The Influence of Soil Salinity, Growth Form, and Leaf Moisture on the Spectral Radiance of Spartina alterniflora Canopies

Changes in the spectral radiance of salt marsh canopies were correlated with biomass, leaf moisture, and soil salinity.

Introduction

S ALT MARSHES dominated by Spartina alterniflora Loisel. extend along the eastern United States from Maine to Florida (Reimold, 1977). This ubiquitous marsh plant also occupies a wide elevational range within the salt marsh. Inundation frequency (elevation) alters edaphic conditions and fosters differential growth by S. alterniflora. The different height forms of S. alterniflora have been attributed to elevation (Adams, 1963), nitro-

upland. The differential growth yields canopy geometry and composition variations related to changes in stem density, leaf to stem ratios, leaf orientation, and proportions of live versus dead tissue maintained in the canopy. Increasing elevation can be associated with increasing soil salinity and decreasing plant height and biomass. Variations in *S. alterniflora* canopies exhibit different spectral signatures, as evidenced by image formation on color infrared film (Reimold *et al.*, 1973).

Abstract: Natural populations of S. alterniflora, growing at apparent soil salinities of 12 to 45%, exhibited a 12 percent range in leaf moisture content. Despite the limited range of moisture content, significant differences in canopy spectral radiance were correlated with changes in leaf and canopy moisture content. Highmarsh and ditchbank S. alterniflora showed a decrease in biomass and leaf moisture content and an increase in spectral radiance as soil salinity increased.

gen limitation (Valiela and Teal, 1974), anaerobiosis (Linthurst, 1980), tidal subsidy (Odum and Fanning, 1973; Steever *et al.*, 1976), interstitial soil salinity (Nestler, 1977), or a combination of these and others. There probably is no singular causal agent; however, salinity is consistently implicated as a major contributor.

Teal (1962) identified four height forms or distinct marsh types supporting *S. alterniflora* in a Georgia salt marsh. For a New England marsh, Niering and Warren (1980) have also characterized several *S. alterniflora* growth forms. *S. alterniflora* is tallest and most productive on the creekbank, becoming progressively less productive as one moves up the elevational gradient toward the

Besides changes in biomass or proportions of live versus dead biomass, an important consequence of increasing soil salinity is physiological changes in the *S. alterniflora* related to plant-soil water relations. Increasing soil salinity requires a lower water potential in plant tissues in order to maintain net water flux into the plant. Water uptake is essential for photosynthesis and the survival of the plant. The osmotic drought induced by soil salinity suggests that a leaf water content gradient may be an aboveground indicator of soil water potential.

Spectral detection of leaf water status has been accomplished in the 1.3 to 2.7 μ m region where infrared radiation is strongly absorbed by water (Allen and Richardson, 1968). Reflectivity from a leaf measured in the 1.3 to 2.7 μ m region results from Fresnel reflections at internal and external interfaces (mainly cell wall-intercellular air

^{*} Presently with the U.S. Army Corps of Engineers, Waterways Experiment Station, P.O. Box 631, Vicksburg, MS 39180.

Photogrammetric Engineering and Remote Sensing, Vol. 49, No. 1, January 1983, pp. 77-83.

^{0099-1112/83/4901-77\$02.25/0} © 1983 American Society of Photogrammetry

spaces) and absorption by water (Allen et al., 1969; Gausman et al., 1970). This phenomenon has been observed and documented by many authors (Gates et al., 1965; Allen et al., 1970; Knipling, 1970; Woolley, 1971; Gausman, 1974; Gausman et al., 1974; among others). Thomas et al. (1971) demonstrated a higher middle infrared reflectance from corn leaves as leaf water content decreased. Similar results from leaves of agricultural crops monitored over the growing season showed an increase of middle infrared reflectance as moisture content decreased (Sinclair et al., 1971; Gausman et al., 1973).

Soil salinity has also been associated with increased reflectance of single leaves in the reflected infrared spectral region. Thomas et al. (1966) working with cotton found reflectance in the infrared to increase below about 80 percent relative turgidity. They also detected increased reflectance from cotton leaves exposed to high concentrations of chloride. Changes in leaf thickness and color were suggested as morphological leaf changes associated with the higher reflectance. Additional work by Gausman et al. (1969) with cotton suggested a decreased leaf water content as a function of higher salinity generally increased infrared reflectance. They attributed near infrared reflectance in the 0.75 to 1.3 μ m region to changes in cellular arrangement within the leaf.

