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Preliminary Energy Budget For a Salt Marsh

In the Cape Fear River Estuary, North Carolina

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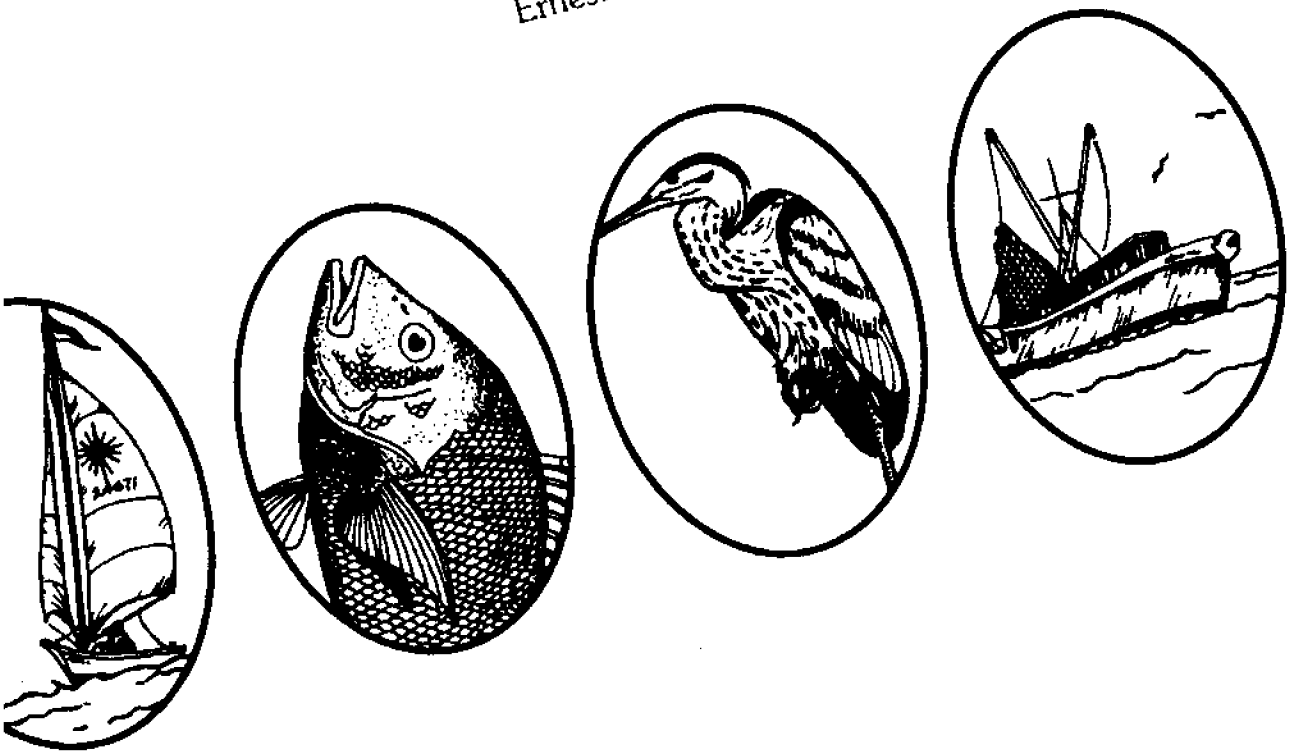

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PRELIMINARY ENERGY BUDGET FOR A SALT MARSH IN THE CAPE FEAR RIVER ESTUARY, NORTH CAROLINA

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INTRODUCTION

A band of salt marshes dominated by the cordgrass Spartina alterniflora extends along much of the East and Gulf Coasts of the United States. These marsh systems are important both as nursery grounds for many commercially important fish and shrimp species (Odum, 1961; McHugh, 1966; Newsom, 1968; Day et al., 1973; Daiber, 1974; Birkhead et al., 1977; Copeland and Hodson, 1977; Pendleton, 1979; Laney, in preparation) and as areas where excess nutrients are removed from the overlying water in a manner similar to tertiary waste treatment (Gosselink et al., 1974; Valiela et al., 1975).

Although there have been several studies of energy flow through individual components of salt marshes, there have been only two comprehensive studies of emergent marsh systems. Energy flow has been studied for populations of the fiddler crabs Uca pugnax (Shanholtzer, 1973; Krebs, 1976; Cammen et al., 1980) and U. minax (Cammen et al., 1980), the marsh periwinkle Littorina irrorata (Odum and Smalley, 1959; Alexander, 1976; Shirley et al., 1978; Cammen et al., 1980), the mussel Geukensia demissa (= Modiolus demissus) (Kuenzler, 1961), and the grasshopper Orchelimum fidicinium (Smalley, 1960). Energy flow through the entire emergent marsh system has been studied only in Georgia (Teal, 1962) and Louisiana (Day et al., 1973); the investigation of a Rhode Island salt marsh by Nixon and Oviatt (1973) emphasized the embayment, not the emergent marsh.

There is some disagreement in the literature as to the role of the emergent marsh in supplying nutrients to the surrounding waters and the degree to which the biota in these waters depend on those nutrients. The energy budgets of Teal (1962) in Georgia and Day et al. (1973) in Louisiana suggested that about 45% and 50%, respectively, of net primary production was available for export in salt marsh ecosystems. Measurements of material transport in tidal creeks indicate that some marshes export detritus (Odum and de la Cruz, 1967; Schultz and Quinn, 1973; Boon, 1974; Settlemyre and Gardner, 1975; Axelrad et al., 1976; Valiela et al., 1978), some import detritus (Hackney, 1977; Woodwell et al., 1977), and some have no net exchange (Nadeau, 1972; Heinle and Flemer, 1976). Haines (1977) has suggested on the basis of stable carbon isotope data that only a minor fraction of the organic seston in shallow salt marsh estuaries in Georgia is made up of marsh plant detritus, but since variability between systems is so high, her findings may not apply to other areas; Peterson et al. (1980) have suggested that the importance of the detritus may be to supply energy, rather than carbon, to the microbes. It appears that the lack of agreement as to the transport of detrital material into or out of marsh systems may be due to the large variability of hydrographic regimes in different marshes.

In order to examine more closely the exchange of material between the emergent marsh and the estuary in North Carolina, we have constructed an energy budget for the emergent marsh at Walden Creek, part of the Cape Fear River Estuary system. This budget is a synthesis of our own measurements of the major pathways of energy flow through this site and adjacent sites (Blum et al., 1978; Cammen et al., 1980) plus values drawn from the literature to estimate the pathways which we did not measure. We have adjusted the literature values whenever possible to reflect the conditions present in our marsh. By including estimates of belowground production and release of

dissolved organic carbon (DOC) by Spartina alterniflora and estimates of production of methane by sediment anaerobes, we have attempted to construct a more complete and realistic budget than those previously published. Since salt marshes along this section of the coast have received relatively little study, despite the fact that impact from both development and industry is rapidly increasing, this initial systems analysis will be useful in: 1) providing basic information into the functioning of the emergent marsh ecosystem in North Carolina, and 2) predicting and evaluating the effects of various management techniques on this system.

DESCRIPTION OF WALDEN CREEK MARSH

The study area was a Spartina alterniflora marsh located approximately 10 km from the mouth of the Cape Fear River Estuary, NC (33° 55' N, 78° 01' W). The marsh consisted of 23.6 ha short-form Spartina (< 50 cm high), 63.8 ha medium Spartina (50-100 cm), and 18.9 ha tall Spartina (> 100 cm), a total of 106.3 ha (Pendleton, 1979). The marsh sediment had an organic content of 13-30% and temperatures at the marsh surface ranged from 2 to 42°C. The marsh is drained by Walden Creek, which has a salinity range of 0 to 30 °/oo and a temperature range of 3 to 30°C (W. Laney, Department of Zoology, North Carolina State University, Raleigh; personal communication).

COMPONENTS OF THE MARSH ECOSYSTEM

The energy budget for Walden Creek marsh is discussed in three sections. In the first section, separate energy budgets for functional components of the ecosystem are developed. These components include the Spartina, the benthic microalgae, the ephiphytes, the fiddler crabs, the periwinkles, the insects, the mussels, the macrofauna, the meiofauna, and the microbiota. In the second section, the energy budget for the entire emergent marsh is presented. In the third section, we compare this energy budget with those developed for other marsh systems and discuss some of the factors affecting the form and amount of export of carbon to the Cape Fear River Estuary ecosystem.

Primary Producers

Spartina

Gross primary production (GPP) of the emergent marsh flora and respiration of both the flora and fauna were estimated by CO_2 analysis (described in Blum et al., 1978). Chambers were placed over several Spartina plants at low tide and sealed to the marsh surface and the changes in CO_2 concentration within light and dark chambers were monitored. Vegetable oil was used in the dark chambers to partition sediment respiration from aboveground respiration; however, the oil was not completely effective and 36 ± 16% of the sediment respiration was included in the measurement of aboveground respiration (Blum et al., 1978). We corrected for this error when calculating gross production and respiration (Appendix Section I).

