Reports

Water Uptake by Roots Controls Water Table Movement and Sediment Oxidation in Short *Spartina* Marsh

Abstract. *Downward movement of the water table during both day and night in the short grass zone of intertidal salt marshes is due not to drainage but to water uptake by roots. Removal of water from the sediment results in the entry of air into the sediment, suggesting a feedback between plant growth, water uptake, and sediment oxidation. The water balance of* Spartina alterniflora *appears to influence the internal morphology of its roots, potentially giving rise to a new mechanism for the mass flow of gas in plants.*

Salt marshes are considered to be among the world's most productive natural plant communities (*1*). Factors controlling the productivity of the dominant marsh grass *Spartina alterniflora* have been a major focus for research. Plants along the banks of natural and man-made creeks tend to be taller (more productive) than those away from creeks, with the difference most likely due to accelerated drainage of interstitial water. The relation between plant production and drainage has been variously explained by the periodic tidal flushing of sediment water transporting nutrients to the roots, oxidizing the sediment, or exporting toxic end products of bacterial metabolism (*2*).

The surface of the short grass marsh is typically inundated for several hours a day during spring tides, and somewhat more briefly and irregularly during neap tides. The floodwater infiltrates into the sediment and saturates interstitial pore spaces. Interstitial water drains from the tall grass zone along creek banks at low tide, but there are discrepancies in the literature about what occurs in the large expanse of short grass marsh farther than a few meters from creeks. Earlier workers in Great Sippewissett Marsh, Massachusetts, have reported both downward pore-water drainage (*3*) and upward ground-water intrusion in the short grass zone (*4*). In contrast, investigators studying systems in Massachusetts, South Carolina, and Georgia inferred, on the basis of temperature and geochemical profiles, that pore water in the short *S. alterniflora* marsh is stagnant (*5*). The role of plants in determining the movement of sediment water has not been defined. As far as we know, our research represents the first attempt to evaluate the role of evapotranspiration in determining sediment pore-water movement in intertidal marshes (*6*).

Our experiments were conducted during summer months at four sites in Great Sippewissett Marsh, Falmouth, Massachusetts, between May 1981 and July 1983, and at one site near Gardner's site (*5*) at the Belle W. Baruch Institute, Georgetown, South Carolina, in August 1982. We found no measurable drainage in the short grass marsh; virtually all the drop in the water table is due to evapotranspiration. We measured the rate of evapotranspiration by monitoring the drop in the water table in lysimeters during low tide (*7*). Our lysimeters consisted of 22-liter sections of vegetated sediment collected with a sharpened fiber glass tube (26.3 cm inside diameter, 100 cm long) and extruded directly into watertight fiber glass tubs (40 cm deep, 26.3 cm inside diameter). Each lysimeter was placed in the hole from which the core had been removed so that the grass was exposed to the same wind and thermal regime as the surrounding marsh. Since the lysimeters were sealed at the bottom, the only pathway for water loss was to the atmosphere. Since there was no significant difference in the rate of water loss from lysimeters and from the surrounding marsh (Fig. 1) (*8*), drainage must therefore be negligible. These results may be generalizable to the short *S. alterniflora* zone in other marshes since the two marshes studied have widely divergent sediment characteristics (0 to 30 cm of organic matter: Sippewissett, ~ 50 percent; Baruch, ~ 20 percent).

Typically, evapotranspiration from plant communities is maximum at midday (*9*). However, the water table in lysimeters dropped at night, even while

