Title

Salinity-Productivity Relationships of Selected Plant Specis from the Suisun March, California

Permalink

https://escholarship.org/uc/item/57j3289c

Authors

Pearcy, Robert W
Bayer, David E
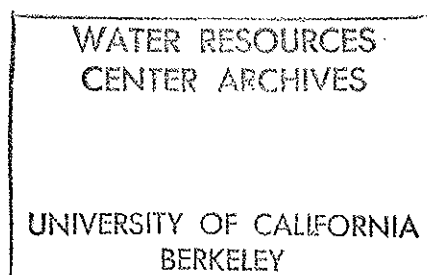Ustin, Susan L

Publication Date

1982-11-01

SALINITY-PRODUCTIVITY RELATIONSHIPS OF SELECTED
PLANT SPECIES FROM THE SUISUN MARSH, CALIFORNIA

by

ROBERT W. PEARCY, DAVID E. BAYER and SUSAN L. USTIN

Department of Botany
University of California, Davis

Office of the Director
CALIFORNIA WATER RESOURCES CENTER
University of California   Davis, California   95616

TECHNICAL COMPLETION REPORT

November 1982

ABSTRACT

The influence of salinity on the productivity of four plant species occurring or potentially occurring in Suisun Marsh was investigated with laboratory measurements of growth, photosynthetic responses and competitive interactions, and field measurements of water relations, growth and carbohydrate reserves. Special emphasis was placed on the responses of Scirpus robustus and its competitors because of its importance as a waterfowl food source. The results showed that photosynthesis and growth were much more reduced by increased salinity in Scirpus than in Spartina foliosa, Salicornia virginica or Cotula cornupifolia. However, at low salinities Scirpus had the highest growth rates. Competition studies showed a strong shift in competitive advantage from Scirpus at low salinities to Salicornia at high salinities. Field studies showed that at most sites where Scirpus occurs, there is a strong seasonal change in salinity from nearly fresh water in the spring to high summer salinity levels. The rapid growth of Scirpus at the low salinities present during the spring may give it a competitive advantage over Salicornia. Scirpus also exhibited considerable tolerance to high salinities--defined here as an ability to survive even though growth was completely stopped. This tolerance may be important, since high summer salinities could prevent encroachment of less salt tolerant but highly competitive and less desirable species such as Scirpus acutus or Typha latifolia. We conclude that management plans designed to enhance Scirpus productivity should put as much weight on maintaining an annual cycle of salinity as reducing the yearly average salinity.

INTRODUCTION

The Suisun marsh comprises 59,000 acres or about 10% of California's remaining "natural" wetlands and is of major importance to waterfowl of the Pacific Flyway. These waterfowl winter primarily in the Central Valley of California and in dry years, up to 25% of the total population may be found in the Suisun marsh (Miller et al., 1975). Present land management practices are directed primarily at maintenance and enhancement of these marshes as waterfowl habitat (Mall, 1969). This land and the ducks that it supports provide a valuable recreational resource with over 200 duck hunting clubs operating in the marsh (Mall and Rollins, 1972). With the projected additional loss of up to 20% of California's remaining wetlands in the future (Calif. Dept. of Fish and Game, 1967), the value of the Suisun marsh in ecological, recreational, and economic terms will increase considerably.

Future water development in California represents a major problem for protection and maintenance of the Suisun marsh. Flows of fresh water into the Sacramento River Delta have been reduced from 33.6 to 15.9 million acre feet through diversion and storage for primarily agricultural use (Miller et al., 1975). A further 30% reduction is anticipated by 1990 (Skinner, 1972). The major impact of this decrease in water outflow through the Delta on the Suisun marsh will be an increase in the salinity of the sloughs and channels that flush the marsh. Total dissolved solids (TDS) now range from 1 to 4 parts per thousand (ppt) from October to January in the sloughs and bays in and around the marsh (Miller et al., 1975) but are predicted to reach 17 ppt for at least 80% of the year as a result of the decreased flushing.

Increased soil salinities could potentially have a marked adverse impact on the productivity of the Suisun marsh (Mall, 1969). The most valuable plant species, in terms of waterfowl food, apparently require intermediate salinities for maximum competitive ability and seed production. Currently,

management practices based on flooding in winter and spring for salinity control have apparently led to increases in productivity of these species (Miller et al., 1975). Future increases in salinity are likely to reduce the effectiveness of marsh management practices and the distribution and productivity of the desirable species. This will, in turn, have a major impact on the use of Suisun marsh by waterfowl. Currently, the marsh supports 5.0 ducks per acre as compared to 0.9 ducks per acre in the more saline marshes of San Francisco Bay (Calif. Dept. of Fish and Game, 1966-1967). Extrapolation based on the predicted future changes in the Suisun marsh indicates that a significant proportion of the wintering waterfowl population of the Pacific Flyway will be lost (Mall and Rollins, 1972).

Considerable research has gone into potential effects of increased salinities based on the current understanding of plant-salinity relationships developed from field observations (Mall, 1969). Possible management plans to preserve the quality of the marsh, based on the studies, include the importation of fresh water in order to reduce salinities. This importation will be expensive, in terms of both the cost of the facilities required and the amount of water used. Currently, cumulative annual water requirement in the marsh for salinity control and vegetation management amounts to 430,000 acre feet (Miller et al., 1975). Detailed knowledge of the responses of plant productivity and distribution are required in order to optimize management practices.

The research supported by this grant had the objective of providing insight into the effects of salinity on plant productivity of important plant species in the Suisun marsh. Species that are important wildlife food sources or that compete with food species were investigated. The effects of salinity on photosynthetic CO_2 exchange, relative growth rate and patterns of dry weight allocation were determined in laboratory measurements on

plants grown at different salinity levels. Field measurements were made of growth, phenology, and carbohydrate storage reserves in the plants, and of biomass at several sites that differed in water and salinity regimes. These sites were also utilized for measurements of plant water relations, stomatal conductances and field photosynthesis rates which were helpful in interpreting the laboratory responses. Finally, competition experiments between Scirpus robustus and its major competitor, Salicornia virginica, were conducted to investigate how competitive interactions would be influenced by higher salinity levels.

MATERIALS AND METHODS

I.   Description of the Species

Experiments on the effects of salinity on growth and CO_2 exchange rates were made on 4 species found in Suisun marsh, or potentially found there if salinities increase. These 4 species were alkalai bullrush (Scirpus robustus), pickle weed (Salicornia virginica), cord grass (Spartina foliosa) and brass buttons (Cotula coronopifolia). Because of the critical importance of Scirpus robustus as a waterfowl food source, a heavy emphasis was placed on this species. Brass buttons is also an important food source for waterfowl. The other two species are not important waterfowl food sources but do compete with food species and, thus, may be important factors regulating the distribution and abundance of waterfowl food.

Two other species, salt grass (Distichilis spicata) and Atriplex patula, are found in the marsh and work was originally planned to include them in this project. However, during the course of the research the results of other studies on the effects of salinity effects on growth and photosynthesis in these two species was published. Therefore, our efforts were concentrated on the other species. A review and description of this published research is included in this report for comparison to our results.

Field work concentrated primarily on the perennial species <u>Scirpus</u> <u>robustus</u> and the two competitors <u>Salicornia</u> and <u>Spartina</u>.

Following is a description of each species, including the taxonomy, morphology, and general distribution.

1. <u>Scirpus robustus</u>

This species is a member of the Cyperaceae or sedge family which is widely distributed in marshes. <u>Scirpus robustus</u> is widespread in North America, occurring in both east and west coast marshes. In California, it is most common in brackish marshes, although populations do occur in quite saline marshes of San Pablo Bay. It is morphologically similar to the European marsh species <u>S</u>. <u>maritimus</u> and to the Mediterranean species <u>S</u>. <u>tuberosus</u>. The latter has been introduced into some marshes in the Sacramento River Valley. A closely related species, <u>S</u>. <u>fluviatilis</u> (river bullrush), is found in the Sacramento River Valley in primarily freshwater marshes. This species, while very similar in appearance to <u>S</u>. <u>robustus</u>, is not a heavy seed producer and is therefore less desirable as a waterfowl food source. Hybrids between <u>S</u>. <u>robustus</u> and <u>S</u>. <u>fluviatilis</u> have been reported (Mason, 1957). Thus, they represent a very interesting species complex extending from very saline to essentially freshwater marshes.

Morphologically, <u>S</u>. <u>robustus</u> is a leafy sedge 0.5 to 1.5 m tall with leaves 5-15 mm wide and up to 50 cm long. The rhizomes form tubers which serve to regenerate the plant each year. Our excavations show that most of the roots occur in the upper 15 cm of soil, although some roots extend much deeper.

Previous work on <u>Scirpus robustus</u> has been limited to taxonomic treatments (e.g., Koyama, 1962; Schulyer, 1974-1975) and to Mall's field studies of salinity-productivity relationships.

2. Salicornia virginica

This perennial species is in the family Chenopodiaceae and is abundant in the most saline parts of the marsh. It is widespread, occurring also in east coast salt marshes. The European equivalent is S. europea. Several annual species of Salicornia also occur in California.