Gross production of Spartina was determined by correcting ecosystem GPP (Appendix Table 3) for the production contributed by the benthic microalgae; epiphytic production was insignificant (see below). Production of benthic microalgae, estimated from Pomeroy (1959), assuming continuous exposure to air in order to simulate conditions in the chambers, was subtracted from ecosystem GPP to give Spartina GPP (Table 1).

Net primary production (NPP) of Spartina was estimated by subtracting Spartina respiration from GPP. Aboveground respiration of Spartina, as measured by Blum et al. (1978), included contributions from insects, arachnids and snails. We estimated faunal respiration (see later sections) and subtracted this amount from total aboveground respiration to give aboveground Spartina respiration (Table 2). Using the estimated ratios of aboveground to belowground respiration, derived from measurements of short Spartina respiration in Georgia (Teal and Kanwisher, 1961, 1966) and measurements of above- and belowground biomass in the three height-forms in Walden Creek marsh (Seneca et al., 1976) (see Appendix Section II for derivation), we estimated belowground Spartina respiration for the three marsh areas (Table 2). Finally, we subtracted the estimates of respiration from GPP to give NPP of Spartina (Table 3). Production was divided into aboveground and belowground portions using estimates from Blum et al. (1978) for belowground production (Table 3). Spartina NPP averaged 64-80% of GPP, lowest for tall and highest for short Spartina areas (Table 4).

Benthic Microalgae

Production of benthic microalgae was estimated from published data for other Atlantic Coast Spartina marshes. Annual gross production was estimated to be 79 g C m^{-2} in tall Spartina and 99 g C m^{-2} in short Spartina areas in a Delaware marsh (Gallagher and Daiber, 1974). In Georgia, estimated annual production (g C m^{-2}), taking into account the actual time of exposure and submergence of the marsh surface, was 219 in tall, 193 in medium, and 172 in short Spartina areas (Pomeroy, 1959). We used intermediate values (g C m^{-2}) of 150 for tall, 142 for medium, and 135 for short Spartina areas as the annual gross production of benthic algae in this marsh. Net production was at least 90% of gross production (Pomeroy, 1959); we assumed 90% and estimated total gross and net primary production for the marsh along with total producer respiration (Table 4), multiplying by 10 to convert g C to kcal for the benthic microalgae.

Epiphytes

Production by the epiphytes growing on Spartina was estimated from published data for two other North Carolina marshes (Lyon, 1975). Epiphyte production in medium Spartina areas of those marshes was 2 μg C hr^{-1} $plant^{-1}$ when the plants were exposed and 55 μg C hr^{-1} $plant^{-1}$ when the plants were submerged. We estimated time of exposure of medium Spartina in this marsh with tide-height data taken each 30 min from March 1975 to March 1976 near Walden Creek and elevation of medium Spartina areas (Fig. 1). We assumed that epiphyte growth was limited to the lower half of the plants and thus estimated that medium Spartina epiphytes were submerged 1.4% of the time. With a 12-hr day and 226 plants m^{-2} (Seneca et al., 1976) annual epiphyte production would

Table 1. Gross primary production (GPP) of Spartina. Estimated annual gross production of benthic microalgae (Pomeroy, 1959), calculated assuming continuous exposure, was subtracted from production estimates of the whole system (Appendix Table 3) to give Spartina gross production. Overall production takes into account the extent of each height-form in Walden Creek marsh. All values are kcal m^{-2} yr^{-1}.

Spartina type	Total ecosystem GPP	Benthic algal GPP	Spartina GPP
Short	6916	970	5946
Medium	11766	1280	10486
Tall	15678	1130	14548
Overall	11386	1184	10201

Table 2. Respiration of Spartina. Estimated aboveground faunal respiration (including Littorina, insects and arachnids) was subtracted from estimates of total aboveground respiration (Appendix Table 3) to give aboveground Spartina respiration. Aboveground Spartina respiration was divided by the ratio of above- to belowground respiration (Appendix Section II) to give belowground Spartina respiration. Overall respiration takes into account the extent of each height-form in Walden Creek marsh. All values (except ratios) are kcal m^{-2} yr^{-1}.

Spartina type	Total aboveground respiration	Faunal respiration	Aboveground Spartina respiration	Ratio of aboveground to belowground Spartina respiration	Belowground Spartina respiration
Short	590	101	489	0.72	679
Medium	2620	120	2500	1.87	1337
Tall	4528	1	4527	6.53	693
Overall	2509	95	2414		1076

Table 3. Net primary production (NPP) of Spartina. Estimated total Spartina respiration (from Table 2) was subtracted from estimated gross production (Table 1) to give total net production. Belowground Spartina production (Blum et al., 1978) was subtracted from total net production to give aboveground net production. Overall values take into account the extent of each height-form in Walden Creek marsh. All values are kcal m^{-2} yr^{-1}.

Spartina type	Total GPP	Total respiration	NPP		
			Total	Belowground	Aboveground
Short	5946	1168	4778	1869	2909
Medium	10486	3837	6649	1806	4843
Tall	14548	5220	9328	889	8439
Overall	10201	3491	6711	1657	5054

Table 4. Summary of primary production in Walden Creek marsh. Overall values take into account the extent of each height-form in Walden Creek marsh. All values are in kcal m^{-2} yr^{-1}.

Spartina type	NPP			Producer respiration			GPP		
	Spartina	Benthic algae	Total	Spartina	Benthic algae	Total	Spartina	Benthic algae	Total
Short	4778	1215	5993	1168	135	1303	5946	1350	7296
Medium	6649	1278	7927	3837	142	3979	10486	1420	11906
Tall	9328	1350	10678	5220	150	5370	14548	1500	16048
Overall	6711	1277	7987	3491	142	3633	10201	1419	11620

have been 12.0 mg C plant^{-1} or only 2.7 g C m^{-2}. The areas studied by Lyon (1975) had a greater abundance of epiphytes than the Walden Creek marsh; thus, epiphyte production was probably insignificant in relation to Spartina and benthic microalgae production and it will not be considered further.

DOC Release From Spartina

From 5 to 19% of the gross production of Spartina was released as dissolved organic carbon (DOC), highest in tall Spartina and lowest in short Spartina (Table 5). Gallagher et al. (1976) found DOC release rates during submergence from 42 to 275 µg C (g dry wt Spartina)$^{-1}$ hr^{-1} in a Georgia marsh; however, the majority of measurements were between 42 and 163 µg C g^{-1} hr^{-1}. Turner (1978) found release rates (µg C g^{-1} hr^{-1}) which varied from about 50 to 900 in another Georgia marsh, with a fall-winter average of about 225 and a spring-summer average of about 430 (calculated from his Fig. 6, p. 447). Gallagher et al. (1976) apparently incubated their leaves in untreated marsh water while Turner used either filtered or artificial seawater. Since the microbial populations in natural marsh water utilize significant amounts of DOC (Gallagher et al., 1976), Turner's estimates were probably closer to the actual release by Spartina. Whole plants apparently release DOC at the same rate per unit weight as isolated leaves (Turner, 1978). Therefore, we used an overall average release rate of 325 µg C g^{-1} hr^{-1} for release of DOC by submerged Spartina. When Spartina is exposed, it releases DOC at a rate of about 21 µg C g^{-1} hr^{-1} (Turner, 1978). We used the tide data taken near Walden Creek, the elevations of short, medium, and tall Spartina areas (Fig. 1), and the heights of the respective plants to estimate the average percent submergence for the plants in each area. With the percent submergence and the distribution of each height-form within the marsh, we calculated the overall release of DOC by living Spartina (Table 5).

After the Spartina dies, but before it falls to the marsh surface and decomposes completely, a small amount of DOC is released from the plants (Gallagher and Pfieffer, 1977). The average standing dead in this marsh (g dry wt m^{-2}) was 259 in short, 417 in medium, and 638 in tall Spartina areas (calculated from Seneca et al., 1976 and Stroud and Cooper, 1968). With an average release rate of 140 µg C (g dry wt)$^{-1}$ m^{-2} hr^{-1} (Gallagher and Pfieffer, 1977), taking into account the amount of submergence, the release of DOC from standing dead Spartina (kcal m^{-2} yr^{-1}) was estimated to be 27 in short, 26 in medium, and 541 in tall Spartina; the release rate for the marsh as a whole was 118 kcal m^{-2} yr^{-1}. Gallagher and Pfieffer measured release from standing dead in the same manner as release from live plants (Gallagher et al., 1976). As a result, they probably underestimated the true release rate since they did not account for uptake of released DOC by microbes in the water during their incubations.