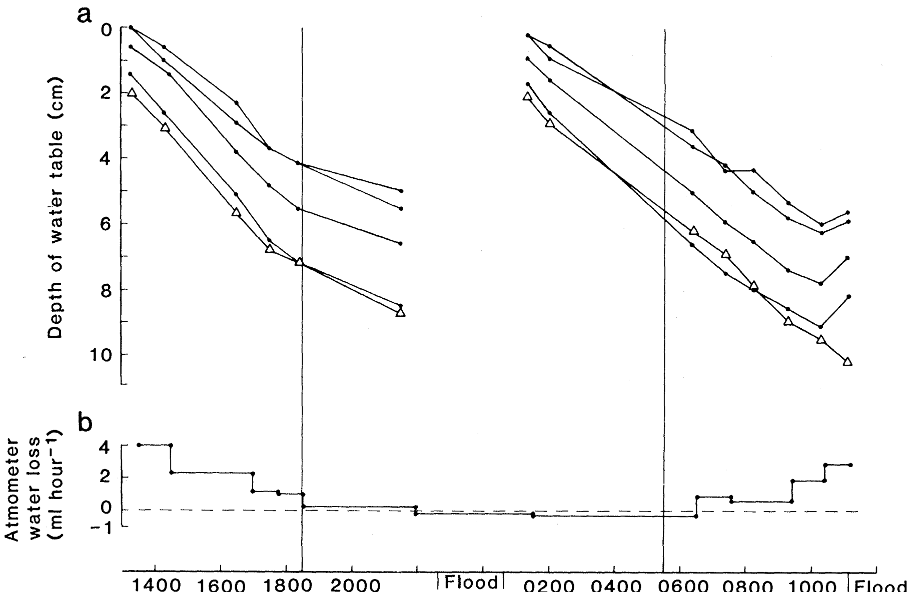

Fig. 1. (a) Drop in the water table in lysimeters (△—△) and in the adjacent marsh (•—•) during low tide. The sediment was saturated by a flood tide during late morning on the first day, at midnight, and again at the end of the run. The water table dropped more slowly at night, probably because of dew formation and lower water uptake by *S. alterniflora*. Shortly before the flood tide (1106 hours), the water table began to rise in control wells but continued to drop in the lysimeters until flooded by surface water. These data are representative of water table movement in all of our runs (more than 50 daytime and 11 night runs). Rates varied about twofold from day to day (on sunny days) and about fourfold from site to site depending on grass biomass. (b) Potential water loss from the marsh surface as measured with a porous porcelain atmometer.

dew was forming on the marsh surface (as represented by negative atmometer readings in Fig. 1). Since lysimeters do not allow drainage, the nighttime drop in the water table must be due to water uptake by the plants. In laboratory experiments, *S. alterniflora* absorbed water at nearly the maximum rate for roughly 6 hours after transpiration had ceased, and at measurable rates for at least 16 hours (Fig. 2) (*10*). Our observation that root water uptake occurs 24 hours a day (Fig. 1) has important implications for marsh biogeochemistry. For example, earlier workers mistakenly concluded that, since evapotranspiration is negligible at night, the nighttime drop in the water table must represent downward drainage (*3*).

We conducted laboratory and field experiments to quantify how much water must be removed from the sediment to yield a given drop in the water table (*11*). Even though these sediments are "waterlogged" (water occupies 75 to 90 percent of the sediment volume), the specific yield of water from this sediment is only 2 to 3 percent. Twelve hours after draining a core section, 97 percent of the sediment water remained above the water table. Therefore a drop of 6 cm in the water table between flooding tides in short grass areas of Great Sippewissett Marsh corresponds to a water loss of about 2 liter m^{-2} (4 liter m^{-2} day^{-1}).

Since we measured no change in sediment volume in lysimeters as water was removed, each volume of water removed from the sediment must have been replaced by an equal volume of air. Air entry was corroborated by the rapid rise in the sediment redox potential (*Eh*) in the top 3 cm of the sediment as water was removed (*12*). This suggests that air enters in fairly well-defined channels, which may represent a major mechanism for increasing sediment *Eh* and plant production in drainage experiments (*2*).

The strong correlation between aboveground biomass and sediment *Eh* has led a number of researchers to hypothesize that increased drainage allows increased oxidation of the sediment, thereby increasing plant production (*2, 12*). We propose that the obverse is also true: increased plant production leads to greater water table fluctuation ("drainage"). At sites where plant production has been increased through nitrogen fertilization (*13*), evapotranspiration (root water uptake) was higher, the water table drop was greater, and the sediment was more oxidized than in the adjacent control marsh (*12*). This suggests a potential positive feedback: increased water uptake by plants results in increased air entry into the sediment, increasing sediment oxidation and plant production.