Morphologically, S. virginica is a suffruticose perennial, usually less than 0.5 m tall. The leaves are strongly reduced and the photosynthetic tissue consists of modified succulent leaves fused around the stem. Vegetative reproduction occurs via horizontal rhizomes. Growth begins in late April and continues through the summer. Flowering occurs in September and the seeds are shed in November.

3. Spartina foliosa

This grass species is common along the edges of the salt marsh and on the tidal flats of San Francisco Bay. It is restricted in distribution to the coastal salt marshes of California and Mexico. However, several other Spartina species occur in east coast and interior marshes, and the genus is widespread in salt marshes throughout the world. S. foliosa does not now occur in Suisun marsh but may become established if salinities increase. Apparently, it was originally absent or occurred only infrequently in San Francisco Bay and San Pablo Bay. However, as salinities have increased due to changing water uses and flood management, Spartina has become much more widespread. It is now the dominant species throughout the "low" marsh at elevations from mean tide level to mean high tide level (Miller et al., 1975).

Growth begins in April and continues through the summer. Flowering occurs in late summer or early fall and the seed matures and is shed in November. Dormancy is incomplete and shoots initiated in early fall remain suppressed until spring when vegetative growth is completed.

Phelger (1971) has previously determined the effects of salinity on the growth and composition of Spartina foliosa, which showed maximum growth at about 25% seawater. Somewhat similar results were obtained by Mahall and Park (1976b).

4. Cotula coronopifolia

This species is a herbaceous facultative perennial (depending on salinity and soil moisture) of the Compositae that was introduced from South America. It occurs extensively in Suisun marsh and other brackish marshes as an often almost aquatic plant with decumbent branches up to 30 cm long. Flowering occurs throughout the spring, summer and fall, and large quantities of very small seed are produced. These appear to be dispersed primarily by flotation and, in some places, seed layers up to several inches deep can be found along the water's edge.

To our knowledge, there has been no information published on the ecology of this species or its responses to salinity.

II. Description of the Field Sites

1. Suisun Marsh

Suisun marsh consists primarily of a series of levied ponds that are seasonally flooded. Species distributions within these ponds depend on elevation, salinity, extent of recent disturbance and flooding duration. Pond management practices, which involve mainly flooding and drainage control, have a marked effect on salinity levels and soil moisture and ultimately on species distributions. The impact of alternative management schemes on species distributions and productivity is discussed in Miller et al. (1975).

Three primary field sites that differed in soil salinity were selected for measurements of seasonal patterns of growth and carbohydrate reserve. These sites were selected on the basis of their visual appearance and the records in Miller et al. (1975). The locations are shown in Figure 1 and

cover estimates for the most important species are given in Table 1. Below is a description of each site.

a. High Salinity Site (Tract 100, Joyce Island)

Vegetation at this site was dominated by Salicornia virginica with Scirpus robustus occurring in only small localized patches. Even within these patches, cover of Scirpus was low. Large areas of bare ground were present.

b. Intermediate Salinity Site (Tract 131, Grizzly Island)

The vegetation at this site consisted primarily of large, nearly mutually exclusive patches of Scirpus robustus and Salicornia virginica. Salicornia appeared to occupy slightly higher elevations (0.1 to 0.5 m) than Scirpus. At still higher elevations Distichilis spicata and Juncus balticus were abundant. Small areas of bare ground within the site supported stands of Cotula coronipifolia.

c. Low Salinity Site (Tract 100, Joyce Island)

This site is dominated by Scirpus robustus with only a small amount of Salicornia virginica present. Areas not supporting Scirpus were occupied by Distichilis spicata, Juncus balticus, Atriplex patula, and Typha latifolia.

2. Sonoma Creek

This natural tidal marsh is at the high end of the salinity gradient for Scirpus robustus. It is located in the San Pablo Bay marsh system along the banks of Sonoma Creek. Scirpus robustus occurs in a narrow band (3-6 m wide) about 10 m from the water's edge and about 1.8 m elevation above the mean tide level. At lower elevations in the intertidal zone towards the creek, a pure stand of Spartina foliosa is found. Above the Scirpus, the marsh is occupied by an extensive pure stand of Salicornia. This site is regularly flooded by tidal waters from Sonoma Creek.

3. Gray Lodge

A site at the low end of the salinity gradient for Scirpus was selected
at Gray Lodge Wildlife Refuge north of Marysville, CA and along the Sacramento
River. Scirpus robustus does not occur at this site but the very closely
related species, Scirpus fluviatilis, occurred in extensive nearly pure stands
surrounding slightly lower areas containing either Scirpus acutus or Typha
latifolia. The remainder of the site was occupied by annual grasses and
broad-leafed herbs. The site was flooded from September through early March.

III. Methods - Laboratory

A. Growth of Plants

All plants used in the laboratory measurements were grown in a greenhouse
on the University of California, Davis campus. Plants were grown either from
seeds, rhizomes or tubers, depending on the species, collected in the field.
For both growth rate determinations and measurements of CO_2 exchange, single
plants were grown in 5 cm dia x 20 cm long, bullet-shaped plastic pots con-
taining sand and perlite. The pots were placed in large 26 L plastic-lined
tanks so that the bottom 15 cm was submerged in nutrient solution. The
solution consisted of a full-strength Hoagland mixture which was salinized to
different levels (10, 20, 30 ppt) with an artificial sea-salt mixture (Rila
mix). Salinity was gradually increased over a 5-15 day period to avoid osmo-
tic shock to the plants. The nutrient-salt solution was continuously aerated.

Supplemental light was provided in the greenhouse by two 1500 W metal-
halide lamps so that the irradiances received were similar to those present
under field conditions during the growing season. The photoperiod was 14
hours and total daily quantum fluxes were 2900 μE cm^{-2} on cloudy days and 4300
μE cm^{-2} on clear days. During the late spring, summer and early fall, the
greenhouse was whitewashed to reduce the heat load. This, coupled with the
thermostatically-controlled heating and evaporative cooling, kept temperatures

in the range of 25 to 33 C during the day and 10 to 18 C at night. These temperatures are similar to those found in Suisun marsh during the growing season.

B. Measurement of Photosynthetic CO_2 Exchange

The plants used in the gas exchange measurements were generally allowed to grow at each final salinity level until new leaves were produced for the gas exchange measurements. Thus, measurements were made on leaves that had developed at the desired salinity level. On the night prior to the gas exchange measurements, the plant was transferred from the greenhouse to the laboratory.

Photosynthetic CO_2 and water vapor exchange rates were measured with apparatus detailed previously (Pearcy, 1977; DeJong et al., 1981). A single attached leaf for Scirpus and Spartina and a branch for Salicornia or Cotula was enclosed within a glass-windowed, circular brass chamber with a thermo-statted water jacket in the base and the lid. A fan in the chamber rapidly mixed the air and maximized the boundary layer conductances and heat exchange between the leaf or branch and the chamber. Leaf or branch temperatures were measured with 0.7 mm diameter copper-constantan thermocouples. Light received by the leaf was measured with a silicon cell mounted on the lid of the cham-ber. Air of known CO_2 concentration was supplied to the chamber by mixing CO_2-free air with air containing 1% CO_2 from compressed air cylinders at known ratios with calibrated metering valves or with rotameters. The air stream was humidified in a glass washing bottle and then dehumidified to a known dewpoint in a thermostatted glass condenser. The flow rate was measured either with a Mass flowmeter (Flow Technology, Inc.) or with a differential pressure transducer (Validyne Engineering, Inc.) mounted across a flow re-strictor made from a scintered glass disc to provide a pressure differential. CO_2 concentration was determined with a differential infrared gas analyzer

(Beckman Inst. Inc. Model 865 or Horiba, Inc. model VIA 500-R) and water vapor concentration with a solid-state relative humidity probe (Weathermeasure model HM-111P). Light for the photosynthesis measurements was supplied from a 1500 watt metal halide lamp and intensities were controlled with neutral density filters constructed from aluminum wire screens of varying mesh sizes.

Leaf conductances to CO_2 flux (g_1') were calculated from the simultaneous measurements of CO_2 and water vapor exchange, while mesophyll conductances (g_m') were calculated from the initial slopes of intercellular CO_2 dependence curves according to procedures outlined by Jarvis (1971). Rates of gas exchange and the leaf resistances were calculated on the basis of the surface area of one leaf side in Scirpus and Spartina and, so that the measurements were comparable, on the basis of 1/2 of the round shoot surface area in Salicornia.

C. Growth Measurements

Relative growth rates were measured using 22 seedlings for each salinity treatment selected from a much larger group on the basis of uniformity of size. These seedlings were transplanted to the pots described above. Growth conditions in these experiments were the same as those used for the photosynthesis measurements. After the gradual salinization period, the plants were allowed to equilibrate for 7-10 days at the final salinity. Harvests of 4-5 plants each were then made at 7-10 day intervals and weights were determined after oven drying.

Leaf growth rates of Scirpus robustus were measured at each salinity treatment by marking leaves with small tags at the time that leaf expansion began. Thereafter, leaf length was measured daily. Curves were constructed of leaf length versus time so that leaf expansion rates could be calculated from the slopes.

D. Water Potentials

Leaf water potentials were measured with a Scholander pressure chamber (Scholander et al., 1965).