Biomass Production

Taking into account respiration and release of DOC by living plants, only 57% of the total gross production of Spartina was available for consumption by herbivores. Short Spartina was the most efficient producer of biomass (75% of gross production), medium Spartina was next (58%), and tall Spartina was least

Table 5. Release of dissolved organic carbon (DOC) by Spartina. To determine average submergence, the plants were divided into 3-cm sections, percent submergence calculated from each section, and the mean of the percents was calculated. Overall values take into account the extent of each height-form in Walden Creek marsh.

Spartina type	Average % submergence	DOC release (kcal m^{-2} yr^{-1})	DOC release as % NPP	DOC release as % GPP
Short	0.9	315	6.6	5.3
Medium	0.6	596	9.0	5.7
Tall	7.7	2775	29.7	19.1
Overall		921	13.7	9.0

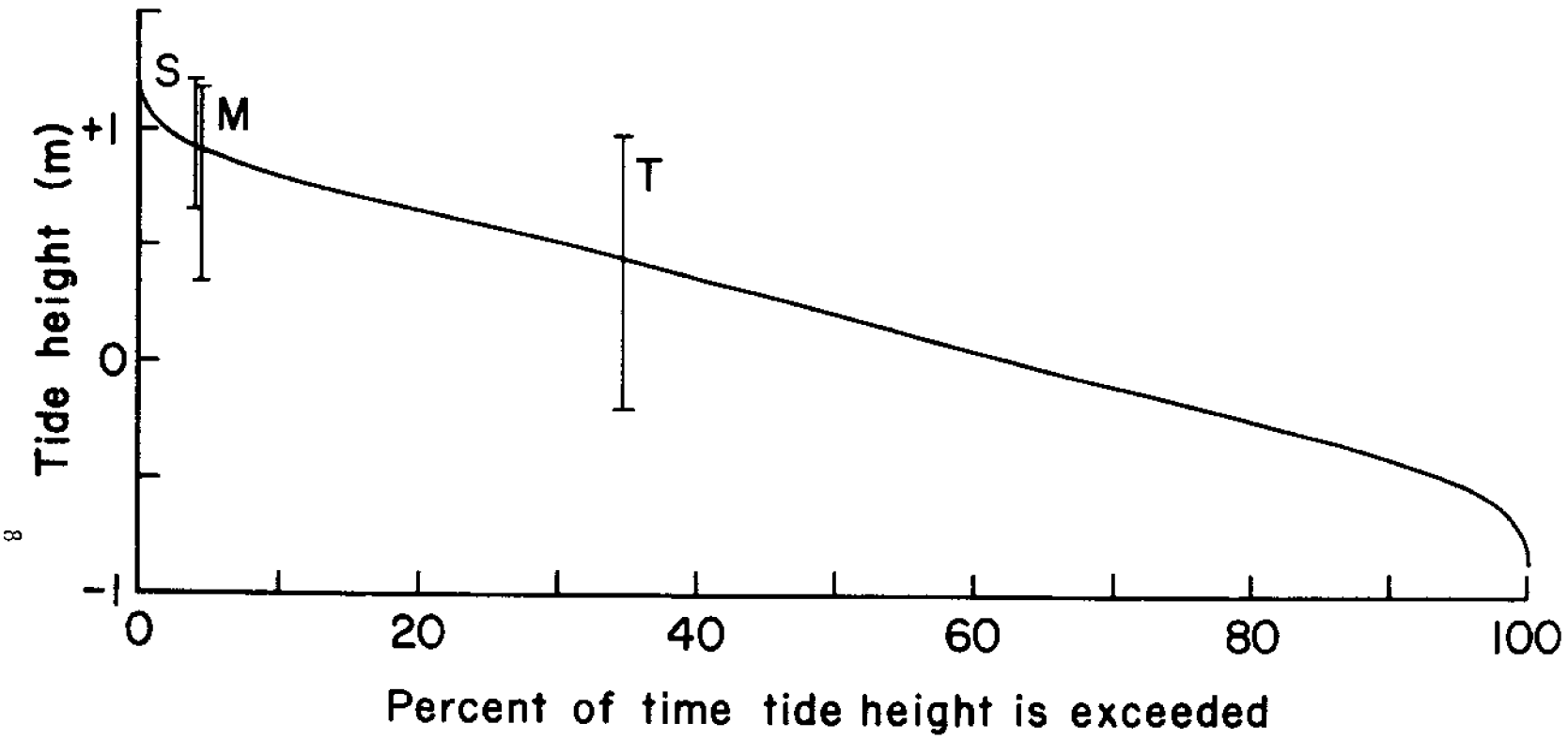

Fig. 1. Distribution of tide heights from March 1975 to March 1976 in Walden Creek along with the range in elevation (vertical bars) of the three marsh areas: short (S), medium (M), and tall (T). The intersection of the tide height distribution with the elevations of the marsh areas indicates the mean percent submergence for each area

efficient (45%). Interestingly, even though gross production of tall Spartina was 2.4 times that of short Spartina, biomass production was only 1.5 times as much. Due to the compensating effects of respiration and DOC losses, production of Spartina biomass was fairly uniform across the marsh, averaging 5789 kcal m^{-2} yr^{-1}. Considering the contribution of benthic microalgae as well, biomass production averaged 7066 kcal m^{-2} yr^{-1}.

Fiddler Crabs

Fiddler crabs of the genus Uca are widespread and abundant in salt marshes along the Atlantic and Gulf Coasts. Two species, U. pugnax and U. minax, are common in this marsh and a third species, U. pugilator, is observed infrequently. Fiddler crabs are deposit feeders (Teal, 1958; Marples, 1966; Shanholtzer, 1973) and do not feed directly on live Spartina. However, $^{13}C:^{12}C$ isotopic data indicated that much of the carbon in U. pugnax was derived from C_4 plants [probably Spartina (Haines, 1976a,b)].

Samples from all three marsh types were taken seasonally from summer 1974 to summer 1975. Only crabs with carapace widths greater than 2 mm were retained. Using a population model developed from our field data along with equations derived from the literature relating growth, respiration and egestion rate to body size of the crabs and temperature, we estimated energy budgets for the two most abundant crabs, U. pugnax and U. minax; details have been presented elsewhere (Cammen et al., 1980).

Energy flow through the crabs was greatest in tall Spartina and least in short Spartina areas (Cammen et al., 1980). Production (kcal m^{-2} yr^{-1}) was 32 in short, 37 in medium, and 195 in tall Spartina areas, while respiration (kcal m^{-2} yr^{-1}) was 40 in short, 72 in medium, and 269 in tall Spartina. On an overall basis, production was 64, respiration was 100, and total assimilation was 164 kcal m^{-2} yr^{-1}. The growth efficiency was 48% for U. pugnax, 23% for U. minax, and 39% for the combined crab populations.

Snails

The marsh periwinkle Littorina irrorata is also abundant in Atlantic and Gulf Coast salt marshes. L. irrorata graze on the stems of Spartina and on the sediment surface ingesting epiphytes, benthic algae, microbes, and plant detritus (Smalley, 1958; Marples, 1966; Alexander, 1976, 1979); $^{13}C:^{12}C$ isotopic ratios indicate that some of the carbon assimilated by the periwinkles may be derived from Spartina (Haines, 1976b).

The periwinkles were sampled at the same times as the fiddler crabs. Since the population size was small in the tall Spartina areas, we concentrated our sampling in short and medium Spartina and assumed that energy flow through the tall Spartina areas was negligible. A population model similar to that developed from the fiddler crabs was used to predict energy flow through the periwinkles and the details have been presented elsewhere (Cammen et al., 1980).

Energy flow through L. irrorata was similar in both short and medium Spartina areas (Cammen et al., 1980). Production (kcal m^{-2} yr^{-1}) was 8 in

short and 9 in medium Spartina; respiration (kcal m^{-2} yr^{-1}) was 100 in short and 119 in medium Spartina. On an overall basis production was 8, respiration was 93 and assimilation was 101 kcal m^{-2} yr^{-1}. Growth efficiency for the periwinkles was only 8%.

Insects and Arachnids

Insect and arachnid populations in the marsh were sampled once each season. Sweep-nets were used to sample two 100 m^2 plots; a total of 1000 sweeps in sets of 100 were made within each plot with 5-min intervals between each set. The organisms were dried in the laboratory at 55-90 C and a value of 5 kcal per g dry weight was used as a conversion factor.

