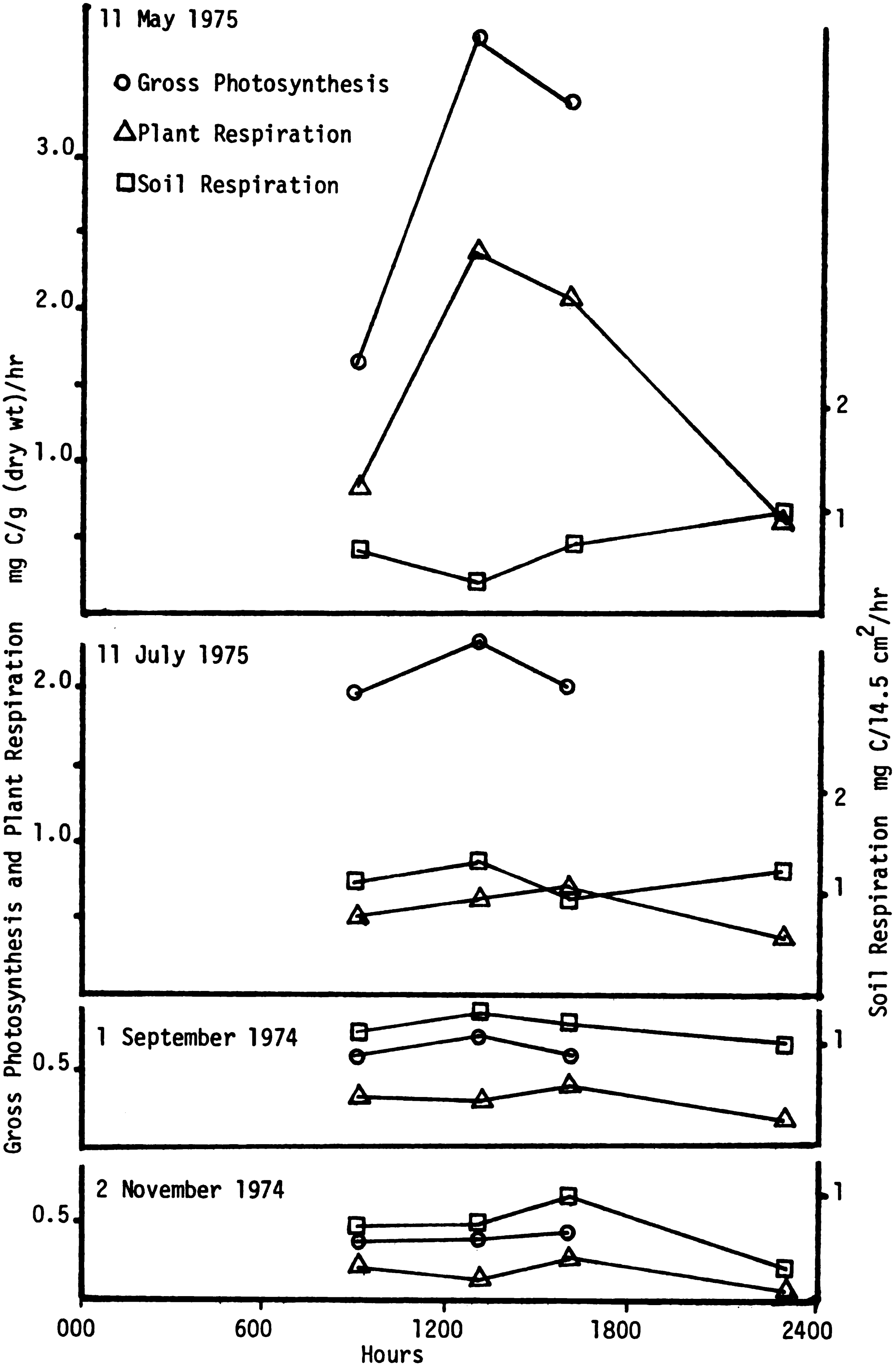
(3) g Cal/cm^2/day (50% of total)

summer and fall are presented in Figure 12.

Rates of gross photosynthetic assimilation during April and May increased from morning to early afternoon and then decreased during late afternoon. During this time the greatest rates per gram of plant tissue were recorded. During the rest of the sampling period, early afternoon rates did not exhibit any consistent trends. At the time the late afternoon measurements were made there was a trend for the rate of gross photosynthetic assimilation to return to that which had been measured in the morning. During the period of June through July, the morning, early afternoon and late afternoon rates generally decreased for each consecutive sampling date. There was no consistent trend for early afternoon rates. Late afternoon rates tended to return to rates measured in the morning regardless of whether early afternoon rates had increased or decreased.

The efficiency indices (gross photosynthesis/solar radiation) increased from early afternoon to morning to late afternoon. During

Figure 12. Hourly rates of gross photosynthetic assimilation, plant respiration and soil respiration.