Plant-water relations also appear to affect the ability of plants to transport O_2 internally, which is an adaptation in marsh grass for life in the anaerobic sediment (*14*). We propose that the dynamics of root water uptake and transpiration directly impact the ability of the plants to achieve that transport. Typical amounts of water uptake at night in Great Sippewissett Marsh (about 2 liter m^{-2}; Fig. 1) suggest that the plants lost about 20 percent of their tissue water during daylight (*15*). We have measured diurnal changes in the water content of shoots to be no more than 1 to 2 percent in Massachusetts and South Carolina. Therefore, the water deficit is not in leaves but in roots and rhizomes. In terrestrial plants water deficit has been accompanied by root shrinkage, and water uptake by increased root volume (*16*). Since we measured a drop in the water table at night while there was no evapotranspiration (Fig. 1 and 2) and no measurable change in the volume of the sediment, water was taken up by roots without changing their external diameter. Therefore, the absorbed water must be replenishing some internal reservoir (presumably root parenchyma), causing it to expand into lacunar gas spaces (aerenchyma) in the roots (*17*).

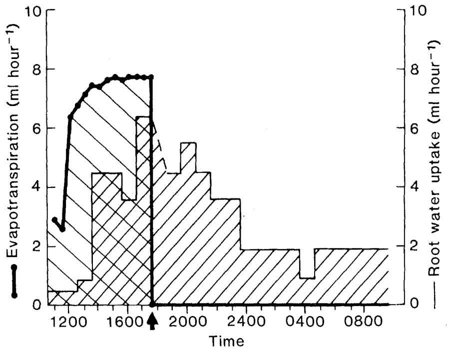

Fig. 2. Evapotranspiration and root water uptake in *S. alterniflora*. Water uptake in the laboratory continued after transpiration had ceased. Evapotranspiration was measured in a flow-through polyethylene chamber sealed over a lysimeter. Dry room air was pumped into the chamber, and the dew point of effluent air was measured to calculate evapotranspiration. Water loss from the sediment was measured by monitoring the water table (*11*). After 7 hours (arrow), transpiration was stopped by turning off the lights and sealing the chamber. Water continued to be removed from the sediment until the end of the experiment. The total evapotranspiration during the first 7 hours was 47 ml. Water uptake was 25 ml during the first 7 hours and 59 ml during the experiment. The discrepancy is most likely due to a plant water deficit that existed before the experiment was begun. This pattern is representative of water table movement in six separate experiments.

This change in lacunar volume gives rise to a previously undescribed mechanism for the mass flow of air in plants. As the water deficit in the plant tissue develops during daylight there must be a mass flow of air into the plants, and a mass flow out as the water deficit diminishes at night. This mass flow should equal the water deficit (that is, 2 liter m^{-2}). We estimate that the plant lacunar volume in short grass is 9 to 15 liter m^{-2}, so lacunar volume changes about 15 to 20 percent diurnally. We do not know the significance of this mass flow in delivering O_2 to the roots; it may be more important that increased lacunar cross-sectional area decreases the resistance to the diffusive transport of O_2. Both mechanisms accelerate O_2 transport to the roots and are bound to be important in root aeration.

Aside from the physiological aspects of this work, our observations have profound implications for the interpretation of the biogeochemistry of short *S. alterniflora* marshes and probably tidal marshes in general. For example, it has long been held that marshes import nutrients and export organic matter to the estuaries and ocean. However, most of the productivity of this ecosystem goes into belowground biomass (*1*), which can only be exported in dissolved form, either as dissolved organic carbon or reduced sulfur compounds (*3*). Our observation of negligible pore-water drainage in the short *Spartina* zone implies that very little export of dissolved compounds is possible from this part of the marsh.