Insect and arachnid standing stock was low in the marsh, ranging from 0.01 kcal m^{-2} in the winter to 0.23 kcal m^{-2} in the summer. The mean standing stock was 0.12 kcal m^{-2}. The insect population in another North Carolina salt marsh was assumed to turn over about three times each year (McMahan et al., 1972) and a grasshopper population in a Georgia marsh was estimated to turn over 2.8 times each year (Smalley, 1958). Assuming three turnovers each year for the insects and arachnids in this marsh gives a production estimate of 0.4 kcal m^{-2}. The ratio between respiration and production in the grasshopper population was 1.7:1 (Smalley, 1960) and this gives an estimate of 0.6 kcal m^{-2} for annual respiration for the insects and arachnids in this marsh. Total assimilation is estimated to be 1 kcal m^{-2} yr^{-1}. Net growth efficiency for the insects and arachnids was 40%.

Mussels

The ribbed mussel Geukensia demissa (= Modiolus demissus) is found throughout Atlantic and Gulf Coast marshes. It commonly occurs in clumps attached to plant roots and each other by byssal threads. The mussels are filter feeders, consuming suspended detritus and algae (Kuenzler, 1961).

Mussel populations in Walden Creek marsh were estimated from published data for other marshes. Mean population density in a Georgia marsh was 6.66 m^{-2} (Kuenzler, 1961) and the mussels were completely absent from tall Spartina edge marsh. In three Spartina marshes near Beaufort, NC, densities ranged from 0.1-7.5 mussels m^{-2} with an average of about 3 m^{-2} (Stiven and Kuenzler, 1980). We have assumed the population size in Walden Creek was similar to that in Georgia.

Energy flow was assumed to be the same as found in Georgia. Total assimilation of the mussels was estimated to be 56 kcal m^{-2} yr^{-1} of which 39 kcal were respired and 17 kcal were used for growth and gamete production (Kuenzler, 1961). Net growth efficiency was 30%.

Macroinfauna

Macroinfaunal communities in North Carolina salt marshes are dominated by polychaete worms and isopods (Cammen, 1979). These animals are mostly

deposit feeders, utilizing benthic microalgae, detritus and its associated microbiota, and smaller metazoans.

Macroinfaunal standing stock was estimated from published data for other southeastern salt marshes. Macroinfaunal data from five other marshes were summarized by Cammen (1979); the range in average standing stock was 1.9-3.1 g ash-free dry weight m^{-2}. Average standing stocks of the three North Carolina marshes that have been studied ranged from 2.4-3.1 g ash-free dry weight m^{-2} (Cammen, 1976, 1979). We have assumed an average standing stock of 3 g ash-free dry weight m^{-2} for this marsh; this is equivalent to 15 kcal m^{-2} if we assume that ash-free dry weight is 69% of dry weight for marsh macroinfauna (Cammen, unpublished data) and that 1 g dry weight is equivalent to 3.5 kcal (value for polychaetes from Cummins and Wuycheck, 1971).

Production and respiration were also estimated from published values. A value of 2 has been used to convert average biomass to annual production when no better data were available (Sanders, 1956; Gerlach, 1971; Cammen, 1976). In addition, the actual production: biomass (P/B) ratio for Nereis succinea, which dominated the macroinfauna of a Spartina marsh near Beaufort, NC, was 1.97 (Cammen, in press). With a P/B ratio of 2 for the macroinfauna in this marsh, annual production was 30 kcal m^{-2}. The ratio between production and respiration (P/R) for Nereis succinea was 2.1:9.4 in the salt marsh near Beaufort. Using this P/R ratio for the macroinfauna in this marsh, annual respiration was 134 kcal m^{-2}.

The completed annual energy budget for the macroinfauna in this marsh has a production of 30 kcal m^{-2} and respiration of 134 kcal m^{-2} for an average standing stock of 15 kcal m^{-2}. The growth efficiency for the macroinfauna was 18%.

Meiofauna

Nematodes dominate the meiofauna in salt marshes both in terms of numbers and biomass (Rogers, 1969; Brickman, 1972; Sikora et al., 1977). For example, in a Spartina marsh in New Jersey, the nematodes accounted for 97% of the total meiofaunal numbers and 93% of the biomass (Brickman, 1972). Therefore, we have concentrated on the nematode fauna in this study. Nematodes feed on benthic algae and microbes in addition to preying on other meiofauna (Coull, 1973; Tietjen and Lee, 1977).

Standing stock of the meiofauna was estimated using literature values from other salt marsh studies. We converted the various biomass measures used in other studies of marsh nematodes to energy by assuming that dry weight was 25% of wet weight (Wieser, 1960) and 1 g dry weight was equivalent to 3.84 kcal (derived from Sikora et al., 1977). Average standing stocks of nematodes in tall Spartina areas in other marshes (kcal m^{-2}) were 26.3 in New Jersey (Brickman, 1972), 24.2 in South Carolina (Sikora et al., 1977), 8.4-17.7 in Massachusetts (Wieser and Kanwisher, 1961), and 0.2-7.3 in Georgia (Teal and Wieser, 1966).

Although nematodes were more numerous in the Georgia marsh (12.9 x 10^6 m^{-2}) than in the other marshes (NJ, 4.3 x 10^6 m^{-2}; SC, 2.2 x 10^6 m^{-2}; MA, 1.4-2.1 x 10^6 m^{-2}), the standing stock in Georgia was much lower than the others because the mean individual size of the Georgia nematodes was less (GA, 0.15 µg dry weight individual^{-1}; MA, 1.55-2.19; NJ, 1.59; SC, 2.83). The data from the Massachusetts marsh came from an area adjacent to a salt marsh, but not actually within the area covered by Spartina growth. Therefore, for this study we considered the best estimates of nematode biomass to be those found in New Jersey and South Carolina and we assumed an average nematode biomass of 25 kcal m^{-2}. If nematodes were 93% of total meiofaunal biomass, as in New Jersey (Brickman, 1972), then total meiofaunal biomass in tall Spartina was 27 kcal m^{-2}. The only applicable information on distribution of the meiofauna within the marsh is from Georgia (Teal and Wieser, 1966) where nematode standing stocks had a ratio of 14.3:4.9:1 for tall:medium:short Spartina. We apportioned total meiofaunal biomass with these ratios to give average standing stocks (kcal m^{-2}) of 27 for tall, 9 for medium, and 2 for short Spartina. Taking into account the distribution of the three Spartina types in this marsh, the average meiofaunal biomass was 10.7 kcal m^{-2}.

Respiration and production of the meiofauna were also estimated from literature values. Average respiration rates of nematodes from two locations in a Massachusetts salt marsh were 755 and 586 mm^3O_2 (g wet weight)$^{-1}$ hr^{-1} at 20°C (mean of 670 mm^3O_2 g^{-1} hr^{-1}) (Wieser and Kanwisher, 1961). Respiration rate of nematodes from a Georgia marsh averaged 625 mm^3O_2 g^{-1} hr^{-1} at 20°C (Teal and Wieser, 1966). In a summary of all the available respiration data on marine meiofauna, median respiration for all taxa other than nematodes was 420 mm^3O_2 g^{-1} hr^{-1} (Gerlach, 1971). Since the nematodes dominate the meiofauna, we used 650 mm^3O_2 (g wet weight)$^{-1}$ hr^{-1} as the average respiration for the meiofauna in this marsh. With an oxy-calorific coefficient of 4.8 cal (ml O_2)$^{-1}$ and a conversion factor of 1 g wet weight of meiofauna (nematodes) to 0.96 kcal, this respiration rate is equivalent to 28.5 kcal respired (kcal biomass)$^{-1}$ yr^{-1}; this rate is for 20°C which is in the middle of the yearly temperature range for this marsh. With this value, we estimated annual respiration (kcal m^{-2}) to be 57 in short, 257 in medium, and 770 in tall Spartina. Gerlach (1971) estimated that annual meiofauna production averages nine times the mean standing stock. Meiofauna production in this marsh (kcal m^{-2} yr^{-1}) was thus estimated as 18 in short, 81 in medium, and 243 in tall Spartina areas.

The annual energy budget for the meiofauna on a whole marsh basis showed a production of 96 kcal m^{-2} and respiration of 304 kcal m^{-2}. The growth efficiency for the meiofauna was 24%.

Sediment Microbiota

The sediment heterotrophic microbiota consists of bacteria, fungi and protozoans. These organisms are responsible for most of the decomposition of organic material in the marsh.

No direct measurement of energy flow was made for individual components of the sediment system, but total aerobic respiration was measured by Blum et al. (1978). We subtracted the respiration attributable to belowground

Spartina, benthic microalgae, fiddler crabs, macroinfauna and meiofauna to obtain an estimate of aerobic respiration for the microbiota (Table 6).