11 May 1975
○ Gross Photosynthesis
△ Plant Respiration
□ Soil Respiration
11 July 1975
1 September 1974
2 November 1974
3.0
2.0
1.0
0.5
2
1
mg C/g (dry wt)/hr
Gross Photosynthesis and Plant Respiration
Soil Respiration mg C/14.5 cm²/hr
000
600
1200
1800
2400
Hours

late afternoon measured insolation was usually decreased by increased cloud cover. The daily and hourly efficiencies indicate that beachgrass was light saturated at least during the early afternoon period and possibly most of the day during much of the year when skies were clear (Zelitch, 1971).

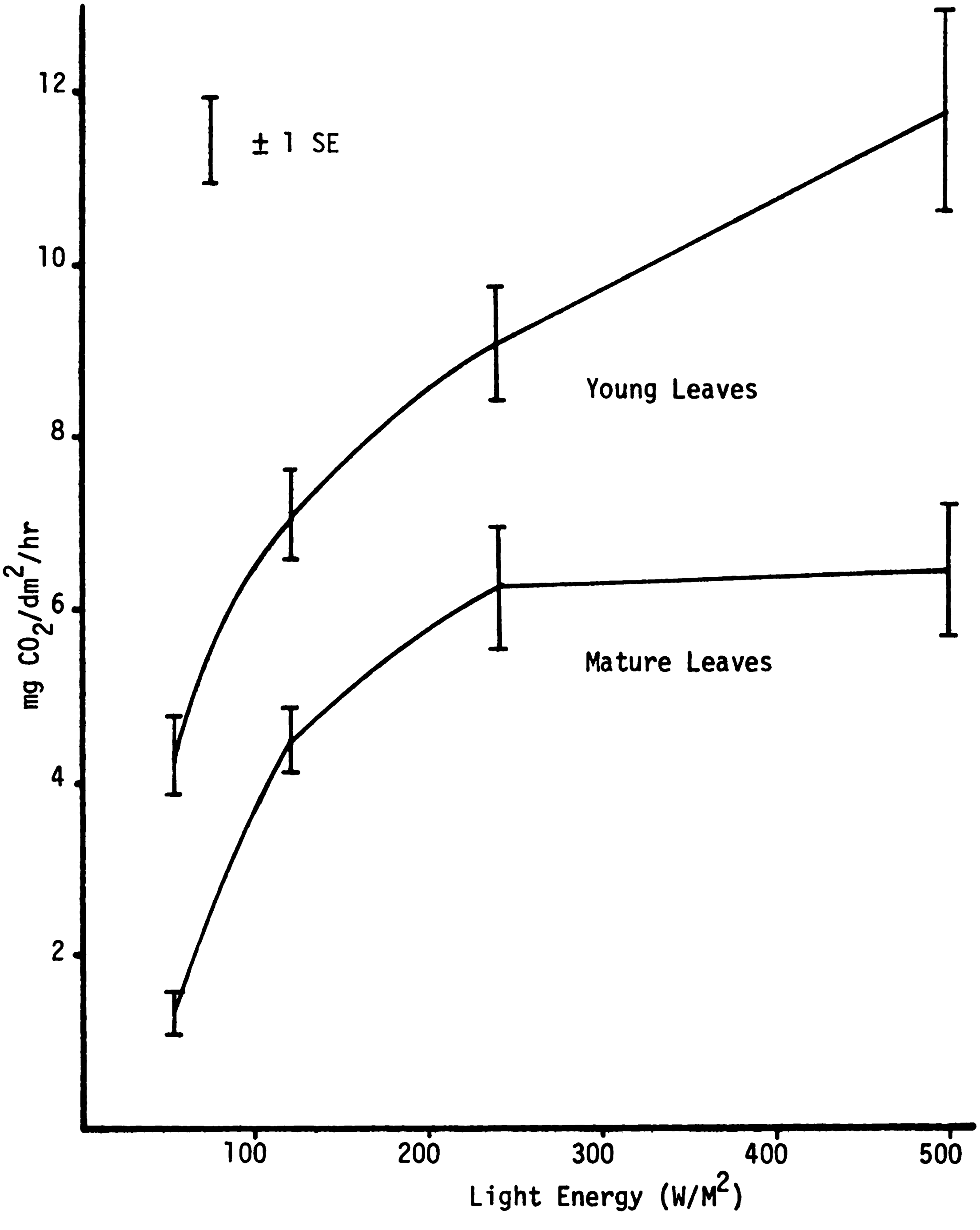
The highest rates of plant respiration per gram of plant tissue per hour were recorded during the period of March through May. From March through August, plant respiration rates increased during the day and at night decreased to a point lower than the morning rates. During the period of June through August plant respiration generally decreased at each consecutive sampling period: however, there was much fluctuation. The rates decreased from morning to early afternoon and increased to a high in the late afternoon during the period of September through November. During this period the night rates were at their lowest levels.

Hourly soil respiration rates did not exhibit any general day time trends. During the period of June through September, night rates were lower than the mean day rates. Rates measured at night during March and during the period of September through November were lower than any hourly day rates.