Laboratory measurements of increased infrared reflectance as moisture content decreased were reversed when spectral signatures of field canopies were considered. Thomas *et al.* (1967) and Meyers *et al.* (1966) found nonsaline cotton to be more reflective than salt-affected cotton. This they attributed to smaller leaves, fewer leaves, and increased amounts of soil reflectivity, characteristic of the salt affected canopies. These observations for salt-affected cotton can be related to canopy variations in height forms of *S. alterniflora*.

The present research was concerned with canopy structure changes in height forms of *S. alterniflora* and how spectral characteristics changed relative to growth form. Sampling of *S. alterniflora* canopies relative to a salinity gradient seemed to be a logical approach. The objectives of this study were to identify the vegetative components of the canopy most related to the observed spectral changes and to equate leaf water content, canopy water content, and spectral response to ambient soil salinity regimes.

METHODS

SITE DESCRIPTION-HIGHMARSH

The *S. alterniflora* salt marshes selected for study were within the drainage basins of Canary Creek and Old Mill Creek in the vicinity of Lewes, Delaware. Brackish and saline marshes supporting *S. alterniflora* were sampled in both creeks. A total of four sampling stations were cho-

sen, representing the range of soil salinities under which highmarsh *S. alterniflora* would normally be found growing in the field.

SITE DESCRIPTION-DITCHBANK

A mosquito ditch, colloquially known as Renegade Ditch, was selected for study from within the Old Mill Creek drainage. Renegade Ditch extended approximately 343 m from the mouth to the nodal point (the point from which tidal water ebbs or floods from opposite directions) and supported an even gradation of creekbank *S. alterniflora* along its banks. Five stations were identified to describe the gradual reduction in plant height and aboveground biomass as one progressed up the ditch to the nodal point. The stations were not evenly spaced up the ditch.

HARVESTING PROCEDURE

The aboveground vegetation was harvested at each of five stations on Renegade Ditch on 30 August 1980 and at the four highmarsh areas on 12–15 September 1980. A 0.1 square metre circular ring was placed in a representative area at each station and all the plants within were clipped at soil level. Three replicate harvests were performed at each sampling station in both the highmarsh and ditchbank areas.

In the laboratory, a representative subsample was drawn from the harvested vegetation. The plant material was sorted into live leaves, live stems, and dead material. The sorted plant parts and the unsorted residual were washed with tap water, dried at 60°C to a constant mass, and weighed to determine dry weight biomass. Each plant component was estimated for the whole sample based on the biomass proportions determined for the sorted subsample.

MOISTURE CONTENT DETERMINATION

Approximately 25 green healthy leaves were clipped from S. alterniflora plants directly adjacent to each harvested plot. The leaves were immediately bagged and put on ice. Within three hours, the leaves from each sample were wiped clean with Kimwipes and the fresh weight determined to the nearest 0.1g. After drying at 60° C to a constant mass, the dry weight of the leaves was determined. The moisture content of the leaves was expressed as the percent moisture content based on the fresh weight of the leaf; $PMC = (1-(DW/FW) \times 100)$, where PMC was percent moisture content, and FW and DW were fresh and dry weight biomass, respectively.

SOIL SALINITY

Soil salinity was determined from soil cores extracted from each harvested plot. A small sample of soil was extracted from 15 to 20 cm below the soil surface and salinity was determined to the nearest part per thousand (%) with a refractome-

ter. Soil salinity determinations were from below the most active root zone. Because salinity was a concentration measurement, water uptake by the plant, rainfall, or time since last tidal inundation likely caused variations in salinity concentrations within the active root zone. The deep salinity determination was thought to be more representative of the salinity regime experienced by the *S. alterniflora* over the long term or the equilibrium salinity (Lord, 1980).