Energy loss from the sediment through anaerobic metabolism was estimated to range from 0.1 to 15% of the energy lost through aerobic metabolism, greatest in short Spartina and least in tall Spartina areas (Table 6). These estimates were based on measurements of methane release from a Georgia marsh (g CH_4-C m^{-2} yr^{-1}): 53.1 for short and 0.41 for tall Spartina (King and Wiebe, 1978); release from medium Spartina areas is about 15 g CH_4-C m^{-2} yr^{-1} (W.Wiebe, personal communication). These release rates were measured only when the marsh surface was exposed, but in short and medium Spartina, where methane production is greatest, the marsh surface is exposed 94-95% of the time. Therefore, these estimates should be close to the actual value for the marsh as a whole.

Annual production of the microbiota was estimated by summing losses to the meiofauna, macroinfauna, and fiddler crabs. A steady-state condition exists in salt marshes for both bacterial standing stock (Rublee et al., 1978) and total microbial carbon (Christian et al., 1975; Rublee et al., 1978), which implies that any temporary increase in microbial biomass is either consumed or exported. The minimum energy required by the meiofauna, macroinfauna, and fiddler crabs was the amount respired (kcal m^{-2} yr^{-1}): 231 in short, 463 in medium, and 1173 in tall Spartina; the maximum energy required was the amount assimilated (kcal m^{-2} yr^{-1}): 311 in short, 611 in medium, and 1641 in tall Spartina. The actual energy required by these fauna was between these values since some of the meiofaunal and macroinfaunal production represented recycling within the respective trophic groups. Therefore, on an overall marsh basis, the energy required by all the consumers was between 538 and 728 kcal m^{-2} yr^{-1}. Not all of this energy came from the microbes, however. In another North Carolina marsh, the most abundant polychaete, Nereis succinea, obtained only 13% of its requirement from "microbial" carbon (Cammen, in press); since the measurement of "microbial" carbon in that study may have included some meiofaunal carbon, 13% represented the maximum contribution of the microbes to the carbon budget of the worms. If 13% of the energy assimilated by the meiofauna, macroinfauna, and fiddler crabs in this marsh came from the microbes, then microbial production (kcal m^{-2} yr^{-1}) was at least 30-40 in short, 60-79 in medium, and 152-213 in tall Spartina. On a whole marsh basis, microbial production was between 70 and 95 kcal m^{-2} yr^{-1}.

Total energy flow through the microbes (kcal m^{-2} yr^{-1}) was thus estimated as 3824-3834 in short, 3766-3785 in medium, and 5105-5206 in tall Spartina. On a whole marsh basis, energy flow through the microbes averaged 4025-4050 kcal m^{-2} yr^{-1}. Net growth efficiency for the microbes was only 2%.

DOC Release From Sediment

Release of DOC from the sediment, resulting from microbial action on decomposing Spartina and loss from benthic microalgae, was relatively minor in the marsh. We used a release rate of 6 mg C m^{-2} hr^{-1}, estimated from measurements taken in tall and short Spartina areas in a Georgia marsh

Table 6. Respiration of microbes and total sediment. Sediment respiration was calculated from Blum et al. (1978) using Spartina respiration from this paper. All values are in kcal m^{-2} yr^{-1}. Overall respiration takes into account the extent of each height-form in Walden Creek marsh.

Spartina type	Microbial			Total sediment (aerobic)
	Aerobic	Anaerobic	Total	
Short	3287	507	3794	4332
Medium	3575	131	3706	5517
Tall	4989	4	4993	7005
Overall	2763	192	3955	5519

(Pomeroy et al., 1977); there was no significant difference in release rate between tall and short Spartina. We assumed that release of DOC from the sediment could occur only when the marsh surface was inundated and calculated release rates (kcal m^{-2} yr^{-1}) of 20 in short, 22 in medium and 165 in tall Spartina areas. The overall marsh average was a release from the sediment of 47 kcal m^{-2} yr^{-1} as DOC.

Secondary Consumers

Secondary consumers in this marsh consisted of the arachnids (discussed previously), the marsh crab Sesarma spp., the rice rat Oryzomys palustris, and some 60 species of birds. Quantitative population data were collected only for the arachnids, but in other marshes the other taxa were found to be relatively unimportant in the total energy flow, at least as far as the fraction of the total production they consume (Teal, 1962; Day et al., 1973; Nixon and Oviatt, 1973). Therefore, we have not attempted to include these other taxa in this energy budget.

COMMUNITY ENERGY FLOW

The information on component energy flow from the previous sections has been summarized in Fig. 2 and Table 7. The data were summarized in Table 7 by functional groups, not by trophic levels since we felt that in a salt marsh system such as Walden Creek, where detritus is so important, any division into trophic levels would have been too artificial. Most of the fauna are omnivorous, feeding on a variety of smaller animals, detritus, benthic microalgae and microbes.

Gross production in the marsh was 1.1% of the incident solar energy (Fig. 2); net production was 0.7% of the solar input. Spartina accounted for 88% of gross and 84% of net production, and benthic microalgae accounted for the remainder. The producers in the marsh respired 31% of their gross production.

Only a minor portion of net production was utilized to produce faunal biomass. The consumers in the marsh assimilated the equivalent of 11% of the total net production in the marsh. Of this amount, about 8% was respired and 3% went to growth. The infauna (macroinfauna and meiofauna) accounted for 64% of the faunal assimilation and 59% of the production. The meiofauna were the most significant faunal component in the marsh, accounting for 45% of both assimilation and production.

More than half of the net production in the marsh was utilized by the microbiota and 98% of this amount was respired. Estimated microbial production was only 33-44% of the production of the infauna and epifauna.

Approximately 42% of the net production was potentially available for export to Walden Creek (Table 8); this was equivalent to an export of 53% of the aboveground net production. About 32% of this material was in the form of DOC on a whole marsh basis, but as much as 78% of the export from tall

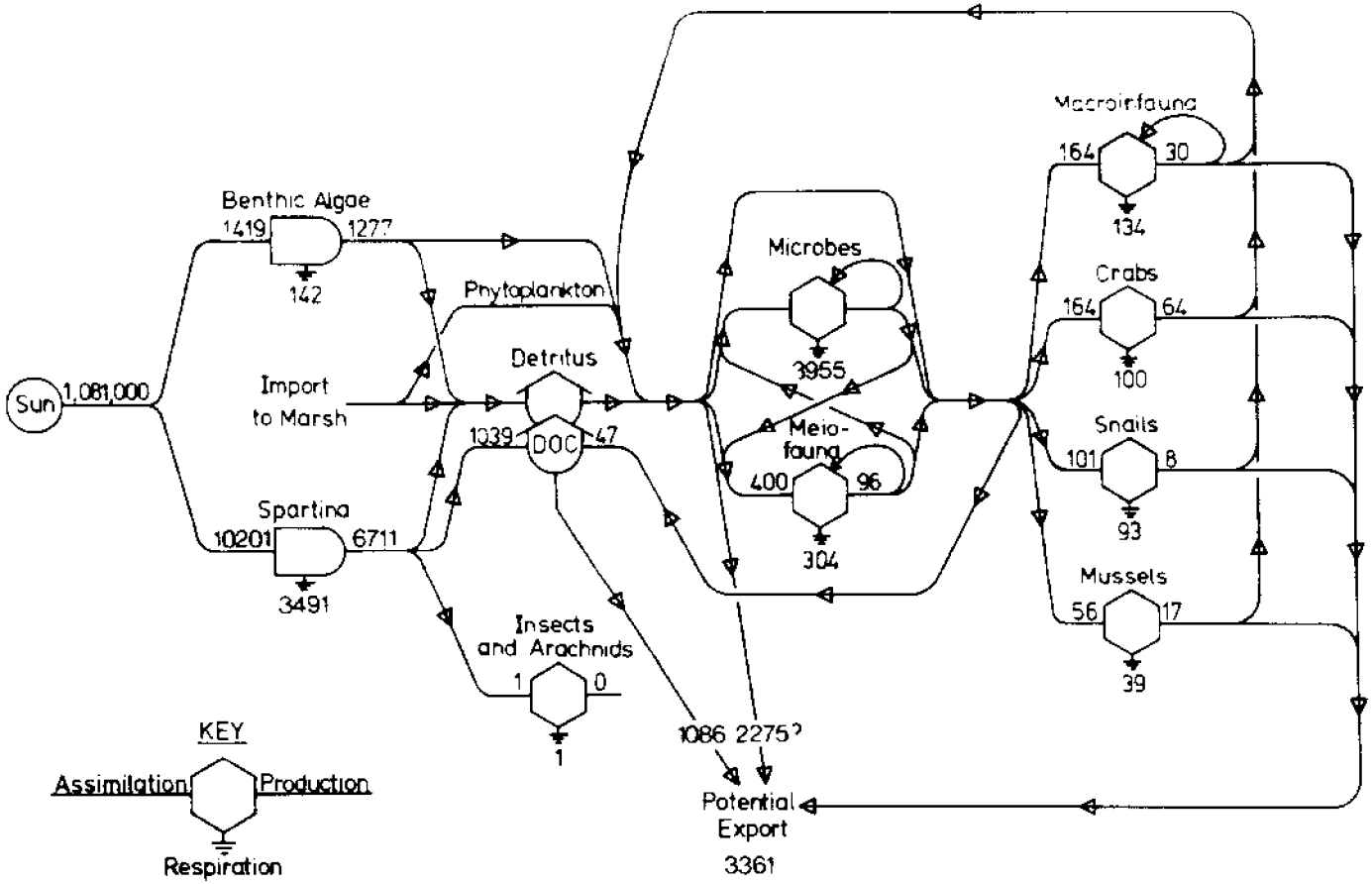

Fig. 2. Energy flow diagram for Walden Creek marsh. The diagram is intended to show the many alternate pathways for energy flow through the system and the magnitude of these flows where they are known. Circle (Sun) represents an energy source, bullet-shapes (Spartina, benthic algae) represent primary producer populations, roofed semi-circles (detritus, DOC) represent passive storage, and hexagons (microbes, meiofauna, insects and arachnids, macroinfauna, crabs, snails, mussels) represent consumer populations. Flows in and out of the compartments are explained in the lower left corner.