Photosynthetic Assimilation Under Different Conditions

Response to varying light intensities. The results in this section and the next are based only on responses measured with assimilation chambers on the lower leaf surfaces, since little to no gas exchange was detected with upper leaf surface assimilation chambers. Young leaves photosynthesized more rapidly than mature leaves (Figure 13): The mature

Figure 13. Net photosynthetic rates of single leaves of *A. breviligulata* in relation to light intensity.


± 1 SE
12
10
8
6
4
2
mg $CO_2/dm^2/hr$
Young Leaves
Mature Leaves
100
200
300
400
500
Light Energy (W/M^2)

leaves reached light saturation at 252.5 W/m^2 (479 x 10^2 lux), whereas the young leaves were not saturated at 500 W/m^2 (947 x 10^2 lux), the highest measurement used.

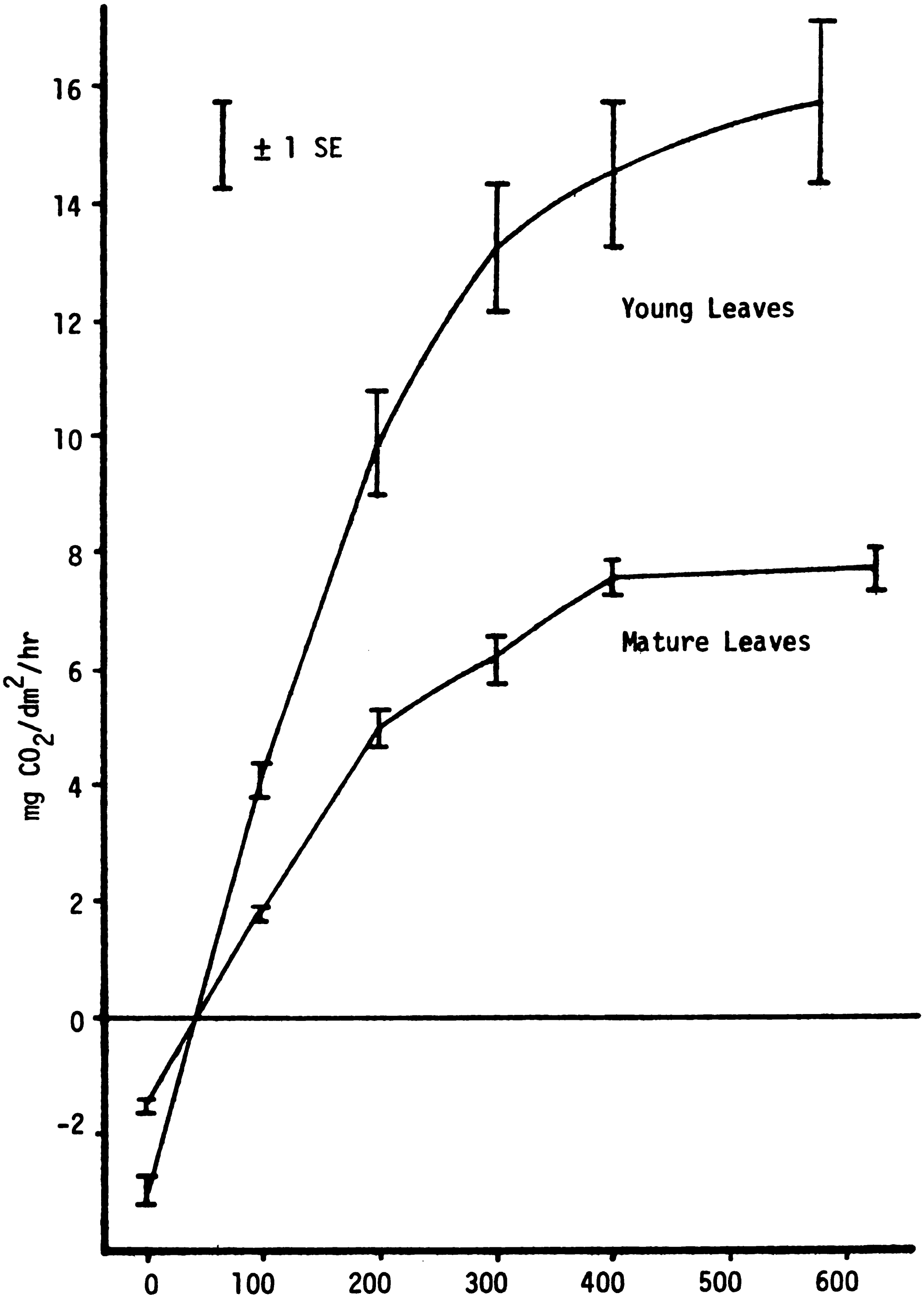
Stomatal oscillations occurred when mature leaves were exposed to a light intensity of 500 W/m^2 (947 x 10^2 lux). Rates of photosynthesis fluctuated between an average low of 5.8 ± 0.6 mg CO_2/dm^2/hr to an average high of 7.3 ± 0.7 mg CO_2/dm^2/hr. Internal CO_2 and conductance were in phase with each other, with periods of 30 minutes.