E. Competition

Competition experiments between _Scirpus robustus_ and either _Salicornia virginica_ or _Spartina foliosa_ were conducted at several salinity levels using the de Wit replacement series technique (de Wit, 1960). In this technique, the density of plants was held constant at 10 plants per 1 gallon pot but the proportions of the two species were varied. Seedlings were grown in flats and then transplanted into the pots in proportions of 10/0, 7/3, 5/5, 3/7, or 0/10 for the competing species pair. The pots were placed in plastic trays and irrigated from below with a Hoagland solution salinized to either 10 or 20 ppt with Rila mix. A control experiment with no added salinity was also established. The pots were periodically rinsed through with the salinized nutrient solution to prevent the buildup of salts in the pots due to evapotranspiration. In some experiments, the solutions were salinized within 3 to 4 days after transplanting, while in the others the salinization was delayed for several weeks. The plants were harvested and the dry weights determined after the _Scirpus_ plants had grown to maturity and flowering had begun.

IV. Methods – Field

a. Growth and phenology.

Field measurements were carried out at the field sites at monthly intervals in 1978 and 1979. Growth of _Scirpus_ and other species was determined by measuring the heights of 50 shoots. For _Scirpus_, seasonal changes in shoot density were also determined by counting the number of shoots in 0.25 m^2 plots. Standing crops were determined at the end of the growing season by clipping 0.25 m^2 plots. Records of phenology, including time of initiation

of shoot growth, flowering and time of dormancy were kept for the major species at each site.

b. Plant water potentials.

Plant water potentials were measured with a Scholander-type pressure chamber (Scholander et al., 1965). Measurements were made on 5-8 plants of each species at dawn and again at 2-3 hr intervals throughout the day. Because of differences in morphology, leaf water potentials were measured for Scirpus and Spartina while shoot water potentials were determined for Salicornia. Water potential measurements were not made on Cotula because the soft, irregular stems were not suitable for the pressure chamber technique.

c. Leaf conductances.

Leaf conductances to water vapor were determined with a null balance type diffusion porometer. Measurements were made on 5 to 7 leaves that were tagged so that repeated measurements could be made. Where necessary, the leaves were rinsed and then dried prior to the start of the measurements to remove salt crystallized on the surface. Measurements were made every 2-3 hours throughout the day.

d. Field photosynthesis.

Measurements of the photosynthetic rates of plants under field conditions were made using the syringe technique (Clegg et al., 1978; Ehleringer and Cook, 1978). A 15X15X3 cm plexiglas chamber containing a fan for rapid air mixing was clamped onto 1 or 2 leaves. An automatic timer system withdrew a 10 cc air sample with a syringe and then withdrew a second 10 cc sample with a second syringe at a predetermined interval (usually 10 or 20 seconds). The needles were capped with rubber stoppers and the syringes were stored in insulated boxes for later analysis. After the measurement, the leaves were harvested so that leaf areas could be determined.

The CO_2 concentrations in the syringes were measured using a Horiba VIA 500R gas analyzer. The 10 cc of air was injected into an airstream flowing through the sample cell of the analyzer at μl min^{-1}. Because the CO_2 concentration in the syringe was different than that in the air stream, a peak deflection occurred as the sample passed through the analyzer. Peak height was related to CO_2 concentration and was calibrated by injection of syringes containing known CO_2 concentrations. Photosynthetic rates were calculated from the decrease in CO_2 concentration over the time interval.

e. Soil moisture and salinity.

Soil samples were collected with a soil auger from the 0 to 15 cm depth zone, where most roots occurred, and were stored in metal soil cans. Soil moisture content was determined gravimetrically from subsamples following oven drying at 105 C. Soil salinities were determined on separate subsamples by addition of distilled water followed by mixing and centrifugation to remove the particulate material. Conductivity of the resulting solution was determined with an aquatronics model 320 conductivity analyzer. Salinities were calculated from the conductivities and then corrected to the original soil moisture values.

f. Carbohydrate content.

Tubers were collected at intervals during 1978, 1979 and 1980 from ponds spanning the range of salinities for Suisun Marsh. Tubers were returned to the lab, cleaned, dried and weighed. The outer epidermis was removed, the remaining storage tissue was ground in a Wiley Mill and analyzed for total non-structural carbohydrate following the procedures of Smith (1969).

RESULTS

I. Laboratory Studies of CO_2 Exchange and Growth

A. Photosynthetic Responses to Light, Temperature and CO_2

Photosynthetic responses to light, temperature and CO_2 were determined for the four species investigated. Measurements of the responses to these environmental factors provide a basis for characterizing differences between species and for identifying conditions required for maximum CO_2 uptake rates. Prior to these determinations, optimum salinity conditions were also determined and shown to be the control solution for Scirpus and Cotula and 10 ppt for Spartina. Plants grown in these concentrations were used for determining the environmental responses. Since, as will be shown later, salinity had little effect on CO_2 uptake in Salicornia, plants grown in control solution were used. Since the plants were grown under high light, high nutrient supplies and moderate temperatures, the photosynthetic rates probably reflect the maximum potential of each species.

High light approaching fall sunlight intensities (2000 μeinstein m^{-2} s^{-1}) was required for maximum photosynthesis in all four species (Figure 2). None of the species showed a clear saturation of CO_2 uptake by light. This was especially pronounced in Scirpus and Spartina. For Spartina and Scirpus, the high photosynthetic capacities probably account for the lack of saturation since this is a commonly observed characteristic in other high photosynthetic rate species (Ehleringer and Björkman, 1978). The lack of light saturation in Salicornia is probably accounted for by the succulent stems which are relatively poor at absorbing light, as compared to flat leaves. This, along with the high dark respiration rate per unit surface area as shown by the intercept at 0 light intensity, accounts for the much poorer performance of Salicornia as compared to the other species at low light levels.

Cotula generally had lower photosynthetic rates than the other species, with the exception of Salicornia at PFD below 500 μEinstein m^{-2} s^{-1}. When compared with the other species, the irradiance at which photosynthesis begins to saturate, that is, the point at which the photosynthetic response

curve begins to deviate from linearity is much lower. In the high irradiance environment of the marsh, Cotula would clearly have a lower photosynthetic capacity.

Large differences were apparent in the temperature responses of photosynthesis. In Spartina, CO_2 uptake increased strongly with increasing temperature up to a maximum of 35 to 36 C (Figure 3). This pronounced temperature dependence is characteristic of the C_4 photosynthetic pathway found in Spartina. The three C_3 species all had much broader temperature responses and lower temperature optima for CO_2 uptake. The temperature optimum for CO_2 uptake was between 27 and 32 C for Scirpus and 25 and 27 C for Salicornia. Cotula had a very broad temperature response with almost no change in photosynthetic rate between 20 and 30 C. At high temperature, photosynthetic capacity is greatest in Spartina. However, at leaf temperatures below 20 C, a temperature that could be commonly expected during midday in the spring growing season in Suisun marsh, Scirpus had the highest rates. Salicornia had lower, and Cotula the lowest photosynthetic rates at all temperatures.

The photosynthetic responses to the calculated intercellular CO_2 concentrations are shown in Figure 4. These curves are most useful for diagnosing the differences in photosynthetic capacity due to the contrasting C_3 and C_4 pathways of these marsh plants. Spartina is highly efficient at low intercellular CO_2 concentrations but exhibits CO_2 saturation above 100 to 150 μbar. These are characteristics typically associated with C_4 photosynthesis. In contrast, the C_3 species are less efficient at low CO_2 but do not exhibit CO_2 saturation. In fact, at high intercellular CO_2, the photosynthetic capacity of Scirpus is substantially higher than that of Spartina. However, the greater photosynthetic capacity of Scirpus than Spartina would never be realized under normal conditions. Normal CO_2 levels in the atmosphere are around 330 μbar, and CO_2 concentrations in the intercellular spaces

are lower than atmospheric concentrations due to the diffusion limitation imposed by the stomata.

B. Photosynthetic Responses to Salinity

The 4 species exhibited a variety of photosynthetic responses to salinity (Figure 5). CO_2 uptake was essentially unaffected by salinity over the range of 0 to 30 ppt in Salicornica. Photosynthesis in Spartina was also quite resistant to salinity stress and rates declined only above 20 ppt. In contrast, photosynthesis in Scirpus and Cotula was strongly inhibited by salinity. At 30 ppt, a salinity commonly reached in Suisun marsh during midsummer (Mall, 1969; Miller et al., 1975; also see Figure 11 of this report), photosynthesis of Scirpus and Cotula was reduced to 36% and 26% of control rates, respectively (Figure 6). While photosynthetic rates of Scirpus were equal to those of Spartina and much higher than those of Salicornia when grown at the lowest salinity, by 30 ppt, the latter two species had much higher CO_2 uptake rates. Thus, increasing salinity has a much more detrimental effect on photosynthesis in Scirpus than on its primary competitor in Suisun marsh, Salicornia, or the potential competitor, Spartina.

The photosynthetic responses to salinity could either be due to stomatal closure restricting the supply of CO_2 to the leaf or to an inhibition of photosynthetic metabolism of CO_2 in the leaf. These two factors can be separated by calculation of the conductances to CO_2 by the leaf (Table 2). The leaf conductance (g_1') expresses the capacity for CO_2 transport across the stomata and boundary layer of the leaf while the mesophyll conductance expresses the capacity for CO_2 uptake across the cell walls and for fixation by the photosynthetic appartus. Both leaf and mesophyll conductances declined in response to salinity in Scirpus and Cotula. No trend was apparent in either conductance for Salicornia. In Spartina, both conductances were constant up to 20 ppt salinities, but both declined at 30 ppt.