Table 7. Summary of energy flow through Walden Creek marsh. All values are kcal m^{-2} yr^{-1}.

Functional group	Input	Output	Efficiency
Insolation	-	1,081,000[a]	-
Primary producers	1,081,000	7987	0.7%
Microbiota	4025-4050	70-95	1.7-2.4%
Infauna	564	126	22.3%
Epifauna	322	89	27.6%

[a]Calculated from data in Blum et al., 1978.

Table 8. Estimate of net ecosystem productivity (NEP) or material available for export from Walden Creek marsh. All values are kcal m^{-2} yr^{-1}. Overall values take into account the extent of each height-form in Walden Creek marsh.

	Spartina type			Overall
	Short	Medium	Tall	
NPP	5993	7927	10678	7987
Microbial and faunal respiration[a]	-4165	-4328	-6206	-4626
NEP or potential export	1828	3599	4472	3361
DOC release from live plants, standing dead, and sediment	-362	-644	-3481	-1086
Potential export of particulate material	1466	2955	991	2275
% NEP of NPP	31	45	42	42
% particulate of NEP	80	82	22	68

[a]Includes methane production.

Spartina could have been in the form of DOC. On a whole marsh basis, an average of 2275 kcal m^{-2} yr^{-1} was available for export as particulate matter and 1086 kcal m^{-2} yr^{-1} was available for export as DOC.

DISCUSSION

Previous salt marsh energy budgets may have greatly underestimated the efficiency of the major primary producer, Spartina alterniflora. Net production in Walden Creek marsh was about 66% of gross production as compared to only 23% in Georgia (Teal, 1962) and 18% in Louisiana (Day et al., 1973). This difference is the result of a discrepancy in respiration estimates along the studies. Assuming that Spartina dry weight is 33% of wet weight (Reimold et al., 1973) and that 1 g dry weight is equivalent to 3.7 kcal (Blum et al., 1978), the ratios of respiration to mean aboveground standing stock of Spartina [kcal respired yr^{-1} (g dry weight)$^{-1}$] were 64.9 in Georgia, 65.5 in Louisiana, and only 6.3 in Walden Creek. On the other hand, the ratios of net production to weight [kcal yr^{-1} (g dry weight)$^{-1}$] were similar: 15.3 in Georgia, 14.0 in Louisiana, and 13.0 in Walden Creek marsh. Respiration estimates for both the Georgia and Louisiana marshes were based on measurements by Teal and Kanwisher (1961) of plants from Georgia and assumed that respiration was continuous for both light and dark periods. However, since Spartina is a C_4 plant, the aboveground portion respires only in the dark (Black, 1973); this would explain about half the difference between the respiration estimates. In addition, the chambers used by Teal and Kanwisher (1961) were short enough to require that the plants be bent over and this may have increased the respiration rate; the chambers used by Blum et al. (1978) were tall enough to fully accommodate the plants. Teal (1962) has suggested that due to the osmotically difficult environment in which Spartina lives, respiratory costs are relatively high. Respiration of Typha in a freshwater marsh in Minnesota was only 15% of gross production, for example (Bray, 1962). However, we estimate that the Spartina in Walden Creek respired only 34% of the gross production which suggests that the energetic costs of surviving in the salt marsh environment are not as high as previously thought.

The energetics of the belowground portion of the Spartina plants, although significant, has not been included in other marsh energy budgets. We have estimated that the belowground biomass accounted for 24% of the gross production, 30% of the primary producer respiration, and 21% of the net production in the marsh; these portions may be even higher in other areas. Belowground production has been estimated to contribute as much as 78 to 89% of Spartina net production in a Massachusetts salt marsh (Valiela et al., 1976) and belowground production in Georgia was about 62% of total net production (Smalley, 1958; Gallagher and Plumley, 1979). Most of the belowground production probably remains in the marsh sediment and is ultimately respired by microbes or buried. Some of the material will be brought to the surface by burrowers such as fiddler crabs, however and may then be exported from the marsh. A portion of belowground production will be lost in the form of root exudates to the surrounding sediment and this material should be rapidly metabolized by the microbial community around the roots.

The release of DOC from live Spartina, decaying litter, and sediment, and the loss of methane from the marsh surface are important pathways of energy flow in the marsh which were not considered in previous marsh energy budgets. Together, these pathways accounted for 16% of the net production in the marsh and 38% of the production remaining after microbial and faunal respiration. The DOC is likely to be a high quality food source for the microbes in the estuarine water column, but represents a portion of the production otherwise unavailable to consumers. Once the methane escapes from the sediment surface of the marsh, it is probably lost to the ecosystem; in earlier budgets, methane loss was tacitly included as export, since it was not actually considered.

Only 8% of the energy fixed by the primary producers was respired by the meio- and macrofauna of the marsh. This pattern was similar to that seen in Georgia, where 8% of net production was respired by consumers (Teal, 1962), and in Louisiana, where 10% was respired (Day et al., 1973).

Most of the energy lost from the marsh by respiration was due to the heterotrophic microbes, which respired the equivalent of 50% of the net production. Microbial production was at least 2% of the net production, since that amount was consumed by larger organisms. We do not know how much of the respiration and production were due to the separate components of the microbial community, namely the bacteria, fungi, and microfauna. Some of the assimilated net production may have been released by the microbes as DOC, but judging from the small amount of DOC released from the sediment, this release was probably not important in the overall energy budget.

The insects and arachnids appeared to be less important in Walden Creek marsh than in other marshes which have been studied. In Georgia, energy flow through the insects was estimated to be 305 kcal m^{-2} yr^{-1} (Teal, 1962) as compared to 1 kcal m^{-2} yr^{-1} in this marsh; energy flow through the insects in a Louisiana marsh was estimated as 26 g organic matter m^{-2} yr^{-1} (Day et al., 1973), which is equivalent to about 120 kcal m^{-2} yr^{-1}. The value from Louisiana is questionable, however, since the insects were assumed to respire 0.7 g organic matter (g dry body weight)$^{-1}$ day^{-1}. Insect dry weight is generally over 90% organic matter (Cummins and Wuycheck, 1971), so the rate assumed by Day et al. represents a minimum loss equivalent to 70% of insect body weight daily; over a 3-month period, the grasshopper population investigated by Smalley (1958) respired the equivalent of only 5% of their standing stock daily. Kuenzler (1961) pointed out that Smalley's study of grasshopper energy flow was carried out in tall Spartina areas, which are the most favorable habitat in the marsh for grasshoppers; Teal (1962) assumed that these values were typical of the marsh as a whole, which resulted in an overestimate of their contribution to the total marsh energy flow. Our values for insect and arachnid standing stock may have been underestimates since organisms were still being collected on the final sweeps, but even if the actual standing stock were twice as high as our estimate, the energy flow would still have been negligible. Insects living within the stems of the Spartina, which have not been considered here or in any of the other marsh energy flow studies, may consume significant amounts of plant tissue (N. Newton, Department of Entomology, North Carolina State University, Raleigh) should be studied in the future.