Response to varying CO_2 concentrations. Under a light intensity of 252.5 W/m^2 (479 x 10^2 lux) and different levels of CO_2 concentration, the rate of photosynthesis of the young leaves was again greater than that of mature leaves (Figure 14). The young and mature leaves had graphically the same CO_2 compensation point of 44 ppm. Using the slope of the curves between the compensation point and 200 ppm as a relative comparison of the efficiency of the leaves for photosynthesis, the young leaves proved to be more efficient than the mature leaves. The points at 0 ppm represent a minimum estimate of photorespiration (Zeltich 1971). The greater photorespiration by the young leaves was increased by a larger rate of dark respiration. The ratio of photorespiration to dark respiration for young leaves was 1.24 and mature leaves was 1.11.

The slight gas exchange from the upper leaf surface during the previous varied conditions was due to the lack of stomates. Stomates occurred in rows on the abaxial surface of the leaves between protruding vascular bundles and averaged 27 stomates per 1.5 x 10^{-3} mm^2.

The CO_2 compensation point (44 ppm) and the crossectional leaf anatomy were similar to a group of plants collectively called low

Figure 14. Net photosynthetic rates of single leaves of _A. breviligulata_ at a constant light intensity of 252.5 W/m^2 and different CO_2 concentrations.


± 1 SE
Young Leaves
Mature Leaves
16
14
12
10
8
6
4
2
0
-2
mg $CO_2/dm^2/hr$
0
100
200
300
400
500
600
PPM CO_2

photosynthetic capacity plants (Black, 1971) or "C_3" plants (Downton and Tregunna, 1968).

Vertebrates

Four species of rodents Peromyscus maniculatus bairdi (prairie deer-mouse), Microtus pennsylvanicus (meadow vole), Zapus hudsonius (meadow jumping mouse), and Mus musculus (house mouse) totaling 54 individuals, were trapped during the 1973 through 1974 trapping period (Table 6). Juvenile male P. maniculatus comprised the largest group of individuals caught. Of the 54 mice trapped, 76% were either juveniles, subadults or young adults; of these 74% were males. In the mornings numerous rodent tracks were observed in the sand of the old dune buggy road and the small blowout just south of the study site. Progressing from the south end toward the north end of the study site, 34 rodents (63% of the total) were trapped in the first 40 m, 8 (15%) from 40 to 140 m, 4 (7%) from 140 to 240 m, and 8 (15%) from 240 to 300 m. Examples of Peromyscus, Zapus and Mus were trapped throughout the study site, whereas those of Microtus were predominantly trapped within the 0 to 40 m area. Trapping during the periods of August through October 1973 and July through August 1974 yielded the most rodents. Although trapping was not done during the winter, rodent tracks were not seen in the snow on the study site either, but were observed further inland.

The stomach contents from these catches were classified as belonging in one of three categories: Insects (including all chitinous material), plants and unknown. The stomachs of Peromyscus contained predominantly insect remains along with some plant material. This

Table 6. The number of species, sex and age groups of rodents trapped within the study site.

Species	Male			Female			Total
	Young adult	Adult	Total	Young adult	Adult	Total	
Microtus pennsylvanicus	7	4	11	4	3	7	18
Zapus hudsonius	1	1	2	1	0	1	3
Mus musculus	0	0	0	1	1	2	2
	Juvenile Subadult	Adult	Total	Juvenile Subadult	Adult	Total	
Peromyscus maniculatus bairdi	14 8	4	26	2 3	0	5	31

predominance of insects in their diets is characteristic (Hamilton, 1941; Jameson, 1952; Whitaker, 1966). The identifiable stomach contents of _Mus_ and _Zapus_ were equally divided between plant and insect materials. Although plants predominated in the diet of _Microtus_, some insects were also consumed, an observation also made by Thompson (1965) and Zimmerman (1965). In only four _Microtus_ stomachs were there any cells which resembled beachgrass. The content of rodent stomachs, in total, consisted of 38% insect parts, 35% plant parts and 27% unknown. Identifiable beachgrass was present in only three of 54 stomachs examined.

Invertebrates

Various species of invertebrates were collected during the sampling period. Species of Diptera formed the largest group of individuals present. Other orders represented were: Hymenoptera, Coleoptera, Orthoptera, Hemiptera, Homoptera, Lepidoptera, Isoptera, and Odonata. Species of Phalangida and Araneida were also present. Of the preceding, only species of the families Acrididae, Cicadellidae, Chrysomelidae and Scarabaeidae may possibly be feeding on the beachgrass, and except for one species of Scarabaeidae (_Phyllophaga rugosa_) only small numbers of individuals of these families were found at any one time.

Larvae, pupae and adults of _Phyllophaga rugosa_ (June bug) were found when separating the sand from the belowground biomass. It was assumed that the larvae were feeding on the roots and/or rhizomes of the beachgrass. It is known that _Phyllophaga rugosa_ larvae annually have done considerable damage to cereal and forage crops in this manner (Anon. 1959; Forbes, 1907; Teetes, 1973). The larvae were found predominantly in areas where the most vigorous beachgrass growth was occurring. During the 1973 sampling period, larvae were found only during August. At this time eight adults, six larvae and four pupae were uncovered in three 1 m^2 samples. From March into June 1974 an average of two adults and two larvae were found per 1 m^2 to a depth of 40 cm. By the end of June through July 1974 none were found in the belowground samples, although adults were seen and heard at night around the Populus deltoides behind the study site. During the rest of 1974 there was an average of one larva/m^2. Larvae were always found in concentrations of at least two or they were entirely absent from belowground samples. During June and into July 1975, larvae averaged seven/m^2 and corresponded with sites of active beachgrass growth.