When salinity stress occurs and reduces photosynthesis, it is clear that both stomatal and mesophyll limitations are involved. The relative importance of these two limitations can be calculated by comparison to a total conductance for CO_2 uptake. As shown in Table 2, changes in leaf conductance account for most of the inhibition of CO_2 uptake by salinity.

C. Salinity Effects on Growth

Growth responses to salinity were remarkably different among the species (Figure 7). There was a substantial stimulation of the final dry weight of Salicornia and Cotula in the 10 or 20 ppt treatments. In contrast, the dry weight of Scirpus was strongly reduced relative to the control at even 10 ppt added salinity. Thus, although Scirpus and Cotula had similar photosynthetic responses to salinity, growth was remarkably different. This contrast was probably due to the succulent nature of Cotula, which may require salt for maximum leaf expansion. A rapid development of leaf area would clearly be required to compensate for the lower photosynthetic rates in this species. Stimulation of surface area expansion in Salicornia would also account for the increased dry weight at 10 and 20 ppt relative to the 0 ppt control. Growth stimulations by moderate salinities have been reported for a number of halophytes, including Atriplex halimus (Gale and Poljakoff-Mayber, 1970) and Salicornia rubra (Tiku, 1979). In these cases, a stimulation of leaf or stem photosynthetic surface area, rather than of photosynthesis, accounts for the increased growth. Our results are in agreement.

Scirpus, in contrast, lacks succulent leaves and, in fact, leaf area expansion was inhibited by salinity (Figure 8). Thus, the strong reduction in growth was due to the combination of both reduced photosynthesis and reduced leaf area expansion. Growth in Spartina, which also has non-succulent leaves, exhibited only a slight stimulation at 10 ppt and a strong inhibition at 20 ppt.

At 30 ppt salinity, growth of Spartina, Scirpus and Cotula was reduced to less than 10% of the control growth, whereas Salicornia still maintained appreciable growth (60% of control). This is consistent with the occurrence of Salicornia in the most saline parts of the marsh to the exclusion of essentially all other species. Salinities frequently reach this level during the summer in Suisun marsh and, thus, could be expected to almost completely limit growth of the two desirable species, Scirpus and Cotula. Relative growth rate (RGR) responses to salinity for Scirpus, Spartina and Salicornia are shown in Figure 9. Despite relatively low photosynthetic rates, Salicornia possessed the highest RGR. Conversely, Spartina possessed the highest photosynthetic rate but the lowest RGR. These differences are apparently due to the fact that over the 5 week growing period, all of the Salicornia shoot was photosynthetic and relatively less biomass was allocated to roots or below-ground rhizomes, as shown by the low root-shoot ratio (Table 4). The large allocation to development of photosynthetic surface area in Salicornia more than compensated for the relatively low photosynthetic rate. Spartina, on the other hand, had a large investment of biomass below ground (high root/shoot ratio) and a relatively small investment in photosynthetic surface area.

RGR was generally more sensitive to salinity than photosynthesis. It was clearly reduced in Salicornia, for example, at 30 ppt while photosynthesis was unaffected. Similarly, 20 ppt salinity had no effect on photosynthesis in Spartina, while RGR was strongly reduced. In Scirpus, the reduced leaf area development shown in Figure 7, and an increasing allocation to below-ground structures (Table 3), are both important in the strong inhibition of RGR with increasing salinity. RGR is determined by two factors: net photosynthetic rate and the allocation to production of new photosynthetic surface versus nonphotosynthetic parts. Our results show that when both factors are con-

sidered, the salinity effects on RGR can be clearly understood. Salinity effects on both photosynthetic rate and allocation patterns are clearly important in determining growth performance. Finally, it should be pointed out that relatively small differences in RGR can lead to large differences in productivity. This is because RGR expresses the expotential growth performance of the plant. Thus, the relatively small stimulations in RGR at moderate salinities seen in figure 9 gave large differences in plant size over the 5 week growth period.

II. Field Studies

Field studies were conducted in 1978, 1979, and 1980 at sites both in and outside of Suisun Marsh. Measurements were made at the 3 primary field sites in Suisun Marsh and at Sonoma Creek and Gray Lodge during 1979 and 1980. In 1978, 1979 and 1980 measurements of growth and tuber carbohydrate reserves were made at an additional 6 sites where Mr. Glen Rollins, California Dept. of Fish and Game, was determining salinity and seed yield relationships.

A. Seasonal Patterns of Soil Moisture and Salinity

The three sites in Suisun Marsh exhibited considerable differences in the seasonal patterns of salinity and soil moisture (Figure 10). Soil moisture levels remained highest at the high salinity site throughout the two year cycle. In contrast, the intermediate site had the lowest soil moisture values in the summer but had high values during the winter. Soil moisture values showed less fluctuation at the low salinity site and ranged from 50 to 100% on a dry weight basis throughout the year.

The high and low salinity sites exhibited large differences in soil salinities throughout the year. At the low site, salinities ranged from 3.5 ppt in the winter or early spring to a maximum of 13 ppt in the summer. In contrast, minimum and maximum salinities were 18 ppt and 43 ppt at the high site. The intermediate site exhibited very large seasonal changes in salin-

ity, having salinity values as low as the low site during the winter, and higher than the high site during the summer. Thus, the intermediate status of this site reflects more the large seasonal changes in salinities rather than the actual salinities measured at any particular season. The large seasonal salinity changes at the intermediate site are in part related to the large soil moisture changes, since as soil moistures decrease the salts in the soil solution become more concentrated.

Seasonal patterns of salinity and soil moisture at Sonoma Creek and Gray Lodge are shown in Figure 11. At Sonoma Creek soil moisture remained at high levels throughout the year. Salinities, however, underwent a marked seasonal change, ranging from 5 to 10 ppt in the winter and early spring to 25 to 35 ppt in the summer. This seasonal change in salinity was due to the winter rain/summer drought climatic pattern and the lower salinities in the tidal waters that flush the marsh in the winter and spring as compared to the summer. Both winter and summer salinites were lower in 1980 as compared to 1979. This is most likely due to the greater runoff in 1980 and especially to late spring rainstorms in that year. The large seasonal changes in salinity at Sonoma Creek are comparable to those at the Suisun intermediate site, except that winter and spring values were higher at Sonoma Creek.

At Gray Lodge, the study site was flooded during the winter. After drainage in the spring, soil moisture decreased to very low values during midsummer before increasing again in the fall when the ponds were reflooded. Salinities were quite low throughout the year at this site and never exceeded 9 ppt. Salinities were lower in 1980 than in 1979, possibly reflecting the greater spring precipitation input in the second year.

B. Plant Growth

The maximum heights attained, standing crop and percent of total above-ground weight in reproductive (flowering) shoots for Scirpus are given

in Table 3. There were considerable yearly differences in plant performances as indicated by these values and no pattern was observed that could clearly be related to salinity. In Suisun marsh, standing crops were highest at the low salinity site and lowest at the high salinity site. However, in 1980 this pattern was exactly reversed. Percent reproduction did not appear to be related to salinity in 1979, whereas in 1980 it appeared to be strongly reduced by increasing salinities. Similarly, no easily discernible pattern of plant height versus salinity was apparent that was consistent over the two years. The existence of what appear to be clear relationships between salinity and plant performance in one year but not the other, suggests that factors other than salinity must be taken into account. Possibly, yearly differences in flooding and drainage used as a management tool in Suisun Marsh are responsible for the inconsistent results. At Sonoma Creek and Gray Lodge the results in 1979 and 1980 were considerably more consistent. Standing crops at these two sites were much higher than those measured at the Suisun Marsh sites. Little difference between responses in 1979 and 1980 was apparent at Sonoma Creek. At Gray Lodge both standing crop and % reproduction were higher in 1980 than in 1979, possibly due to the spring rains and lower salinites in the second year.

C. Carbohydrate Reserves

Scirpus vegetatively reproduces from tubers that also function to store carbohydrate reserves. Carbohydrate concentrations are high in the winter but are depleted in the spring as plant growth commences. A substantial amount of the current year's growth and possibly reproductive seed output in Scirpus is thus dependent on carbohydrate reserves stored during the previous year. During the summer, after shoot growth is completed, carbohydrate reserves in the tuber are again built up. Because of the potential importance of carbohydrate reserves in determining seed production in Scirpus, we deter-

mined the seasonal patterns at the field sites in Suisun Marsh and at 6 additional sites where seed production data were being obtained by G. Rollins.