SPECTRAL DATA COLLECTION

Spectral radiance data were collected immediately before harvesting and directly over the quadrat of marsh to be sampled. In situ spectral data were collected radiometrically using a prototype to the Goddard Space Flight Center Mark II three band radiometer (Tucker et al., 1981). The radiometer contained three wavelength bands spectrally configured with interchangeable interference filters to match bands 3, 4, and 5 of the Landsat-D Thematic Mapper. The sensor head housed a red band (0.63 to 0.69 \mum, RED) sensitive to chlorophyll concentration, a near infrared band (0.76 to 0.90 \mum, NIR) sensitive to plant tissue structure or biomass, and a middle infrared band $(1.55 \text{ to } 1.75 \mu\text{m}, \text{IR})$ sensitive to water content. Data were recorded simultaneously for all three bands.

Three radiance measurements were taken over each plot to be harvested. The detector module was leveled using a bubble level affixed to the top of the module and held 88 cm above the marsh canopy. At 88 cm the instantaneous field of view was 0.1 square metre at the top of the canopy. The instrument operator always held the detector module at arms length over the plot and always stood facing the sun. Spectral data were collected within two hours of solar noon (1100 to 1500 hrs) and under sunny to partly sunny skies.

Radiance data for each plot were averaged and the mean for each band was used in subsequent calculations. Spectral radiance data were expressed as a normalized difference (Kriegler et al., 1969) and are referred to as either the vegetation index (Rouse et al., 1973) or the infrared index. The vegetation index was expressed as VI = NIR -RED/NIR + RED, where VI equals the vegetation index and NIR and RED were the near infrared and red band radiance, respectively. The infrared index (II) was the same as the vegetation index except the middle infrared band (IR) radiance was substituted for the red band in the above expression. Representing spectral radiance data as the vegetation or the infrared index had the effect of correcting for changing levels of irradiance. Because radiance measurements were obtained under sunny skies and at the same time of year, we presume little change in irradiance conditions from site to site or day to day in this study.

Significant differences in this paper will be as-

sumed to be at the 95 percent probability level. Contrasts among variable means were according to Duncan's Multiple Range test.

RESULTS

HIGHMARSH

The results from the destructive harvest of the highmarsh *S. alterniflora* areas are depicted in Figure 1. Spectral data expressed as the vegetation index and the infrared index were similar; therefore, only the infrared index is graphed in Figure 1. Each sample location was represented by the ambient soil salinity on the *x*-axis. The dead component included dead leaves and stems, while the live component represented live leaves, stems, and inflorescences. The letters on the bars or next to point symbols indicated the statistical separability of the respective components (live, dead, or total biomass and radiance) across the salinity gradient. A similar letter for the same component denoted a lack of significant difference.

Total aboveground biomass showed a significant decrease with increased soil salinity (Figure 1). The major differential growth occurred as a reduction in live tissue as soil salinity increased. The dead component was statistically similar for the two areas with soil salinities less than 23% and for the two areas with soil salinities greater than 27%. The infrared index showed a marked decrease for the plant canopies growing on increasingly saline soil. The infrared index values

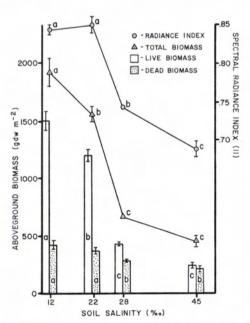


Fig. 1. Biomass and infrared index of highmarsh S. alterniflora canopies experiencing various soil salinity regimes. Bars representing \pm one standard error of the mean are shown wherever they exceeded the size of the point symbol.

Table 1. Comparison of S. alterniflora Canopy Parameters by Soil Salinity For Highmarsh Areas

Soil* Salinity (%00)	Live Biomass (%)	Leaf Moisture (%)	Canopy Moisture $(g m^{-2})$	
12 ± 0 a	74 ± 2 a	$67 \pm 0.6 \text{ a}$	1469 ± 47 a	
$22 \pm 0 \text{ b}$	71 ± 1 a	$68 \pm 0.7 \text{ a}$	$959 \pm 52 \text{ b}$	
$28 \pm 0.3 c$	$59 \pm 0 \text{ b}$	$56 \pm 0.8 \text{ b}$	$280 \pm 7 c$	
$45 \pm 1.2 d$	$52 \pm 1 c$	$55 \pm 0.9 \text{ b}$	$188 \pm 13 c$	

^{*} Values presented are means of three replicates ± one standard error of the mean. Means followed by similar letters were not significantly different.

were not significantly different for the two freshest stations, but the 28% and the 45% areas yielded significantly lower values.