Mycorrhizal Fungi

Throughout the sampling period, balls of tightly compacted sand grains were found when separating the belowground biomass from the sand. The occurrence of small balls of sand has been reported elsewhere (Brown, 1958; Koske et al., 1975; Olsen, 1958a). Koske et al., (1975) have reported an endomycorrhizae of the family Endogonaceae associated with many plant species colonizing dunes on the eastern shores of Lake Huron. Their physical description of the balls of sand is similar to those found in this study.

Staining the "sand balls" with acid fuchsin in lactophenol revealed the presence of a large number of spores. The spores are of a vesicular-arbuscular mycorrhizal fungus and closely resemble those produced by Glomus macrocarpus Tul. and Tul. (J. W. Gerdemann, University of Illinois, personal communication). Dr. Gerdemann suspects that the "sand balls" may be sporocarps although they may must be dense clusters of chlamydospores enclosing a mass of sand.

Staining a small clump of roots showed fungal mycelia in close proximity to beachgrass roots. While positively identified penetration points could not be found, Dr. Gerdemann thinks there is little doubt that the fungus is mycorrhizal on Ammophila breviligulata.

DISCUSSION

Beachgrass Primary Production

The net primary production of the beachgrass community during 1974 was 347 g/m^2 based on aboveground and belowground accumulation and aboveground senescence. Net primary production for 1975 was estimated to be 550 g/m^2. This estimate was based on the extropolation of measurements made during the period of March through July 1975 to the end of the growing season, using the trends established during 1973 and 1974.

The estimated greater productivity during 1975 relative to 1974 would probably be related to two factors: sand accumulation and high amounts of spring precipitation. The growth of beachgrass is known to increase with sand deposition (Hope-Simpson and Jeffereies, 1966; Laing, 1958; Marshall, 1965). During the growing seasons of 1973 and most of 1974, there was no measurable sand deposition on the study site, but between September 1974 and June 1975, 2-3 m of the foredune west of the study had eroded and by July 1975 4-5 cm of sand had accumulated behind this eroded area. Year-to-year differences in precipitation during May and June account for 74% of the variation of forage production in short-grass prairie (Smoliak, 1956). Precipitation on the study site during the period of April through July 1975 was 14.0 cm above the 29 year norm of 33.4 cm, and 52% above that measured during a similar period of time in 1974.

Estimates of beachgrass net primary production were comparable to the average (500 g/m^2) annual temperate grassland net primary production which ranges from 150 to 1500 g/m^2 (Whittaker, 1970). However, since estimates of senescence were not included in the temperate grassland estimates, their values could be up to twice as high, based on the results of Bradbury and Hofstra (1976). Wiegert and Evans (1964) estimated the net primary production of an upland Michigan old field, including estimates of above and belowground production and living aboveground senescence, to be 1991 g/m^2, a substantially greater amount than the beachgrass community. The productivity of beachgrass can be increased with fertilization. Previously, artificially planted and fertilized 1- to 3-yr-old stands of beachgrass when fertilized have produced up to 380 g/m^2 of aboveground living biomass (Woodhouse and Hanes, 1966) compared to the 183 g/m^2 produced during the 1974 growing season of this study. However Woodhouse and Hanes did not determine aboveground senescence or belowground production.

The growing season net production efficiency of the beachgrass community (0.23%) was similar to those of desert (0.19%) (Chew and Chew, 1965) and xeric alpine (0.20%) (Scott and Billings, 1964) regions (as cited in Jordan, 1971), but was less than that of a Missouri tallgrass prairie (0.54%) (Kucera _et al_., 1967). This difference from the Missouri tall grass prairie would be expected because of the clumped growth habit of beachgrass with areas of open sand between clumps instead of a more uniform distribution of leaves which would more completely intercept incident light. The difference was also partly due to the greater nutrient levels present in the prairie soil compared to the dune sand.

The rate of gross photosynthesis increased with increasing aboveground biomass and increasing photosynthetic leaf surface area. Once the beachgrass leaves were fully expanded, there was a gradual decrease in the photosynthetic rates for the remainder of the growing season. The decline in the rate of photosynthesis was probably related to the shading of leaves and the lower photosynthetic rates of mature leaves which were present in a higher proportion in the beachgrass community during the late part of the growing season. Laboratory investigations indicated a decline in net photosynthetic potential with leaf age. This decline also has been described in other species (Hardwick et al., 1968; Treharne et al., 1968; Woledge, 1971; and others). In this study the young beachgrass leaves photosynthesized at a more rapid rate than the mature leaves and were not light saturated at 500.0 W/m^2 (947 x 10^2 lux) whereas the mature leaves were light saturated at 252.5 W/m^2 (479 x 10^2 lux). The decreased rate of photosynthesis could be partially attributable to the increased rate of plant respiration measured in the field, since respiration also decreases in older leaves but at a slower rate than photosynthesis (Zelitch, 1971).