Carbohydrate reserves in % of dry weight and g per tuber are shown in Table 4. Initial carbohydrate concentrations at the start of the growing season were high, averaging 60 percent. For most sites a substantial decline in carbohydrate reserves occurred by the time of seed set in June. Moreover, there was substantial variation in the carbohydrate reserves on an absolute basis as well as in the seasonal change in carbohydrates. This clearly demonstrates, as expected, that stored carbohydrates are heavily utilized to support the rapid vegetative growth and possibly seed production. However, when comparisons are made between seed production estimates provided by G. Rollins and our carbohydrate measurements, no pattern is apparent. This may be due to sampling error since seed production estimates and the carbohydrate estimates could obviously not be done for exactly the same place in the marsh. Local variations in seed production at each site could be quite high due to microtopographic drainage effects, differences in plant densities, etc. An additional factor that we did not take into account was vegetative reproduction. The production of rhizomes and tubers is of considerable significance to the survival of Scirpus since vegetative reproduction is much less risky than seed reproduction; germination and seedling establishment are probably relatively rare events in dense Scirpus stands. Production of new rhizomes and tubers would obviously compete with seed production for reserves and might obscure any relationship between seed production and carbohydrates. It is interesting to note that carbohydrate reserves were much higher at Sonoma Creek where seed production is apparently rare but plants may survive as dormant tubers for at least two years. This suggests that high carbohydrate reserves and tuber production, at the expense of seed production, may be especially favored at this site.

In contrast, sexual reproduction of <u>Scirpus fluviatalis</u> was much higher at Gray Lodge while tuber size was much smaller (carbohydrate contents were not measured). Possibly, this species depends less on vegetative reproduction and consequently invests more in sexual reproduction. The genetic, physiological and environmental controls on vegetative vs. seed production in <u>Scirpus</u> are complex and preclude any simple method of characterizing or predicting potential seed production.

D. Plant Water Potentials

The seasonal course of plant water potentials (ψ) at Gray Lodge, Sonoma Creek and Suisun Marsh are shown in Figure 12. At all three sites water potentials decreased strongly as the season progressed. In Suisun Marsh, dawn plant ψ decreased from −1.5 MPa to less than −3 MPa from mid−May to mid−July. No further measurements were taken after this time as the <u>Scirpus</u> shoots became senescent. Thus, this represents the end of the effective growth period for <u>Scirpus</u>. Midday ψ values showed a similar decline but were always 2 MPa lower than the dawn values. <u>Salicornia</u> had higher dawn but lower midday ψ values than <u>Scirpus</u> throughout the growing season. After early June, midday plant ψ values were too low to measure. The much greater change in ψ from dawn to midday in <u>Salicornia</u> may be due to its occurrence at slightly higher, and therefore possibly slightly drier, microsites than <u>Scirpus</u>. At Sonoma Creek the seasonal decline in plant ψ was more gradual, but since senescence did not occur until the fall, the lowest values reached were similar to those found in Suisun Marsh. Plant values were generally higher at Gray Lodge and senescence occurred earlier at this site than at the other more saline sites. Since soil moistures were quite high throughout the year at Sonoma Creek, the decline in plant ψ can be attributed entirely to seasonal increases in salinity. At Gray Lodge, on the other hand, reduced soil moisture contents account for the decline in plant ψ. In Suisun Marsh, the

situation is complicated since salinities increase primarily because of declines in soil moisture contents and both factors are probably important. The much earlier senescence at Gray Lodge and Suisun marsh than at Sonoma Creek suggests that soil moisture is a very important control on growth and productivity. This is also supported by our observations that in wetter microsites, such as small drainage areas at both Gray Lodge and Suisun marsh, senescence is delayed.

E. Leaf Conductances

The seasonal courses of leaf conductance to water vapor (g_1) are shown in Figure 13. In general, leaf conductances were highest in the early morning when plant ψ values and humidities were highest, and were lower during midday. This was especially pronounced at Sonoma Creek in the spring and at Suisun marsh. A more complete description of the daily courses of g_1 at Sonoma Creek is given by Ustin et al. (1982). The maximum g_1 values were similar at all three sites and occurred during May when salinities were low. After May, g_1 values declined strongly as salinities increased and/or soil moisture values decreased. The large declines in g_1 as salinities increased is consistent with the responses to controlled salinities under laboratory conditions and suggests a strong reduction in photosynthetic productivity by salinity under field conditions. The higher midday conductances after May at Sonoma Creek are consistent with the greater above-ground standing crop accumulation over the season and probably greater vegetative productivity of this population. Since this site reaches high ψ salinities but at the same time maintains high soil moistures, the data suggest that more than salinity alone must be taken into account when considering the productivity responses of Scirpus. Soil moisture may be of particular importance and deserves further consideration.

F. Field Photosynthesis Measurements

Measurements of photosynthesis in the field were made during 1979 in order to provide a check on the laboratory results. Figure 14 shows a typical all-day response of CO_2 uptake measured at Sonoma Creek. Photosynthetic rates were fairly constant throughout the day at about 15 μ mol m^{-2} s^{-1}. Although g_l showed an early morning peak, there was no corresponding peak for CO_2 uptake, possibly because of the variable light conditions due to cloudiness on this day. At Gray Lodge on July 12, CO_2 uptake rates were higher at 8 a.m. and then declined in parallel with g_l values through the rest of the morning.

Table 5 gives the maximum mean photosynthetic rates measured for each date when measurements were taken. The maximum rates measured were at Gray Lodge on May 21. Photosynthetic rates declined over the season as expected from the g_l measurements. Although the variation was greater than found under laboratory conditions, the dependence of photosynthesis on leaf conductance was clearly evident. Moreover, the field behavior of both leaf conductances and photosynthetic rates over the season agree with the predicted behavior from the laboratory measurements. The greater variation in the field data reflects the less precise techniques available for the field measurements, the neccessity of measuring g_l and photosynthesis on separate leaves, and the more variable field environment.

III. Competition

Competition experiments were conducted during 1979, 1980, and 1981. These were done under different day length and temperature conditions during the spring, summer, and fall periods spanning the plants' normal growing season. Although other environmental conditions varied, salinities were held constant and consisted of 1X Hoagland's solution with either 0, 10 or 20 ppt Rila mix. Comparisons of plant competitive responses under different salinity

regimes should allow better interpretation of the ecological significance of the physiological and growth responses to salinity.

As shown in figure 15, the yield of Scirpus in the competitive mixture was greatest in the control solution and was greatly inhibited at both 10 and 20 ppt salinity. In contrast, maximum yields of Salicornia and Spartina occurred at 30 and 10 ppt salinity, respectively. These responses are consistent with both the photosynthetic and growth responses of plants grown in the absence of competition. Thus, the primary determinant of yield in their experiments is the direct effects of salinity. However, competitive effects were also present and these were influenced by the salinity treatment. For each experiment the dashed line shows the expected yield in each mixture if only intra but not interspecific competition were occurring. Where the actual yields fall above the dashed line, it indicates an intraspecific competitive advantage for that species in the mixture. Similarly, where the actual yields fall below the dashed line, it indicates a competitive disadvantage.

As can be seen in figure 15, Scirpus maintained a strong competitive advantage over Salicornia in fresh water, but the advantage shifted to Salicornia as salinities increased. The pattern was less clear for competition between Scirpus and Spartina, primarily because of the very low yields of Spartina at all salinities. The high RGR's and clonal propagation of new shoots from the rhizomes make Scirpus a highly efficient competitor for space when conditions for growth are optimal. Because shoot height in Scirpus is much greater than in either Spartina or Salicornia, early shading is a cause for growth inhibition in these species. Salicornia, while having the highest RGR, lacks the capacity for early clonal growth, and does not develop the height of Scirpus because of its branching physiognomy. The time of the onset of salinity stress appeared important in that it allowed Scirpus, a less salt-tolerant species, to become dominant early and to maintain a height and

shading advantage even after the salt stress drastically curtailed its growth. When the plants were subjected to a salt stress within 3 or 4 days after transplanting, the competitive advantage of Scirpus was much reduced.

The effect of the salinity stress on Scirpus was greater than the effect of competition with either Salicornia or Spartina. However, competition does play an important role in limiting the growth of Salicornia, even at the 20 ppt salinity when Scirpus growth was drastically reduced in both height and biomass. This demonstrates the advantage that the rapid early growth of Scirpus has when salt stress is at a minimum. There was a greater effect on biomass and shoot height from salinity than on the number of shoots per pot in Scirpus. As was found in the RGR experiments, the number of shoots per pot decreased as the salt concentration increased, and the root/shoot ratio in Scirpus was altered under salinity stress, which resulted in a higher precentage of total biomass in the roots and tubers. This same pattern of increased allocation to roots and tubers and reduced shoot growth was noted when the plants were grown in the fall, suggesting that this is part of the general plant response to the induction of dormancy.

Consistent with the RGR experiments, Spartina grew so slowly in these trials that it never became a serious competitor with either Salicornia or Scirpus. It was always smaller and was more severely inhibited by salinity. From these results we can predict that if Spartina becomes established in Suisun Marsh, or other marshes of the delta, it will not primarily compete with these species. The more probable competitive displacement will be with Scirpus acutus, in the more continuously flooded areas along canal and stream banks. This relationship was observed along the tidal marshes on the lower Napa River.

DISCUSSION

Mall (1969) conducted an extensive vegetation survey of Suisun March and on the basis of cover, biomass and seed productivity estimates, developed empirical relationships between competitiveness and the environmental variables of salinity and length of flooding for the major species. He also established relationships between salinity and seed productivity for Scirpus robustus. These relationships, which were based entirely on field correlations, have served to guide much of the management policy for Suisun Marsh. Our results are in general agreement with those of Mall. Additionally, they provide a more experimental basis for understanding the ecological relationships in the Suisun marsh vegetation and especially the salinity responses of Scirpus robustus and its competitors.