JOHN W. H. DACEY
Biology Department,
Woods Hole Oceanographic Institution,
Woods Hole, Massachusetts 02543
BRIAN L. HOWES*
Boston University Marine Program,
Marine Biological Laboratory,
Woods Hole, Massachusetts 02543

References and Notes

1. R. E. Turner, *Contrib. Mar. Sci.* **20**, 47 (1976); R. E. Good, N. F. Good, B. R. Frasco, in *Estuarine Comparisons*, V. S. Kennedy, Ed. (Academic Press, New York, 1982), pp. 139–157.
2. M. L. Shea, R. S. Warren, W. A. Niering [*Ecology* **56**, 461 (1975)] found that tall (creek bank) and short *S. alterniflora* are genetically identical and that growth differences are due to habitat. A variety of growth-regulating mechanisms have been proposed, all of which are directly impacted by interstitial water movement. These include the following: drainage: J. K. Shisler and D. M. Jobbins, *Mosq. News* **37**, 631 (1977); R. G. Wiegert, A. G. Chalmers, P. F. Randerson, *Oikos* **41**, 1 (1983); water table depth: I. A. Mendelssohn and E. D. Seneca, *Estuarine Coastal Mar. Sci.* **11**, 27 (1980); B. L. Howes, R. W. Howarth, J. M. Teal, I. Valiela, *Limnol. Oceanogr.* **26**, 350 (1981); sediment redox potential: B. L. Howes *et al.*, *ibid.*; I. A. Mendelssohn, K. L. McKee, W. H. Patrick, Jr., *Science* **214**, 439 (1981); aeration: R. A. Linthurst, *Am. J. Bot.* **66**, 685 (1979); H_2S and oxidized iron input: G. M. King, M. J. Klug, R. G. Wiegert, A. G. Chalmers, *Science* **218**, 61 (1982); sediment salinity: B. L. Haines and E.

Dunn, *Bot. Gaz. (Chicago)* **137**, 224 (1976); J. Nestler, *Estuarine Coastal Mar. Sci.* **5**, 707 (1977); A. J. Cavalieri and A. H. C. Huang, *Oecologia (Berlin)* **49**, 224 (1981); R. M. Smart and J. W. Barko, *Ecology* **61**, 630 (1980); tidal pumping: E. P. Odum, J. T. Finn, E. H. Franz, *BioScience* **29**, 349 (1979).