The rate of gross photosynthesis when expressed as g C/g (living beachgrass enclosed in a chamber)/hr also decreased during the season. Generally the morning and afternoon rates of gross photosynthesis decreased throughout the annual study period. The noon rates generally also decreased during the annual study period but the comparison of noon rates to morning and afternoon rates did not show any consistent seasonal trend.

Midday fluctuations in the rate of gross photosynthesis appeared to be correlated with light intensity and air temperature. Because winds off Lake Michigan at times moderated air temperatures, high light intensities and high air temperatures did not necessarily occur together. During the periods of April through May and September the trends of increasing light intensity and air temperatures from morning through midday and then declined in the afternoon. During the period of June through August the mi-day rates decreased (compared to morning and afternoon rates) when light intensities approached 10,000 foot candles (measured with a Weston Electric Corp. footcandle meter) and also when air temperatures exceeded 30°C.

During the times of depressed rates of gross photosynthesis the midday rates of plant respiration (dark chamber) increased while those of photosynthesis (light chamber) decreased when compared to morning and afternoon rates. The increased rates of respiration were likely due to increased temperatures and the lower rates of photosynthesis were likely due to increased photorespiration with increasing temperatures. Zelitch (1971) has reviewed different studies relating to these occurrences.

The phenomenon of photorespiration, well known in terrestrial plants, has recently been reviewed by Chollet and Orgren (1975). The gas exchange methods for estimating photosynthesis in the field did not distinguish between mitochondrial (dark) respiration and photorespiration. Because estimates of photorespiration were not included in this study, gross photosynthesis was underestimated, but to what extent is unknown.

The close interrelationship of living above and belowground portions of the beachgrass community can be seen when their respective biomass estimates are compared. The living aboveground beachgrass exhibited a rapid spring increase, a slower summer rate of increase and a fall dieback. In contrast, the belowground biomass showed an inverse pattern of biomass increase except during June and July. This inverse pattern may in part represent seasonal root decomposition, and/or root to shoot and shoot to root carbohydrate translocation. Since results from the belowground litter experiment and the work of Olson (1958a) indicate the rate of decomposition and organic matter build-up in sandy soils to be a very slow process, the former may not be involved in this case. However, Poa pratensis shows a similar spring and fall inverse root and shoot biomass relationship (Bernard, 1974), and Bernard attributes this to translocation of material between above and belowground portions. Carbohydrate concentrations in roots have been shown to decrease during periods of rapid aboveground growth. The carbohydrate concentrations again increased in the belowground portions when the aboveground growth rate slowed down and the photosynthetic leaf area increased (McCarty, 1935).

During the fall the belowground biomass once more increased as the living aboveground biomass decreased. This could possibly represent a shoot to root carbohydrate translocation. Wiemann (1940) and McCarty (1935) have shown that in Chloris gayana, Elymus ambigus and Muhlengeria pracilis the root carbohydrate content in the fall increased while the aboveground carbohydrate content decreased an equivalent amount.

The proportion of the living aboveground biomass that was incorporated into the aboveground dead and belowground biomass between mid September and mid November of 1974 was determined by measuring weight changes in the respective biomass portions. During this period 134 g/m^2

of living aboveground biomass died and the belowground biomass and the dead biomass increased 39 g/m^2 and 108 g/m^2, respectively. This combined increase of 147 g/m^2 exceeded that lost by the living aboveground biomass by 13 g/m^2 but was within 1 SE for both the dead above and total belowground biomass.

The large amount of belowground biomass compared to living aboveground biomass was evident from the root/shoot ratio. However, how much of the belowground biomass was living and functioning was not determined. The ratio of belowground to aboveground production for 1974 was 0.5. Bray (1963) compiled root/shoot ratio data from a large number of sources and showed that the ratio of belowground to aboveground production for certain grasses increased as xeric conditions increased. In Bray's study, plants with a production ratio similar to that of beachgrass were considered to be mesic. Chapman (1964) states that the dry character of a sand dune habitat may be more apparent than real. He states that water tables under dunes tend to be dome shaped. Together with this and the fact that McLeod (1974) found water to be permanently available for plant usage at depths of 25 cm (at a site 2 Km south of the present site) it was felt that the root/shoot production ratio of 0.5 illustrated that either roots were efficient or that water was not a limiting factor in the growth of beachgrass.

Soil respiration increased in the spring until June and then decreased for the remainder of the season. Soil respiration of the beachgrass community, when compared to estimates of other communities including pine oak forest, cedar stand, wet tropical secondary growth and Grape Peninsula grass community as reviewed by Kucera and Kirkham (1971), was most similar to that of a Missouri prairie. However, the total soil carbon flux of the beachgrass community was less than that of the prairie, as expected, since the prairie had a greater belowground biomass (Dahlman and Kucara, 1965).