Additional canopy characteristics for the highmarsh stations are listed in Table 1. The percent live biomass in the respective canopies decreased with increased soil salinity. Leaf moisture content was similar for the two fresher stations and similar for the two saltier stations. The total range of percent moisture was 12 percent. The canopy moisture content represented the water content of live leaves within the canopy per unit ground area. This representation of moisture content showed significant decreases in unit canopy moisture as soil salinity increased. Soil salinity was negatively correlated with leaf moisture (r = -0.79) and with canopy moisture (r = -0.88).

The close association between moisture content and aboveground biomass was evident from the data. Total and live leaf biomass were considered covariates and the ANOVA was repeated. Differences in leaf moisture and canopy moisture remained statistically significant when adjusted for biomass variation among stations.

The vegetative descriptors of the *S. alterniflora* communities associated with the different soil salinity regimes were analyzed with linear regression analysis to determine if any relationships existed between canopy parameters and observed spectral radiance indices (Table 2). All correlation

coefficients were significant at the 0.01 probability level. Leaf moisture content and canopy moisture content correlated well with radiance indices. The infrared index was more highly correlated with all the vegetative descriptors than was the vegetation index.

DITCHBANK

Live and dead components of the *S. alterniflora* along Renegade Ditch are presented in Figure 2. The station numbered 1 was closest to the main creek. Letters denote statistical similarity for biomass or radiance data considered over the five stations sampled. Bars having different letters were significantly different. The infrared index and the vegetation index values were similar, so only the infrared index is shown in Figure 2.

Live biomass density decreased significantly moving up the ditch (Figure 2). The dead component also exhibited a significant decrease up the ditch; however, the magnitude was much less for the dead than for the live biomass. One would expect an increase in soil salinity and a decrease in tidal amplitude moving up the ditch. The reduction in biomass was considered consistent with the increasing osmotic stress of increasing soil salinity. The infrared index declined in a similar pattern to the live biomass. The infrared index for station 1 was significantly greater than all other stations. The infrared index values for stations 2, 3, and 4 were not significantly different but were significantly higher than station 5.

The gradation in soil salinity generally increased toward the nodal point. Although some significant differences in soil salinity were observed, the magnitude of change was small with a fair amount of variability associated with the mean of each station (Table 3). Percent live biomass showed a decreasing trend from station 1 to 5. Leaf moisture content was not significantly different at the lower three stations. Leaf moisture declined significantly at both stations 4 and 5. The canopy water content showed the same trend as did the leaf moisture content. Soil salinity was negatively correlated with leaf moisture (r = -0.65) and with canopy moisture (r = -0.75).

Table 2. Correlation Coefficients (r) Describing the Relationship Between Canopy and Radiance Parameters for Highmarsh S. alterniflora Areas

Radiance* Index	Live Leaf Biomass (gdw m ⁻²)	Total Aboveground Biomass (gdw m ⁻²)	Live Biomass (%)	Leaf Moisture (%)	Canopy Moisture (g m ⁻²)
VI	0.79	0.89	0.89	0.94	0.83
II	0.86	0.92	0.95	0.95	0.89

^{*} v_1 = vegetation index; u_1 = infrared index. gdw u_2 = grams dry weight per square metre.

g m⁻² = grams per square metre.

g m⁻² = grams per square metre. n for all correlations = 12.

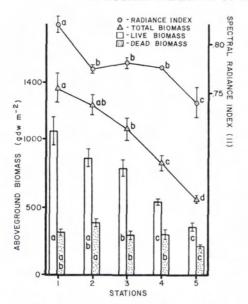


Fig. 2. Biomass and infrared index of ditchbank S. alterniflora canopies along Renegade Ditch. Bars representing ± one standard error of the mean are shown wherever they exceeded the size of the point symbol.

Table 4 presents correlation coefficients between radiance indices and the vegetation parameters. All correlation coefficients were significant at the 0.05 level. The vegetation index was slightly better correlated with moisture content and live leaf biomass than was the infrared index.