3. R. W. Howarth and J. M. Teal [*Am. Nat.* **116**, 862 (1980)] estimated pore-water drainage to be 52 liter m^{-2} day^{-1}. Subsequently R. W. Howarth, A. Giblin, J. Gale, B. J. Peterson, G. W. Luther III [*Ecol. Bull. (Stockholm)* **35**, 135 (1983)] estimated drainage to be 13 liter m^{-2} day^{-1}. Their value was based on differences in water table movement between day and night and was used to calculate export of reduced sulfur compounds. R. W. Howarth and J. E. Hobbie [in *Estuarine Comparisons*, V. S. Kennedy, Ed. (Academic Press, New York, 1982), pp. 183–207] calculated the export of dissolved organic carbon on the basis of a drainage of 13 liter m^{-2} day^{-1}.
4. H. F. Hemond and J. L. Fifield, *Limnol. Oceanogr.* **27**, 126 (1982). Our data suggest that, if such upward transport occurs, it occurs only during the few minutes preceding the surface flooding of the marsh (Fig. 1). Tidal water, rainfall, and ground-water intrusion are major components of water recharge to the sediment.
5. A. C. Redfield, paper presented at the Salt Marsh Conference, Marine Institute, University of Georgia, Athens, 1959; L. R. Gardner, *Southeast. Geol.* **15**, 17 (1973); J. Nestler, *ibid.* **18**, 265 (1977); C. H. Riedeberg, thesis, University of Georgia, Athens (1977); L. R. Pomeroy and J. Imburger, in *The Ecology of a Salt Marsh*, L. R. Pomeroy and R. G. Wiegert, Eds. (Springer-Verlag, New York, 1981), pp. 21–36.
6. J. M. Teal and J. W. Kanwisher [*Ecology* **51**, 690 (1970)] reported transpiration rates in chambers at midday. J. R. Giurgevich and E. L. Dunn [*Oecologia (Berlin)* **43**, 139 (1979)] measured transpiration in laboratory cultures. These data cannot be extrapolated for use in a field water budget.
7. Lysimeters are a standard tool for measuring evapotranspiration in terrestrial systems. We used a 100-cm core tube (to avoid damage to leaves) to remove a 40-cm core. More than 95 percent of the root biomass is in the top 20 cm of sediment in Great Sippewissett Marsh (*13*). The lysimeters have a valve at the base to vent air while the core is being transferred. Initial sediment compression during coring was less than 0.3 cm, followed within hours by gradual rebound. No measurements were taken until 24 hours after the lysimeters were filled. Lysimeters have been monitored periodically weeks and months after placement in the marsh. We measured the drop in the water table with wells (polyvinyl chloride pipe, 0.95 cm inside diameter, 1.3 cm outside diameter, 40 cm long, open at a depth of 27 to 30 cm). The depth of the water table was recorded when two electrical contacts at the end of a graduated glass rod contacted the water surface. Readings were reproducible to 0.1 cm. We used boardwalks to approach wells and made measurements within 10 seconds of approaching the well. In one experiment we prolonged high tide by damming a creek. The water table did not move down in control wells but moved down in lysimeters at the normal rate, confirming that the lysimeters did not leak.
8. Data are water loss by water table drop in lysimeters and in adjacent marsh. For Great Sippewissett Marsh, $P = 0.76$ (paired *t*-test), $N = 38$, June through September; for Baruch, $P = 0.52$ (*t*-test), $N = 13$ (five lysimeters, eight wells) over 3 days at one site, August 1982. The water table drop in lysimeters was 7 ± 6 percent (± standard error) greater than in an adjacent marsh in Great Sippewisset Marsh.
9. We measured evapotranspiration in the field during July 1982 under a flow-through chamber and found that the maximum rate occurred at 1400 hours. The diurnal pattern of water loss paralleled that of a terrestrial grass community [C. H. M. van Bavel, L. J. Fritschen, W. E. Reeves, *Science* **141**, 269 (1963)].
10. Delayed water uptake should occur whenever plants develop a water deficit [P. J. Kramer, *Water Relations of Plants* (Academic Press, New York, 1983)].
11. Known volumes of water were drained from laboratory lysimeters (21.2 cm inside diameter, 40 cm deep), and the change in the water table was measured when the head pressure measured by a pressure transducer at the base reached steady state (usually 30 to 45 minutes). We confirmed this estimate of specific yield by measuring the amount of water required to bring the water table to the sediment surface in field lysimeters.
12. In three separate laboratory experiments we measured a rapid (100 to 300 mV) rise in redox potential in 47 percent of the platinum electrodes ($N = 17$) placed in the top 3 cm of sediment. This, together with the lack of sediment collapse, suggests that air was drawn into the sediment as water was removed by roots. Higher transpiration should lead to greater air entry and therefore more oxidized sediments (B. Howes and J. Dacey, in preparation). This may explain the correlation between sediment *Eh* and fertilization observed by Howes *et al.* [see (*2*)]. The water table typically falls 4 to 8 cm during low tide in Great Sippewissett Marsh and more than 2 cm at our site in Baruch Marsh. At Baruch, the water table drop between flood tides was less because water tended to pool on the surface. However, it was more than 20 cm deep after 5 to 6 days without a flood tide even though 5 cm of rain had fallen during that time.
13. I. Valiela, J. M. Teal, N. Y. Persson, *Limnol. Oceanogr.* **21**, 245 (1976).
14. J. M. Teal and J. W. Kanwisher, *J. Exp. Bot.* **17**, 355 (1966).
15. Plant biomass at this site is about 2.4 kg m^{-2} (dry weight); water content averages about 82 percent of fresh weight in belowground tissue and about 70 percent in shoots. This suggests that the volume of plant water at the study site (Fig. 1) was about 10 liter m^{-2}.
16. M. G. Huck, B. Klepper, H. M. Taylor, *Plant Physiol.* **45**, 529 (1970).
17. M. F. Aston and D. W. Lawlor [*J. Exp. Bot.* **30**, 169 (1979)] concluded that water storage in roots smooths fluctuations in the water supply in leaves. We propose that in *S. alterniflora* water loss from root parenchyma increases the volume of aerenchyma, which occupies about 60 percent of the roots of marsh grass [J. W. H. Dacey, *Oceanus* **24** (No. 2), 43 (1981)].
18. Publication 5533 of Woods Hole Oceanographic Institution. Supported by NSF grants BSR-8021741, BSR-8004701, BSR-7905127, and BSR-8119819. We thank the Belle W. Baruch Institute and J. M. Teal and I. Valiela for use of their experimental plots.