Rates of soil respiration have been found to decrease with decreasing soil moisture (Kucera and Kirkham, 1971; Wiant, 1967a) and to increase with increasing soil temperature (Kucera and Kirkman, 1971; Reiners, 1968; Wiant, 1967b). Monteith _et_ _al_. (1964) have suggested that the availability and depletion of substrate material for microorganisms may also be contributing to the seasonal change in soil respiration. Two other factors which may be involved in the soil respiration of a stabilized dune are decomposition of material from previous years and the possible diffusion of CO_2 within the dune.

The microbial population of developing dunes is low and will remain low until the dune has become stabilized (Brown, 1958). This is due to the continual deposition of sand. The conditions associated with this are unfavorable to microorganisms (Webley _et_ _al_., 1963). Once a dune has become stabilized, the beachgrass root system has been shown to be associated with increased numbers of microorganisms (Kisiel, 1970; Marchant, 1970; Nicolson, 1960; Wahlrab _et_ _al_., 1963). The soil respiration on a recently stabilized dune (such as this study site) may represent decomposition of roots and rhizomes that have been in existence several years but were only recently being used as a substrate for microbial activity.

The measurement of soil respiration may also be complicated by CO_2 diffusion from different areas within the dune. To test this, the belowground biomass was removed from a square meter plot to a depth of 40 cm and the sand was replaced, thus destroying the sites for microbial activity. However, 24 days later the carbon flux from this area was 45% of that measured on undisturbed sites. Possibly the soil respiration measured on the harvested site was due to the diffusion of CO_2 from areas of decomposition and respiration. Another possibility was that by removing the belowground biomass and then replacing the sand favorable conditions for short term microbial activity were created.

These are two factors which may enhance beachgrass growth where there is no sand accumulation. The first is the slow decomposition of dead aboveground biomass and the second is the apparent association of beachgrass roots with a vesicular-arbuscular mycorrhizal fungus.

The region of root initiation in beachgrass communities without sand accumulation is near the surface (Olson, 1958a) where soil temperatures increase and soil moisture decreases (McLeod, 1974). During the period of June through August noon soil (bare sand) temperatures were frequently observed to exceed 30°C during this study and that of McLeod's (1974). Although optimum soil temperatures for root initiation and elongation vary with different species, soil temperatures above 30°C have been found to be detrimental (Hansen, 1971). The slowly decomposing material would provide a physical means of cooling the soil through shading. The ability of beachgrass to cool sand by shading has been previously demonstrated by Salisbury (1934). The accumulation of dead aboveground plant material may also be a means of retaining mineral nutrients in a rapidly leaching sand dune community, where, by its slow rate of decomposition it would release nutrients over a long period of time.

Gerdemann (1968) cited evidence that vesicular-arbuscular mycorrhizal infected plants had enhanced growth compared to non-infected plants. Although A. arenaria has been found to have a mycorrhizal association (Nicolson, 1960), such an association has not been previously reported for A. breviligulata. However, such an association would be expected since conditions of high light intensity and a deficiency of available nitrogen or phosphorus, both present on dunes, make plants more susceptible to mycorrhizal infection (Bjorkman, 1942). The mycorrhizal association of A. arenaria occurred only after the dune surface had become stabilized (Nicolson, 1960). This would also appear to apply to A. breviligulata.

Estimates of Animal Activity

Vertebrates. The presence of only three meadow jumping mice and three house mice in the trapping samples of 1973 and 1974 suggest that these species were only transient and would be found infrequently in the area of the study site. The large majority of juvenile and sub-adult (87%) prairie deer-mice and of young-adult (65%) meadow voles raises the question of whether, in fact, the beachgrass stand supports any permanent rodent population. I do not believe that it does. The literature contains many examples of young mice wandering for a time after leaving the nest (Blair, 1940a,b, 1951; Burt, 1940; Howard, 1949; and others). Only one pregnant mouse (a house mouse) was trapped during the sampling period. If the adult mice represented a resident population it would be expected that more pregnant females would have been trapped. During the entire beachgrass sampling no rodent holes, runways or aboveground nests were found on the study site. Also a resident rodent population would be expected to support some form of predators, none of which were caught. The lack of tracks or trapped predators does not disprove their presence, however if present, they appear to be scarce.

The presence of the meadow voles was surprising since they have previously been reported to prefer more mesic areas in Michigan (Blair, 1940a); and New Jersey (Shure, 1970). Blair (1940b) reports a continuous flow of transients moving through an area without any taking up residence. Of the meadow voles, 83% were trapped within 40 m of the old road along the south side of the study site. Occasionally beachgrass stems showing signs of feeding by meadow voles as defined by Bailey (1924) and Summerhayes (1941) were found in this area of the study site. Meadow voles feed by a continuous process of trial and error (John Fitch, Michigan State University, personal communication). The absence of beachgrass in meadow vole stomachs indicates little to none was in fact eaten. Since at times large amounts of marsh vegetation carried by the Kalamazoo River into Lake Michigan were deposited on the shore and fringes of the SW corner of the study site, it is possible that the meadow voles were feeding on this and occasionally on insects. Zimmerman (1965) has found insect remains in meadow vole stomachs.