The results indicate large differences in the salinity tolerance of photosynthesis among the 4 species tested. The lower tolerances of Scirpus and Cotula all consistent with their occurrence in brackish rather than highly saline sites. Salicornia, on the other hand, is clearly the least affected by salinity, consistent with its occurrence in the most saline sites in Suisun Marsh. The complete lack of any inhibition of photosynthesis in Salicornia is remarkable and indicates an extremely salt tolerant response in this species. While the photosynthetic response of Scirpus is quite sensitive to salinity relative to the other species, it still exhibits a high degree of tolerance as compared to reported responses for crop species (Dowonton, 1977; Gale et al., 1967; Longstreth and Nobel, 1979). Moreover, our measurements were all on leaves that had developed at the particular salinity; there is evidence that Scirpus leaves that were fully developed before the salt concentration was increased were less inhibited (Ustin, unpublished). Since leaves of Scirpus typically expand in the early spring when salinities are low, this may give the plants a greater salt tolerance under field conditions than is apparent in

our laboratory measurements. This is apparent in the field photosynthesis measurements at Sonoma Creek where photosynthesis of Scirpus declined relatively little between April and July despite the large increase in salinity. Unfortunately, there were too many other variables confounded with the changes in salinity, especially in Suisun Marsh where pond draining and subsequent drought stress were clearly important influences, to allow an evaluation of salinity responses under field conditions.

Growth was always more sensitive to salinity than was photosynthesis in all species tested. Nevertheless, there was a good correlation between photosynthesis and relative growth rate responses since both processes were most sensitive in Scirpus and least sensitive in Salicornia. The greater sensitivity of growth than photosynthesis to salinity shows that the latter is not the primary reason for reduced productivity under saline conditions. Instead, productivity may be restricted more by reduced photosynthetic leaf area expansion. Leaf area expansion is dependent on cellular water relations and cell turgor pressures which act as the driving force for cell expansion (Hsiao et al., 1976). Salinity reduces the soil water potential and consequently the plant water potential as is evident in our field measurements. Unless there is an equivalent osmotic adjustment in the cells, turgor will also be reduced. Osmotic adjustment through accumulation of organic acids or salts in the cell may compensate wholly or in part and allow continued growth. This clearly occurs in Salicornia (Pearcy, unpublished data) and apparently in Cotula through accumulation of NaCl. Indeed, in both Salicornia and Cotula moderate salinity appears to be necessary for maximum growth probably because NaCl serves as the osmoticum in the cells. The increased leaf area results in small increases in relative growth rate which compounded over time give large increases in biomass at moderate salinity. The greater productivity of Salicornia at moderate salinity is consistent with other reports.

That this occurs even though photosynthesis per unit leaf area remains constant in Salicornia and declines in Cotula indicates that salinity effects on growth processes other than carbon gain determine the productivity of these species.

Growth is also more inhibited than photosynthesis in Scirpus. The maximum growth rates and biomass at 0 salt concentrations suggest that this species has its maximum potential productivity in fresh water. Its occurrence in brackish to saline sites may involve an ecological displacement rather than an optimum response to the environment, as will be discussed later. Scirpus does not seem to accumulate NaCl to the extent that Salicornia does (Pearcy, unpublished) and may rely primarily on organic compounds for osmotic adjustment. Species that exclude NaCl and utilize organic compounds for osmotic adjustment generally show reduced growth with increased salinity (Greenway and Munns, 1980), indicating that this may be a less efficient or more costly mechanism for adaptation to high salinity (Epstein, 1980).

Two other species in the Suisun Marsh, Distichlis spicata and Atriplex triangularis, have been investigated in other laboratories and the published results can be compared to ours. Both photosynthesis and growth of Atriplex were inhibited by moderate levels of salinity, although not as much as in cotton (Longstreth and Nobel, 1978). Tiku (1976) compared the growth and photosynthesis of Distichlis stricta and Salicornia rubra. For Salicornia rubra, photosynthesis was essentially independent of salinity while growth was increased at moderate salinities, a response identical to that observed here for Salicornia virginica. In contrast, growth and photosynthetic rates of Distichlis were maximum at 0 added salt and declined at even moderate salt levels. A similar inhibition of growth of Distichlis spicata by salinity has been reported by Hansen et al. (1976). Thus, the responses of both Atriplex and Distichlis are similar to those of Scirpus. These responses are consis-

tent with the occurrence of _Atriplex_ primarily in disturbed areas of low salinity and of _Distichlis_ primarily on the higher elevation areas and levee banks where rainwater may reduce salinity levels. Increasing salinities in Suisun Marsh will probably result in a decline in the importance of these two species.

In comparison to our laboratory measurements, the field results are considerably more difficult to interpret. The physiological characteristics, such as plant water potential, leaf conductance and photosynthesis, were clearly influenced by salinity and gave responses that were consistent with the laboratory results. However, growth and seed reproductive output of _Scirpus_ showed no clear relationship to salinity. Similarly, we could find no consistent patterns of carbohydrate reserve that related to either past or present salinities in Suisun Marsh. The complete reversal of results from one year to the next suggests that other factors not accounted for in our measurements are having a major influence. This lack of consistency also suggests that simple regression relationships between seed productivity and salinity, as developed by Mall (1969), are unlikely to provide accurate predictions. While the relationships are undoubtedly qualitatively correct, there are clearly too many other unaccounted-for variables to say more than that, in general, seed produciton will decline with increasing salinity.

Several factors may account for our finding of a poor correspondence between growth, seed production and salinity. We did not take into account year-to-year variations due to flooding and draining. This may be especially important since drought stress following drainage induces dormancy and may greatly reduce productivity. Tradeoffs between sexual (seed) and vegetative (tuber) reproduction may also be important since, if carbon is allocated to the latter, it is not available to the former process. The control of allocation is difficult to investigate in _Scirpus_ since individuals cannot

readily be distinguished. However, we have observed in the greenhouse that tuber production appears to increase at the expense of seed production as salinities increase. Other environmental factors are undoubtedly also important. Under field conditions annual shifts in allocation could be important in determining productivity. Tubers are a more reliable mode of reproduction than seeds and should be favored under stress conditions. In contrast, seed production should be most beneficial in disturbed conditions where seedlings would stand a better chance of establishment. Tubers, on the other hand, provide a mechanism for survival through unfavorable periods. During the 1976 and 1977 drought years Scirpus tubers remained dormant at Sonoma Creek, but sprouted in 1978.

Suisun marsh is intensively managed and most studies, such as those of Mall (1969), have concentrated on the behavior of Scirpus robustus under these managed conditions. Our studies and observations at Sonoma Creek and in other natural marshes provide some insight into the ecology of Scirpus robustus under natural, unmanaged conditions. These, in turn, provide a better basis for understanding its behavior under managed conditions.

Our observations suggest that Scirpus robustus reaches its best development in tidal marshes subjected to large seasonal salinity changes. While there are relatively few of these marshes left, an extensive stand along the Napa River may best typify this habitat. Scirpus robustus occupies nearly all of the high marsh while the low marsh consists of patches of Scirpus acutus separated by zones of Spartina foliosa. Salicornia is nearly absent from the high marsh. Unfortunately, salinity measurements are not available at this site, but it is likely that the water in the Napa River is nearly fresh during the winter months and that salt water encroachment from San Pablo Bay occurs during the summer. This may be a remnant of a more extensive seasonal salinity cycle that occurred in the entire San Francisco Bay-Sacramento Delta

region before flood control (Atwater et al., 1979). Summer salinities were apparently similar to those now found but winter salinities were much lower. Indeed, Scirpus robustus apparently was once much more common in the marshes surrounding San Pablo Bay than it is now (Miller, 1975). This suggests that increasing salinities, particularly the higher winter salinities in the tidal waters, may have been responsible a reduction of Scirpus and an increase of Salicornia.

At the Sonoma Creek site, Scirpus is found only in a narrow zone between the high marsh Salicornia zone and the low marsh Spartina zone. At nearby, higher salinity sites Scirpus is absent from this zone. However, Spartina or Salicornia do not develop significant cover in this zone in the absence of Scirpus, probably because, as Mahall and Park (1976a) suggest, physical factors (flooding for Salicornia, high salinity for Spartina) may be responsible for the zonation patterns. Where Scirpus does occur in this zone it is probably because of the absence of competition from Salicornia. Our competition experiments illustrate the very significant shift in competititve advantage from Scirpus to Salicornia as salinity is increased. We interpret the shift from a Scirpus-dominated high marsh at the Napa River to a Salicornia-dominated high marsh at Sonoma Creek as primarily due to the enhanced competitive ability of Salicornia with the increasing salinities. The occurrence of low spring salinities may be especially important in favoring Scirpus since this is the time of rapid growth of Scirpus which may give it a later competitive advantage for light over Salicornia. Scirpus robustus appears to be tolerant of high summer salinities. Indeed, high summer salinities may favor Scirpus robustus in natural tidal marshes by preventing encroachment of the less salt tolerant but taller species, such as Scirpus acutus, Scirpus californicus and Typha augustifolia. In Suisun Marsh, the draining and subsequent low soil moistures may produce similar results.