* Present address: Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Mass. 02543.

31 October 1983; accepted 1 March 1984

Ocean Circulation: Its Effects on Seasonal Sea-Ice Simulations

Abstract. *A diagnostic ice-ocean model of the Arctic, Greenland, and Norwegian seas is constructed and used to examine the role of ocean circulation in seasonal sea-ice simulations. The model includes lateral ice motion and three-dimensional ocean circulation. The ocean portion of the model is weakly forced by observed temperature and salinity data. Simulation results show that including modeled ocean circulation in seasonal sea-ice simulations substantially improves the predicted ice drift and ice margin location. Simulations that do not include lateral ocean movment predict a much less realistic ice edge.*

The growth, drift, and decay of sea ice are closely related to the circulation of polar oceans. This is especially true in the Greenland and Norwegian seas in winter where warm currents flowing northward encounter rapidly cooling atmospheric conditions together with sea ice advancing southward. In earlier work on modeling the seasonal cycle of Arctic sea ice, the ocean has been approximated by a motionless mixed layer of fixed depth (*1, 2*) with possibly a small constant heat flux from the deeper ocean, and more recently by a one-dimensional mixed layer of variable thickness (*3*). This approach has also been used in most global-climate-model sensitivity studies of the effect of increasing atmospheric carbon dioxide.

In this report we examine the dominant effects of a more realistic treatment of the three-dimensional ocean circulation on seasonal sea-ice simulations. For this purpose we have constructed an ice-ocean model and used it to carry out a series of seasonal simulations of the Arctic, Greenland, and Norwegian seas. The results show that including the ocean circulation yields first-order improvements in the predicted ice margin location and in the ice velocity fields. Moreover, this improvement in the ice margin prediction requires inclusion of the full three-dimensional circulation of the ocean.

Our basic approach in this study was to couple an existing dynamic thermodynamic sea-ice model (*2, 5*) with a multilevel baroclinic ocean model (*6*). The sea-ice model supplies heat flux, salt flux, and momentum-exchange boundary conditions for the top of the ocean. The ocean model, in turn, supplies current and heat-exchange information to the ice model. Since our main concern here is examining the effect of ocean circulation on sea ice, mean annual observed oceanic temperature and salinity data (*7*) are used to weakly force the ocean model (all terms that are externally specified "force" the model) so that its equilibrium time scale is similar to that of the ice model (3 to 5 years). This "diagnostic" (*8*) method allows the ocean model to be relaxed to available climatological ocean data, while at the same time allowing considerable adjustment in the upper ocean as a result of the effects of ice-ocean interaction. In addition, the barotropic mode of the ocean is fully simulated so that time-varying currents due to surface stress fluctuations are part of the model predictions.

The details of the coupling may be outlined as follows. The sea-ice model of Hibler (*2, 5*) is used to calculate ice drift, thickness, and compactness. We determined the momentum transfer from the ocean to the ice (i) by using the ocean velocity at the second level as the ocean current in the ice calculations (the first ocean level of 30-m thickness is a de facto mixed layer) and (ii) by allowing the surface-pressure term in the rigid-lid