WHOLE MARSH

When all stations were considered, leaf moisture and canopy moisture were more closely correlated with the infrared index than with the vegetation index. Moisture content and infrared index data for all height forms of *S. alterniflora* (highmarsh and ditchbank) were analyzed together in Figures 3 and 4. The infrared index explained 70 percent and 61 percent of the variation in leaf moisture and canopy moisture, respectively, for all stations sampled.

DISCUSSION

We would, in some ways, consider the use of the red spectral region (primarily sensitive to chlorophyll absorption) and the near infrared region (primarily sensitive to cellular structure) as an indirect indicator of actual water content. It seems clear that morphological and physiological changes related to moisture stress are readily detected by combining these spectral regions (vegetation index). However, longer wavelength infrared energy would be expected to be a more direct indicator of water content. Tucker (1980), in a recent paper, used a stochastic leaf radiation model (Tucker and Garratt, 1977) to simulate the influence of leaf water content on spectral reflectance. A salient outcome of this work was that maximal differences in reflectance attributed to differences in leaf water content occurred in the 1.50 to 1.75 µm spectral region. Based on this simulation, the middle infrared band used in this study should possess good moisture content discrimination capabilities.

Our radiance data showed an improvement in estimating leaf moisture and canopy moisture content when the infrared index was used as opposed to the vegetation index. This trend was indicated in the highmarsh samples and when both marsh types were considered together, but the infrared index was not clearly superior in the ditchbank samples. Previous work (Hardisky et al., in press) suggested that the vegetation index was more effective in describing tall form S. alterniflora canopy parameters than was the infrared index. The physical limitation of light penetration of taller canopies apparently reduced spectral sensitivity more for the infrared index than the vegetation index and contributed to the observed dichotomy between highmarsh and ditchbank areas. Overall, the infrared index was superior to the vegetation index for moisture content detection.

We used osmotic drought (induced by soil salinities) as opposed to soil moisture drought to study variations in canopy spectral radiance. The spectral responses we obtained were consistent

Table 3. Comparison of Ditchbank S. alterniflora Canopy Parameters by Relative Position Along the Length of Renegade Ditch

Station*	Soil† Salinity (°/00)	Live Biomass (%)	Leaf Moisture (%)	Canopy Moisture (g m ⁻²)
1	$32 \pm 1.2 \text{ a}$	76 ± 2 a	67 ± 0.4 a	1226 ± 95 a
2	$31 \pm 0.9 a$	$69 \pm 2 \text{ bc}$	$68 \pm 0.8 \text{ a}$	1276 ± 167 a
3	$34 \pm 0.9 \text{ ab}$	73 ± 1 ab	$66 \pm 0.3 \text{ a}$	$1165 \pm 77 a$
4	$38 \pm 1.5 c$	$65 \pm 2 c$	$64 \pm 0.6 \text{ b}$	$696 \pm 46 \mathrm{k}$
5	$37 \pm 2.3 \text{ be}$	$62 \pm 3 c$	$60 \pm 1.1 c$	$302 \pm 21 c$

^{*} Station 1 corresponds to the mouth of the ditch and station 5 corresponds to the nodal point.

[†] Values presented are means of three replicates \pm one standard error of the mean. Means followed by similar letters were not significantly different. g m⁻² = grams per square metre.

Table 4. Correlation Coefficients (r) Describing the Relationship Between Canopy and Radiance Parameters for Ditchbank S. alterniflora Stations

Radiance* Index	Live Leaf Biomass (gdw m ⁻²)	Total Aboveground Biomass (gdw m ⁻²)	Live Biomass (%)	Leaf Moisture (%)	Canopy Moisture (g m ⁻²)
VI	0.77	0.74	0.66	0.80	0.74
II	0.73	0.78	0.84	0.72	0.71

* v_I = vegetation index; I_I = infrared index. gdw m⁻² = grams dry weight per square metre. g m⁻² = grams per square metre. n for all correlations = 15.

with laboratory and field results obtained by other authors working solely with soil moisture deficit. The drought switch was successful, but osmotically induced stress is variable temporally and spatially. For the highmarsh stations, the estimate of soil salinity was probably a reliable indicator of the average salinity experienced by the plants. The position of the highmarsh areas away from the creekbank and the slightly higher elevation reduced the frequency of tidal inundation and the rate of soil water movement relative to the ditchbank stations. The ditchbank soil salinity data showed more variability, due to the presumably more rapid soil water movement, and were not as closely correlated with biomass. The influence of differential flooding regimes on the ditchbank as the tidal amplitude decreased up the ditch and lunar controlled variations of the initial tidal amplitude, created a highly variable soil salinity regime. The long term indicator of salinity stress (biomass) was evenly graded up the ditch but the instantaneous estimate of salinity stress (soil salinity or plant moisture content) was not as consistent.