The results show that any future increase in salinity in Suisun marsh will probably reduce the distribution and productivity of Scirpus robustus and favor the less desirable species, Salicornia virginiana. However, this effect could probably be mitigated if management practices maintained low salinities during the spring to favor rapid growth and a competitive advantage for Scirpus during this critical period. During the summer it may be advantageous to allow salinities to rise to reduce competition. Any management plan clearly needs to consider this seasonal cycle of salinity as being of equal or greater importance than average salinities.

We recommend that future research on salinity effects on Scirpus and other species in Suisun Marsh be concerned with the establishment of a series of small (10 x 10 M, for example) experimental marshes where salinities, flooding and draining can be experimentally controlled. Manipulation of these marshes would provide a much sounder basis for understanding the effects of increased salinity or of specific management practices than is possible under uncontrolled field conditions.

LITERATURE CITED

Atwater BF, Conard SG, Dowden JN, Hedel CW, MacDonald RL, Savage W 1980
History, landforms, and vegetation of the estuary's tidal marshes in San
Francisco Bay. In The Urbanized Estuary. Pac Div AAAS, San Francisco,
CA. p 347-85

California Dept Fish and Game 1967 Delta fish and wildlife protection study.
Ann Rept (1966-7), the Resources Agency of California. 120 p

Clegg MD, Sullivan CY, Easten JD 1978 A sensitive technique for the rapid
measurement of carbon dioxide concentrations. Plant Physiol 62: 924-926

Dejong TM, Drake BG, Pearcy RW 1981 Gas exchange responses of Chesapeake Bay
tidal marsh species under field and laboratory conditions. Oecologia 52:
5-11

Downton WJS 1977 Photosynthesis in salt stressed grapevines. Aust J Plant
Physiol 4:183-92

Ehleringer JR, Cook CS 1980 Measurement of photosynthesis in the field:
utility of the CO_2 depletion technique. Plant Cell Env 3:479-482

Ehleringer JR, Björkman O 1978 A comparison of photosynthetic character-
istics of Encelia species possessing glabrous and pubescent _leaves_. Plant
Physiol 62:185-90

Epstein E 1980 Responses of plants to saline environments. In Genetic
Engineering of Osmoregulation: Input on Plant Productivity for Food,
Chemicals and Energy. DW Rains, RC Valentine and A Hollaender, eds.
Plenum Press, New York. p. 7-21

Gale J, Kohl HC, Hagen RM 1967 Changes in water balance and photosynthesis
of onion, bean, and cotton plants under saline conditions. Physiol Plant
20:408-20

Gale J, Poljakoff-Maber A 1970 Interrelationships of growth and photosynthe-
sis of saltbush (Atriplex halimus L.) grown in saline media. Aust J
Biol Sci 23:937-45

Greenway H, Munns R   1980   Mechanisms of salt tolerance in nonhalophytes. Ann Rev Plant Physiol 31:149-90

Hansen DJ, Dayanandan P, Kaufman PB, Brotherson JD   1976   Ecological adaptations of salt marsh grass _Distichilis spicata_ (Gramineae), and environmental factors affecting its growth and distribution.   Aust J Bot 63: 635-50

Hsiao TC, Acevedo E, Ferres E, Henderson DW   1976   Stress metabolism.   Phil Trans R Soc Lond B 273:479-500

Jarvis PG   1971   The estimation of resistances responses to carbon dioxide transfer.   _In_ Z Sestak, J Catsky, PG Jarvis (eds), The Plant Photosynthetic Production: Manual of Methods.   The Hague.   pp 566-631

Koyama T   1962   The genus _Scirpus_ Linn.   Some North American alphlloid species.   Can J Bot 40:913-36

Longstreth DJ, Nobel PS   1979   Salinity effects on leaf anatomy: consequences for photosynthesis.   Plant Physiol 63:700-3

Mahall BE, Park RB   1976a   The ecotone between _Spartina foliosa_ Trin. and _Salicornia virginica_ L. in a salt marsh of northern San Francisco Bay.   I. Biomass and Production.   J Ecol 64:421-33

Mahall BE, Park RB   1976b   The ecotone between _Spartina foliosa_ Trin. and _Salicornia virginica_ L. in a salt marsh of northern San Francisco Bay.   II. Soil water and salinity.   J Ecol 64:793-809.

Mall RE   1969   Soil-water-salt relationships of waterfowl food plants in the Suisun Marsh of California.   Cal Dept of Fish and Game Wildlife Bul #1.   59 p

Mall RE, Rollins G   1972   Wildlife resource requirements: waterfowl and the Suisun Marsh.   _In_ JE Skinner (ed), Ecological Studies of the Sacramento-San Joaquin estuary.   Cal Dept of Fish and Game, Delta Fish and Wildlife Protection Study Rpt #8.   p 60-8

Mason HL 1957 A flora of the marshes. UC Press, Berkeley, CA. 878 p

Miller AW, Miller RS, Cohen HC, Schultze RF 1975 Suisun Marsh study, Solano
County, CA. USDA Soil Conservation Service. 186 p

Pearcy RW 1977 Acclimation of photosynthetic and respiratory CO_2 exchange
to growth temperatures in Atriplex lentiformis (Torr.) Wats. Plant
Physiol 59:795-9

Smith D 1969 Removing and analysing total nonstructural carbohydrates from
plant tissue. U Wisconsin Research Rpt #41. 9 p

Schulyer AE 1974-5 Scirpus cylindricus: an ecologically restricted eastern
North American tuberous bulrush. Bartonia 43:29-37

Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA 1965 Sap pressure in
vascular plants. Science 148:339-46

Skinner JE (ed) 1972 Ecological studies of the Sacramento-San Joaquin
estuary. Cal Dept of Fish and Game, Delta Fish and Wildlife Protection
Study Rpt #8. 94 p

Tiku BL 1976 Effect of salinity on the photosynthesis of the halophyte
Salicornia rubra and Distichlis stricta. Physiol Plant 37:23-8

Ustin SL, Pearcy RW, Bayer DE 1982 Plant water relations in the San Fran-
cisco Bay salt marsh. Bot Gaz (in press)

Wit de CT 1960 On competition. Versl Landbouwk Onderz 66:1-82

Table 1. % cover by the dominant species at the 3 primary field sites in Suisun Marsh.

	Scirpus	Salicornia	Distichilis	Juncus	Annuals[1]
Low	12	3	40	7	7
Intermediate	12	48	9	–	2
High	3	48	–	–	–

[1]Includes both <u>Cotula</u> <u>cornupifolia</u> and <u>Atriplex</u> <u>patula</u>.

Table 2. Effect of salinity on the leaf and mesophyll conductances for CO_2.

| | Salinity Treatment, ppt | | | |
	0	10	20	30
Mesophyll Conductance, $g_m^{(1)}$				
$mm\ s^{-1}$				
Spartina foliosa	.90	.96	.93	.77
Scirpus robustus	.39	.40	.27	.15
Salicornia virginica	.17	.12	.13	.19
Cotula cornupifolia	.28	.19	.18	.06
Stomatal Conductance $g_1^{(1)}$				
$mm\ s^{-1}$				
Spartina foliosa	.52	.51	.56	.22
Scirpus robustus	1.35	1.26	.34	.05
Salicornia virginica	.49	.47	.35	.37
Cotula cornupifolia	.57	.25	.21	.11

Table 3. Maximum plant height, standing crop and percent weight in reproductive stems of Scirpus species at sites differing in salinity during 1979 and 1980.

Site	1979			1980		
	Height	Standing[3] Crop	%[4]	Height	Standing[3] Crop	%[4]
	cm	gm^{-2}	Repro	cm	gm^{-2}	Repro
High salinity[1]	82	65	30	32	460	10
Medium salinity[1]	55	223	46	48	386	40
Low salinity[1]	75	282	25	109	151	57
Sonoma Creek[1]	100	800	0	100	783	2
Gray Lodge[2]	108	706	56	100	1576	90

[1] Scirpus robustus

[2] Scirpus fluviatalis

[3] Standing crops measured for 0.25 m^{-2} quadrats containing Scirpus species. Samples not containing Scirpus were not included in the analysis.

[4] Weight of reproductive shoots/total shoot wt X100.

Table 4. Carbohydrate reserves in <u>Scirpus</u> <u>robustus</u> tubers, seed production, and salinity in Suisun Marsh and at Sonoma Creek in 1978 and 1979.

| Site | Carbohydrate reserves[1] | | | | Seed Production[4] |
| | % dry weight | | $g\ tuber^{-1}$ | | $g\ m^{-2}$ |
	initial[2]	seed set[3]	initial	seed set	
			1978		
1	50	10	.242	.080	76
2	45	11	.542	.070	123
3	53	43	.505	.375	2
4	39	68	.269	.412	0
5	---	68	---	.515	5
6	---	81	---	.802	18
			1979		
1	79	18	.520	.133	70
2	39	20	.170	.128	28
3	71	22	.636	.180	7
4	---	21	---	.125	44
5	61	---	.669	---	43
6	---	---	---	---	---
high	41	20	.280	.020	---
med.	---	20	---	.158	---
low	49	2	.380	.020	---
Sonoma Ck.	86	33	1.420	.650	---

[1]Carbohydrate contents are the means of two replicate samples drawn from a random sample of tubers at each site.