The equivalent of 42% of the net production was not dissipated in the marsh and was presumably available for export into Walden Creek (Table 8). Of this amount, 14% was accounted for as DOC and probably was exported. The fate of the remaining 28% in the form of particulate matter, was uncertain. Some of this material was exported but some was also incorporated into the sediment. Accretion often occurs in marshes (Redfield, 1972), but no estimates were available of accretion rate for Walden Creek marsh. Some simple calculations can be made, however, to examine the range of possibilities. If no sediment was accreting, then all the particulate material, or 2275 kcal m^{-2} yr^{-1} (Table 8), would have been exported from the marsh. On the other hand, if no export of particulate material were occurring, then the marsh would have been accreting an average of 4 mm of sediment each year; this calculation assumes that the newly accreted sediment has the same organic content as the existing sediment (25%), that the density of the sediment is 0.6 g dry wt cm^{-3} (R. A. Linthurst, Department of Botany, North Carolina State University, Raleigh), and that 1 g of accreted organic matter is the equivalent of 3.7 kcal (overall marsh average). Accretion in a Long Island salt marsh was estimated to be 2.0-4.25 mm yr^{-1} (Richard, 1978) and if the accretion rate in Walden Creek marsh were near the upper end of this range, then export of particulate matter from the marsh would be minimal. Export of material from Walden Creek (Pendleton, 1979) was equivalent to 8911 kcal m^{-2} of marsh as DOC and 466 kcal m^{-2} of marsh as particulate carbon, but these amounts do not necessarily represent export from the marsh for two reasons: 1) some of the material exported from the marsh is undoubtedly metabolized or retained in Walden Creek itself without ever being exported from the creek; and 2) there is probably additional input of material to Walden Creek from upstream pocosin and forest areas (Pendleton, 1979). In the case of DOC, in particular, release from the marsh was estimated to be 1086 kcal m^{-2} (Table 8), much less than the amount actually exported from Walden Creek.

Potential export of material from Walden Creek marsh was similar to that estimated for marshes in Georgia (Teal, 1962) and Louisiana (Day et al., 1973). Potential export from Walden Creek marsh was estimated to be 42% of net production, as compared to 45% in Georgia and 50% in Louisiana, but the similarity of these values is misleading. The Georgia and Louisiana studies did not consider belowground production and therefore underestimated net production of the marshes; since export was calculated by subtracting faunal and microbial respiration from net production, the result was an underestimate of potential export equal to the underestimate in net production. Comparison between the marshes is further complicated by large differences in estimated microbial and faunal respiration. Despite having similar aboveground production (kcal m^{-2} yr^{-1})--Walden Creek, 6331; Georgia, 8205; Louisiana, 6948 [assuming organic matter is 50% C and 9 kcal $(g\ C)^{-1}$]--microbial and faunal respiration was much greater in Walden Creek marsh (4626 kcal m^{-2} yr^{-1}) than in Georgia (3090, excluding planktonic respiration) or Louisiana (3393, assuming organic matter is 50% C and 9 kcal $(g\ C)^{-1}$). We measured respiration directly throughout the year (Blum et al., 1978), while the Georgia value was based on only one measurement in each of the three different marsh areas (Teal and Kanwisher, 1961) and the Louisiana value was obtained by estimating faunal respiration and assuming the same ratio between faunal and microbial respiration as found in Georgia. It is unlikely that microbial and faunal respiration was actually less in the Georgia and Louisiana marshes than in Walden Creek and,

therefore, we feel that respiration was underestimated in the previous studies. If we assume that the ratio between aboveground and belowground production was similar for all three marshes and that our respiration values would apply to all three marshes, then potential export would be 42-55% of net production. Most export probably comes from aboveground material and these figures are equivalent to an export of 53-70% of the aboveground production.

We have not included energy transfer through the anaerobic processes of denitrification (respiration of organic matter using nitrate as the terminal electron acceptor) and sulfate reduction (respiration of organic matter using sulfate as the terminal electron acceptor). Denitrification has been measured for a Massachusetts salt marsh and accounted for the respiration of less than 0.1% of the belowground production (Kaplan et al., 1979). Sulfate reduction results in the production of reduced end-products such as H_2S which diffuse toward the surface where they are oxidized; if a steady-state exists in the marsh, with all the reduced end-products eventually being oxidized at the sediment surface, then measurement of oxygen consumption by the sediment (as in this study) would give an estimate of energy flow including both the organic matter respired anaerobically by sulfate reduction and that respired aerobically. Sulfate reduction was the main pathway for organic matter decomposition in the Massachusetts salt marsh, possibly accounting for all the belowground production (Howarth and Teal, 1979). In addition, as much as one-third of all the reduced end-products may have moved through the sediment to tidal creeks where it was exported from the marsh system (Howarth and Teal, 1979). Since belowground production in Walden Creek marsh (Table 3) was much less than in the Massachusetts marsh (Valiela et al., 1976), we could predict that sulfate reduction would also be less. However, it is not possible to predict the proportion of reduced end-products that might be exported from the marsh in the waters of Walden Creek since we have no knowledge of the flow through the marsh sediment.

Since there were a variety of sources of organic material available to the organisms in the marsh, including imported material, it was not possible to determine the exact fate of the primary production of the marsh. It is necessary to think of the animals as consuming the "equivalent" of some portion of the net production, since an unknown fraction of this material may have been phytoplankton or suspended detritus carried into the marsh with the tide. In addition, estimates of transport of material into or out of marshes actually are estimates of net transport, only. It is possible in a system such as Walden Creek marsh that much of the aboveground production could actually be exported from the marsh but replaced by an equivalent amount of imported material from upstream; net export would be zero, but also a poor measure of the functioning of the system. This problem is important because the material leaving the marsh may be younger and less refractory, and thus more nutritious, than the older material entering the marsh. Even though the marsh did not appear to be important quantitatively in the carbon budget of Walden Creek, the material coming from the marsh may be increasing the quality of the food supply for estuarine detritivores. Indeed, the fact that it is difficult to find evidence of Spartina detritus in the waters surrounding Georgia marshes using isotopic ratios (Haines, 1977) may actually be an indication of how rapidly the exported material is being utilized. This effect may be especially significant in Walden Creek, itself, where a large export of energy

to the Cape Fear Estuary in the form of juvenile shrimp and fish is supported (Laney, in preparation; Pendleton, 1979).

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APPENDIX

Section I. Calculation of Ecosystem Respiration and Primary Production

The data used to estimate ecosystem respiration and primary production in this paper were used previously by Blum et al. (1978). Since we wished to treat the data in a slightly different manner, we have presented the original data here (Appendix Table 1); these data were the basis of Table 7 in Blum et al. (1978).

Ecosystem respiration

A major difficulty of the method used by Blum et al. (1978) to partition sediment respiration from aboveground respiration, pouring a layer of vegetable oil onto the marsh surface, was the failure of that oil to completely seal the surface. Approximately 36 ± 16% of sediment respiration was estimated to escape through the oil seal; thus, aboveground ecosystem respiration was overestimated and sediment respiration was underestimated. We attempted to correct for this error as follows:

Let the quantities actually measured be total ecosystem respiration (Rs_E) and aboveground respiration (Rs_{SC}); sediment respiration (Rs_S) was calculated as the difference between the two. Although the values for ecosystem respiration are correct, those for aboveground and sediment respiration differ from the true values (Rs_{SC}^* and Rs_S^*) due to the inclusion of 36% of sediment respiration as aboveground respiration. Thus

$$1) \quad Rs_{SC} = Rs_{SC}^* + 0.36\ Rs_S^*$$

and

$$2) \quad Rs_E = Rs_{SC}^* + Rs_S^* .$$

Therefore

$$3) \quad Rs_S^* = (Rs_E - Rs_{SC})/0.64$$

and

$$4) \quad Rs_{SC}^* = Rs_E - Rs_S^* .$$

Using Eq. 3 and 4, we have recalculated the original data in Appendix Table 1 to estimate the true values for aboveground and sediment respiration given in Appendix Table 2. We treated light and dark periods separately and assumed that aboveground respiration in the light was negligible since Spartina is a C_4 plant (Black, 1973). As an example, the calculations for Feb. 16 in the short Spartina area were:

Light $Rs^*_S = (0.69 - 0.33)/0.64 = 0.56$

$Rs^*_{SC} = 0.00$ (by assumption)

Dark $Rs^*_S = (0.57 - 0.27)/0.64 = 0.47$

$Rs^*_{SC} = 0.57 - 0.47 = 0.10$

Total $Rs^*_S = 0.56 + 0.47 = 1.03$ g C m^{-2} day^{-1}

$Rs^*_{SC} = 0.00 + 0.10 = 0.10$ g C m^{-2} day^{-1}.

Primary production

In order to estimate ecosystem gross production (GPP), it was necessary to correct the quantity actually measured, net ecosystem photosynthesis (NEP_S), for ecosystem respiration during the measurement. Since the measurements were carried out in the light, we assume there was no aboveground respiration.