Fig. 3. Relationship between infrared index and leaf moisture for all *S. alterniflora* growth forms sampled.

Conclusions

Spectral radiance measurements along naturally occurring salinity gradients have shown a reduction in spectral radiance indices as soil salinity increases for the salt marsh plant *S. alterniflora*. Aboveground live biomass, spectral radiance indices, and leaf moisture content showed a significant negative correlation with soil salinity.

The infrared index was more closely correlated with moisture and other canopy variables than the vegetation index in the highmarsh areas. This was attributed to the better moisture detection capabilities of the middle infrared spectral region. Ditchbank (tall form) *S. alterniflora* characteristics were best described by the vegetation index.

Remote spectral detection of plant vigor is possible using a combination of spectral bands. The interdependence of aboveground biomass, leaf moisture content, and canopy height permitted the spectral discrimination of variation in canopy characteristics with both spectral radiance indices tested. Because natural, presumably equilibrium, communities of *S. alterniflora* were observed in

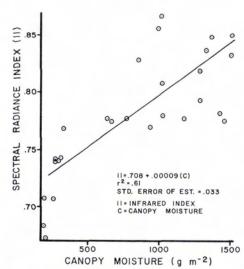


Fig. 4. Relationship between infrared index and canopy moisture for all *S. alterniflora* growth forms sampled.

this study, we were not able to demonstrate direct spectral alteration solely from leaf moisture changes; rather, the composite reaction of the plant community to salinity stress was detected.

ACKNOWLEDGMENTS

We thank Dr. C. J. Tucker and NASA Goddard Space Flight Center for the loan of the radiometer. We thank Dr. Frank Daiber and Dr. John Gallagher for reviewing an earlier version of the manuscript. We also acknowledge the assistance of Mrs. Barbara MacKenzie in preparing the manuscript. This work was supported with funds from the College of Marine Studies, University of Delaware.

REFERENCES

- Adams, D. A., 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. *Ecology* 44:445-456.
- Allen, W. A., and A. J. Richardson, 1968. Interaction of light with a plant canopy. J. Opt. Soc. Am. 58:1023-1028.
- Allen, W. A., H. W. Gausman, A. J. Richardson, and J. R. Thomas, 1969. Interaction of isotropic light with a compact plant leaf. J. Opt. Soc. Am. 59:1376-1379.
- Allen, W. A., H. W. Gausman, A. J. Richardson, and C. L. Wiegand, 1970. Mean effective optical constants of thirteen kinds of plant leaves. Appl. Opt. 9:2573-2577.
- Gates, D. M., H. J. Keegan, J. C. Schleter, and V. R. Weidner, 1965. Spectral properties of plants. Appl. Opt. 4:11-20.
- Gausman, H. W., 1974. Leaf reflectance of near-infrared. Photogram. Eng. 40:183-191.
- Gausman, H. W., W. A. Allen, and R. Cardenas, 1969. Reflectance of cotton leaves and their structure. Remote Sensing of Environment 1:19-22.
- Gausman, H. W., W. A. Allen, R. Cardenas, and A. J. Richardson, 1970. Relation of light reflectance of histological and physical evaluations of cotton leaf maturity. Appl. Opt. 9:545-552.

——, 1973. Reflectance discrimination of cotton and corn at four growth stages. Agron. J. 65:194-198.