Even though prairie deer-mice were trapped throughout the study site, 62% were trapped within 40 m of the old road on the south. This area contained some of the densest beachgrass clumps and it was likely that it contained the highest concentrations of June bug larvae. Several times in this area small holes were found in the soil approximately 10 cm deep. Upon excavation there were no noticeable chewed beachgrass roots or rhizomes. It is felt that praire deer-mice dug these looking for June bug larvae, pupae or adults. Deer mice appeared to utilize whatever was available such as insects (larvae and adults), spiders, seeds and occasionally portions of plants as also seen by Hamilton (1941), Jameson (1952), Whitaker (1963) and Williams (1959).

Invertebrates. Although a large variety of insects were present in and around the beachgrass community, only June bug larvae were found to be residents of the community and feeding on it. The concentration of 0.4 larvae/m^2 in 1974 and 1.1 larvae/m^2 in 1975 would be classified as a light infestation compared to a severe infestation of 63 to 125 larvae/m^2 (Hammond, 1948). The herbivorous insects present were thought not to be residents of the beachgrass community but blown into the community by on or offshore winds. The beachgrass community does support a population of spiders and insects (ants, tiger-beetles, wasps, etc) which are predators and scavengers that utilize these transient invertebrate populations (Shelford, 1913).

In conclusion it is felt that beachgrass has a major structural and perhaps minimal nutrient relation to the majority of vertebrates and invertebrates found in its community. Beachgrass not only binds sand but also catches material blown from the shore which may be later consumed by the vertebrates and gives insects resting and hiding places. These insects in turn support a population of predators and opportunists (spiders, ants and rodents). These predators and opportunists are in turn hidden by beachgrass from other predators (e.g. wasps and whatever might prey on the rodents). Invertebrates survive on dunes by being able to tolerate great temperature extremes or avoiding them by only short exposures (Chapman et al., 1926). Beachgrass undoubtedly also aids insects by creating an environment of lower temperatures by shading (Salisbury, 1934). Beachgrass, though not contributing directly to most invertebrate and vertebrate diets does provide a structural benefit within which they are able to exist.

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LITERATURE CITED

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APPENDIX

Appendix Table 1. *A. breviligulata* living biomass(1) harvested during 27 July 1973 from 25 plots on the study site.

Distance (m) from the west boundary of the study site					
37	120	123	204	104	112
28	178	128	116	107	143
19	128	113	114	150	157
10	154	165	121	161	211
0	142	209	113	129	170
	262	202	142	82	22

Distance (m) from the south boundary of the study site

(1) dry weight (g)/m^2

Appendix Table 2. Living leaf surface area and leaf dry weights used for development of leaf surface area linear prediction equation.

Leaf dry weight (g)	Leaf surface area (mm^2)
5.4	407.4
14.6	831.1
4.9	293.9
12.3	590.3
8.3	500.5
8.4	578.3
4.3	296.1
6.2	366.5
8.2	492.5
10.0	584.3
9.2	705.5
8.8	528.5
22.0	1534.0
6.4	474.2
16.0	1104.0
18.4	1248.6
13.1	907.2
23.2	1368.3
6.1	400.3
13.6	831.5
10.6	537.3
14.1	886.2
6.0	431.4
8.7	593.4
27.1	1645.0

Appendix Table 3. *A. breviligulata* daily mean harvested dry weights.

Date	Aboveground living	Aboveground dead	Total belowground
	(1) (2)		
7/27/73	138 (18)	261 (32)	
8/11/73	151 (16)	246 (21)	
8/30/73	201 (23)	339 (41)	
9/17/73	230 (30)	312 (19)	
10/6/73	194 (16)	318 (33)	
10/27/73	183 (18)	338 (30)	
11/17/73	66 (7)	396 (48)	
3/7/74	0	392 (51)	795 (47)
4/6/74	5 (1)	381 (33)	749 (45)
4/27/74	23 (2)	425 (37)	655 (67)
5/18/74	48 (4)	380 (27)	586 (68)
6/10/74	106 (10)	457 (49)	783 (54)
6/28/74	118 (8)	373 (34)	778 (50)
7/17/74	131 (7)	359 (27)	771 (53)
8/9/74	142 (7)	382 (29)	701 (75)
9/1/74	162 (13)	415 (31)	623 (64)
9/21/74	183 (18)	437 (44)	886 (74)
10/12/74	159 (6)	471 (21)	891 (89)
11/2/74	97 (8)	468 (27)	981 (91)
11/23/74	49 (4)	545 (39)	925 (86)
3/20/75	0	573 (50)	954 (54)
4/22/75	8 (1)	584 (55)	944 (61)
5/11/75	30 (2)	502 (41)	970 (63)
6/3/75	86 (4)	547 (62)	876 (60)
6/24/75	143 (13)	587 (28)	748 (53)
7/11/75	166 (17)	634 (65)	955 (51)

(1) dry weight (g)/m^2

(2) ± 1 SE