Therefore

$$5) \quad GPP = NEP_s + Rs^*_{S(light)}.$$

The calculated values of daily gross production are presented in Appendix Table 2. As an example, the calculation for Feb. 16 in the short Spartina area was:

$$GPP = 0.80 + 0.56 = 1.36 \text{ g C } m^{-2} \text{ day}^{-1}.$$

Seasonal and annual totals

The daily values of gross production, aboveground and sediment respiration were multiplied by the appropriate number of days in the season [winter (Feb. 16), 90; spring (Apr. 19), 92; summer (Jul. 18), 94; and fall (Nov. 3), 89] to give seasonal totals (Appendix Table 3). These seasonal totals were summed to give annual totals which were then converted from g C to kcal by multiplying by the appropriate conversion factor (short, 9.44; medium, 8.52; and tall, 8.98; calculated from factors given in Blum et al., 1978, for converting g C to g dry weight and g dry weight to cal).

Section II. Calculation of Belowground Spartina Respiration

Although it was possible to partition aboveground Spartina respiration from total aboveground respiration by subtracting the estimated contribution of aboveground fauna (Table 2), a corresponding treatment of the sediment respiration data in order to estimate belowground Spartina respiration was not

possible because we had no independent figures for sediment faunal and microbial respiration. Therefore, we attempted to estimate belowground Spartina respiration from aboveground respiration.

Aboveground respiration in the dark accounted for 59% of the total respiration of short Spartina in a Georgia marsh (Teal and Kanwisher, 1961, 1966); in the light aboveground respiration is assumed to be negligible in Spartina since it is a C4 plant (Black, 1973), but belowground respiration should proceed at the same rate in the light and in the dark (assuming other extrinsic variables such as temperature are unchanged). If we let Rs_{ABOVE} be the total aboveground respiration during the average 12-hour dark period and Rs_{BELOW} be the total belowground respiration during the same period, then respiration during the dark (Rs_{DARK}) will be

$$6) \quad Rs_{DARK} = Rs_{ABOVE} + Rs_{BELOW} .$$

Respiration during the light period will be belowground only and the belowground rate will be the same as during the dark, so

$$7) \quad Rs_{LIGHT} = Rs_{BELOW} .$$

For the entire day, respiration (Rs_{TOT}) will be

$$8) \quad Rs_{TOT} = Rs_{DARK} + Rs_{LIGHT} = R_{ABOVE} + 2 \cdot Rs_{BELOW} .$$

From Teal and Kanwisher's experiments and Eq. 6:

$$9) \quad Rs_{ABOVE}/Rs_{DARK} = Rs_{ABOVE}/(Rs_{ABOVE} + Rs_{BELOW}) = 0.59 .$$

Combining Eq. 8 and 9 we can determine the fraction aboveground respiration makes up of the entire daily respiration:

$$10) \quad Rs_{ABOVE}/(Rs_{ABOVE} + 2 \cdot Rs_{BELOW}) = 0.42 .$$

In Walden Creek the aboveground portion of short Spartina accounted for 27% of the total biomass (Seneca et al., 1976). If we assume the biomass ratio was similar in Georgia, then the aboveground portion of the short Spartina accounted for 42% of the daily respiration while making up only 27% of the biomass; similarly, the belowground portion accounted for 58% of the respiration and 73% of the biomass. We can compare the relative rate of respiration of the aboveground to belowground Spartina by comparing the respiration:biomass (R:B) ratios. For the aboveground portion, R:B is 42:27 or 1.56:1; for the belowground portion, R:B is 58:73 or 0.79:1. Assuming that these same R:B ratios hold for medium and tall Spartina tissue as well, we can calculate the distribution of respiration between aboveground and belowground portions simply by knowing the distribution of biomass. In medium Spartina areas in Walden Creek, aboveground biomass accounts for 49% of the total and belowground for 51%. The portion of respiration accounted for by the aboveground portion will be

$$(1.56 \cdot 0.49)/(1.56 \cdot 0.49 + 0.79 \cdot 0.51) = 0.65 .$$

Similarly, for tall Spartina, where aboveground biomass is 77% of the total, aboveground respiration will account for

$$(1.56 \cdot 0.77)/(1.56 \cdot 0.77 + 0.79 \cdot 0.23) = 0.87$$

of the total. For the three height-forms of Spartina, then, the portion of total respiration accounted for by the aboveground portion of the plants is: short, 42%; medium, 65%; and tall, 87%. The ratio of aboveground to belowground respiration for the three height-forms is: short, 0.72:1; medium, 1.87:1; and tall, 6.53:1.

Appendix Table 1. Calculated carbon exchange data for net ecosystem photosynthesis (NEP_s), ecosystem respiration (Rs_E) during light and dark periods, and aboveground respiration (Rs_{SC}) during light and dark periods in g C m^{-2} day^{-1} for Walden Creek marsh. These data were used to construct Table 7 in Blum et al. (1978).

Date	Spartina type	NEP_s	Rs_E		Rs_{SC}	
			Light	Dark	Light	Dark
Feb 16	Short	0.80	0.69	0.57	0.33	0.27
Apr 19	"	2.50	0.73	0.17	0.35	0.07
Jul 18	"	0.19	2.36	1.62	1.56	0.94
Nov 3	"	1.33	0.94	0.09	0.42	0.00
Feb 16	Medium	1.85	1.26	1.24	0.88	0.91
Apr 19	"	3.81	1.89	0.97	1.26	0.78
Jul 18	"	2.42	3.85	2.88	2.81	2.00
Nov 3	"	2.73	1.79	1.01	1.09	0.65
Feb 16	Tall	2.60	2.17	2.31	1.69	1.86
Apr 19	"	4.36	2.35	1.36	1.37	0.88
Jul 18	"	3.56	4.82	3.70	3.45	2.55
Nov 3	"	3.43	2.19	1.49	1.75	1.43

Appendix Table 2. Calculated carbon exchange data for aboveground (Rs^*_{SC}) and aboveground (Rs^*_S) respiration during light and dark periods and gross primary production (GPP) in g C m^{-2} day^{-1} for Walden Creek marsh.

Date	Spartina type	Light		Dark		Total		GPP
		Rs^*_{SC}	Rs^*_S	Rs^*_{SC}	Rs^*_S	Rs^*_{SC}	Rs^*_S	
Feb 16	Short	0.00	0.56	0.10	0.47	0.10	1.03	1.36
Apr 19	"	0.00	0.59	0.01	0.16	0.01	0.75	3.09
Jul 18	"	0.00	1.25	0.56	1.06	0.56	2.31	1.44
Nov 3	"	0.00	0.81	0.00	0.09	0.00	0.90	2.14
Feb 16	Medium	0.00	0.59	0.72	0.52	0.72	1.11	2.44
Apr 19	"	0.00	0.98	0.67	0.30	0.67	1.28	4.79
Jul 18	"	0.00	1.63	1.50	1.38	1.50	3.01	4.05
Nov 3	"	0.00	1.09	0.45	0.56	0.45	1.65	3.82
Feb 16	Tall	0.00	0.75	1.61	0.70	1.61	1.45	3.35
Apr 19	"	0.00	1.53	0.61	0.75	0.61	2.28	5.89
Jul 18	"	0.00	2.14	1.90	1.80	1.90	3.94	5.70
Nov 3	"	0.00	0.69	1.40	0.09	1.40	0.78	4.12

Appendix Table 3. Annual and seasonal totals for gross primary production (GPP), aboveground (Rs^*_{SC}), and belowground (Rs^*_S) respiration calculated from daily values (Table 2) assuming winter, spring, summer, and fall have 90, 92, 94, and 89 days, respectively. Conversion factors for kcal per g C for the three marsh areas were: short: 9.44; medium, 8.52; and tall, 8.98. Overall totals take into account the extent of each height-form in Walden Creek marsh.

Season	Spartina type	GPP	Rs^*_{SC}	Rs^*_S
Winter (Feb 16)	Short	122.4	9.0	92.7
Spring (Apr 19)	"	284.3	0.9	69.0
Summer (Jul 18)	"	135.4	52.6	217.1
Fall (Nov 3)	"	190.5	0.0	80.1
Total (g C m^{-2})	"	732.6	62.5	458.9
Total (kcal m^{-2})	"	6916	590	4332
Winter (Feb 16)	Medium	219.6	64.8	99.9
Spring (Apr 19)	"	440.7	61.6	117.8
Summer (Jul 18)	"	380.7	141.0	282.9
Fall (Nov 3)	"	340.0	40.1	146.9
Total (g C m^{-2})	"	1381.0	307.5	647.5
Total (kcal m^{-2})	"	11766	2620	5517
Winter (Feb 16)	Tall	301.5	144.9	130.5
Spring (Apr 19)	"	541.9	56.1	209.8
Summer (Jul 18)	"	535.8	178.6	370.4
Fall (Nov 3)	"	366.7	124.6	69.4
Total (g C m^{-2})	"	1745.9	504.2	780.1
Total (kcal m^{-2})	"	15678	4528	7005
Overall total (kcal m^{-2})		11386	2509	5519