- Gausman, H. W., W. A. Allen, and D. E. Escobar, 1974. Refractive index of plant cell walls. *Appl. Opt.* 13:109-111.
- Hardisky, M. A., R. M. Smart, and V. Klemas. Seasonal spectral characteristics and aboveground biomass of the tidal marsh plant, *Spartina alterniflora*. In press. *Photogram*. *Eng. and Remote Sensing*.
- Knipling, E. B., 1970. Physical and physiological basis for the reflectance of visible and near-infrared radiation from vegetation. Remote Sensing of Environment 1:155-159.
- Kriegler, F. J., W. A. Malila, R. F. Nalepka, and W. Richardson, 1969. Preprocessing transformations and their effects on multispectral recognition. Proc. Sixth International Sym. on Remote Sensing of Environment, Michigan, pp. 97-131.
- Linthurst, R. A., 1980. A growth comparison of Spartina alterniflora Loisel. ecophenes under aerobic and anaerobic conditions. Am. J. Bot. 67:883-887.
- Lord, III., C. J., 1980. The chemistry and cycling of iron, manganese, and sulfur in salt marsh sediments. Ph.D. dissertation, University of Delaware. 177p.

- Meyers, V. I., C. L. Wiegand, M. D. Heilman, and J. R. Thomas, 1966. Remote Sensing of soil and water conservation research. Proc. Fourth International Sym. on Remote Sensing of Environment, Michigan pp. 801-813.
- Nestler, J., 1977. Interstitial salinity as a cause of ecophenic variation in Spartina alterniflora. Est. Coast. Mar. Sci. 5:707-714.
- Niering, W. A., and R. S. Warren, 1980. Vegetation patterns and processes in New England salt marshes. *Bioscience* 30:301-307.
- Odum, E. P., and M. A. Fanning, 1973. Comparison of the productivity of *Spartina alterniflora* and *Spartina cynosuroides* in Georgia coastal marshes. *Bull. Ga. Acad. Sci.* 31:1-12.
- Reimold, R. J., 1977. Mangals and salt marshes of eastern United States. In V. J. Chapman, ed. Wet Coastal Ecosystems. Elsevier Scientific Publ. Co. Amsterdam, pp. 157-166.
- Reimold, R. J., J. L. Gallagher, and D. E. Thompson, 1973. Remote sensing of tidal marsh. *Photogram*. Eng. 39:477-488.
- Rouse, J. W., R. H. Hass, J. A. Schell, and D. W. Deering, 1973. Monitoring vegetation systems in the Great Plains with ERTS. Third Earth Resources Technology Satellite-1 Symposium. NASA, pp. 309-317.
- Sinclair, T. R., R. M. Hoffer, and M. M. Schreiber, 1971. Reflectance and internal structure of leaves from several crops during a growing season. Agron. J. 63:864-868.
- Steever, R. Z., R. S. Warren, and W. A. Niering, 1976. Tidal energy subsidy and standing crop production of Spartina alterniflora. Est. Coast. Mar. Sci. 4:473-478.
- Teal, J. M., 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614-624.
- Thomas, J. R., V. I. Meyers, M. D. Heilman, and C. L. Wiegand, 1966. Factors affecting light reflectance of cotton. Proc. Fourth Sym. on Remote Sensing of Environment, Michigan. pp. 305-312.
- Thomas, J. R., C. L. Wiegand, and V. I. Meyers, 1967. Reflectance of cotton leaves and its relation to yield. Agron. J. 59:551-554.
- Thomas, J. R., L. N. Namken, G. F. Oerther, and R. G. Brown, 1971. Estimating leaf water content by reflectance measurements. Agron. J. 63:845-847.
- Tucker, C. J., 1980. Remote sensing of leaf water content in the near infrared. Remote Sensing of Environment 10:23-32.
- Tucker, C. J., and M. W. Garratt, 1977. Leaf optical system modeled as a stochastic process. Appl. Opt. 16:635-642.
- Tucker, C. J., W. H. Jones, W. A. Kley, and G. J. Sundstrom, 1981. A three-band hand-held radiometer for field use. Science 211:281-283.
- Valiela, I., and J. M. Teal, 1974. Nutrient limitation in salt marsh vegetation. In R. J. Reimold and W. H. Queen, eds. *Ecology of Halophytes*. Academic Press, New York, NY, pp. 547-563.
- Woolley, J. T., 1971. Reflectance and transmittance of light by leaves. Plant Physiol. 47:656-662.

(Received 3 August 1981; revised and accepted 21 July 1982)