[2]Initial carbohydrate contents are for dates.

[3]Carbohydrate contents at flowering are for samples taken at the approximate time of seed set.

[4]Data of G. Rollins, Calif. Dept. of Fish and Game.

Table 5. Mean maximum photosynthetic rates and corresponding leaf conductances for Scirpus species at 3 sites in 1979.

Site	Date	Photosynthesis[1] $mol\ m^{-2}\ s^{-1}$	g_l $mm\ s^{-1}$
Suisun Marsh			
	4-27	$17.3 \pm .2$	11.7
	5-17	$9.6 \pm .1$	6.5
	5-30	$10.3 \pm .2$	6.1
Gray Lodge			
	4-19	$19.9 \pm .2$	8.3
	5-21	$28.5 \pm .6$	14.9
	6-1	$13.7 \pm .1$	8.9
	7-12	13.0	—
Sonoma Creek	4-30	$18.1 \pm .1$	4.9
	6-4	$15.4 \pm .4$	8.7
	7-10	$14.0 \pm .3$	—

[1] mean maximum rates (3 to 5 independent determinations) measured for each date. The leaf conductances correspond to the approximate time of the photosynthesis measurements.
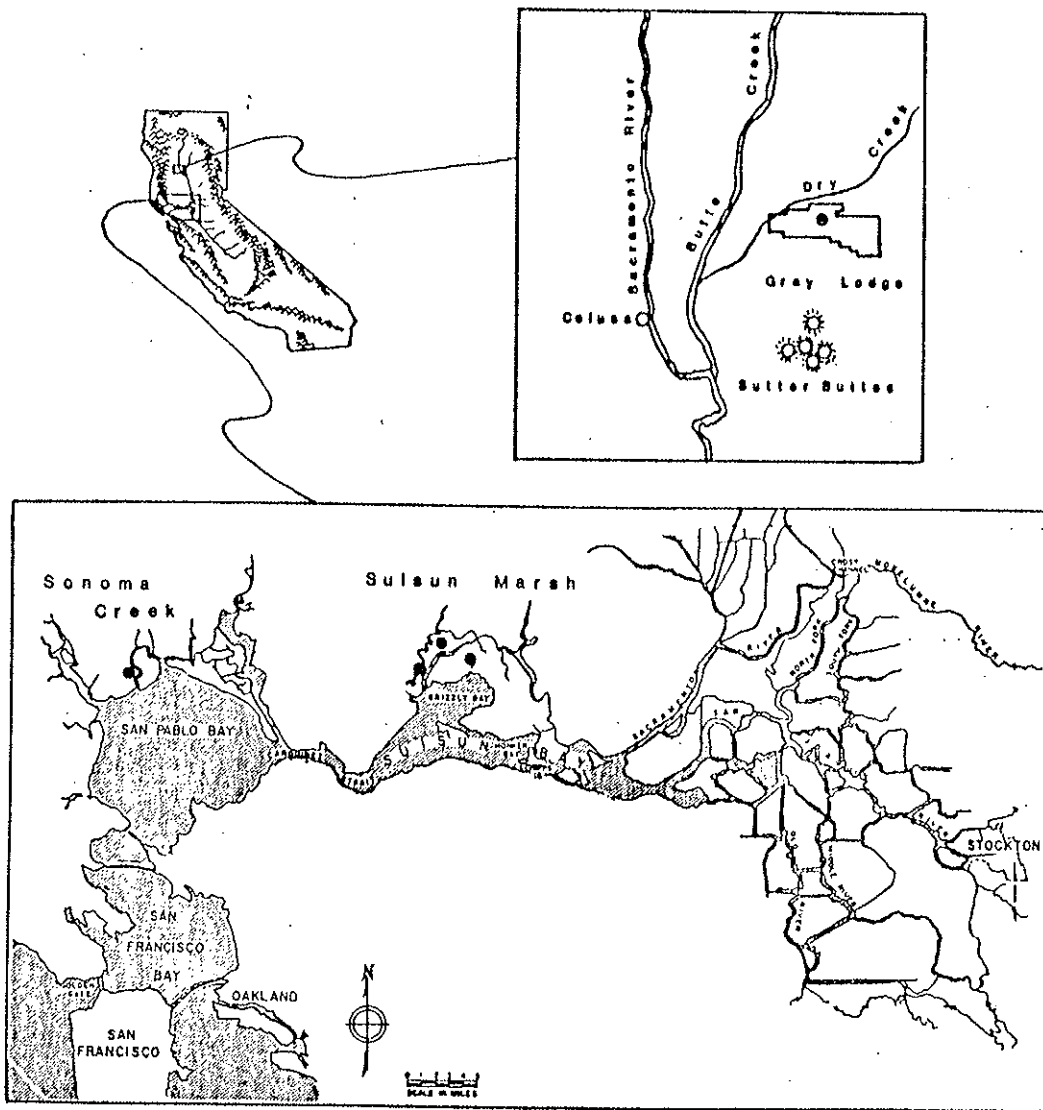
Figure 1. Map showing locations of the study sites (●).
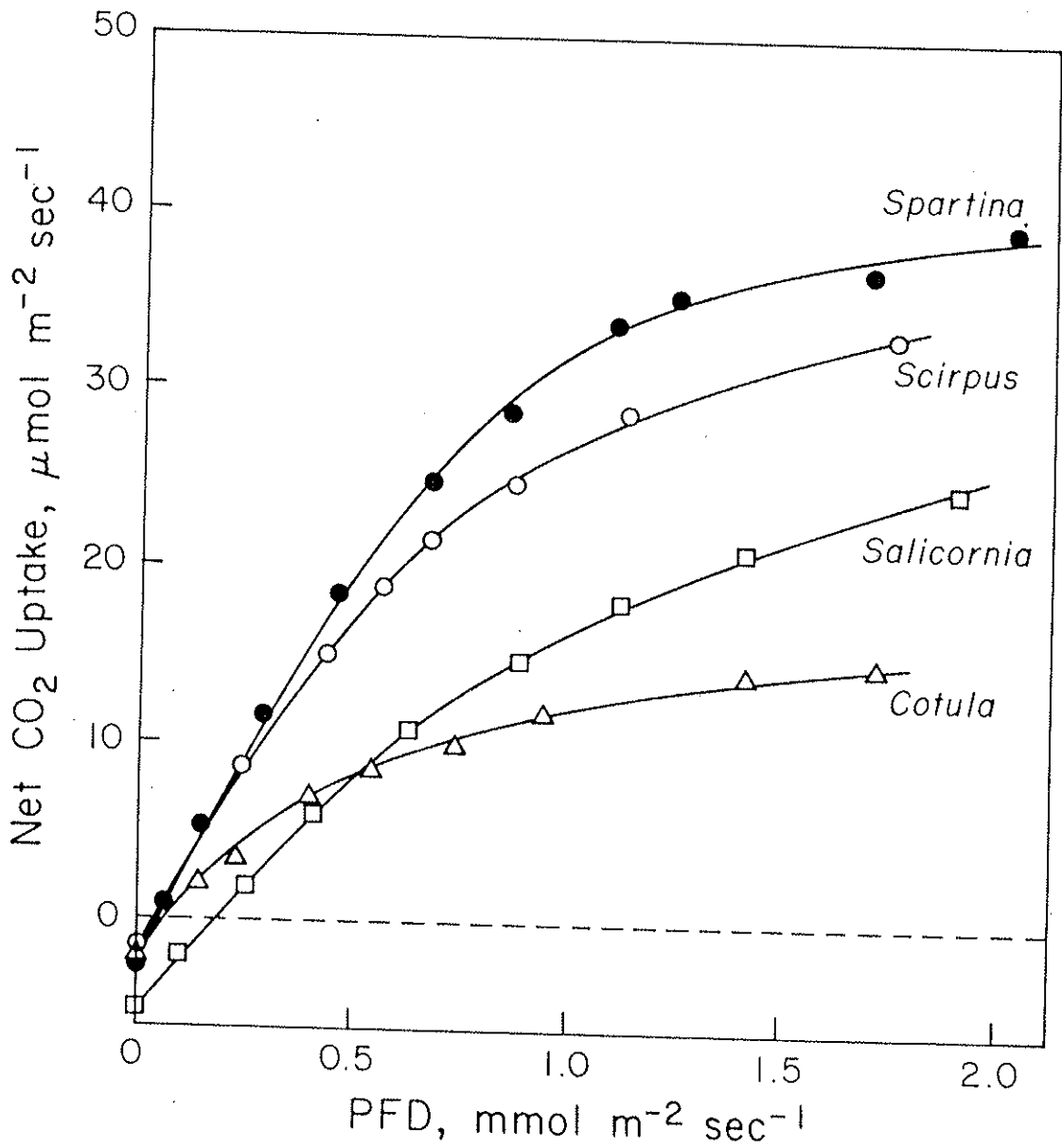
Figure 2. Photosynthetic CO_2 uptake as a function of photon flux density, for

Spartina foliosa (●), Scirpus robustus (O), Salicornia virginica (□), and

Cotula coronopifolia (△). Measured at 30°C leaf temperatures, 320 μbar

CO_2 pressures, and a VPD of 5-10 mbar. The Spartina plant was from the

10 ppt treatment, whereas the other species were from the control.
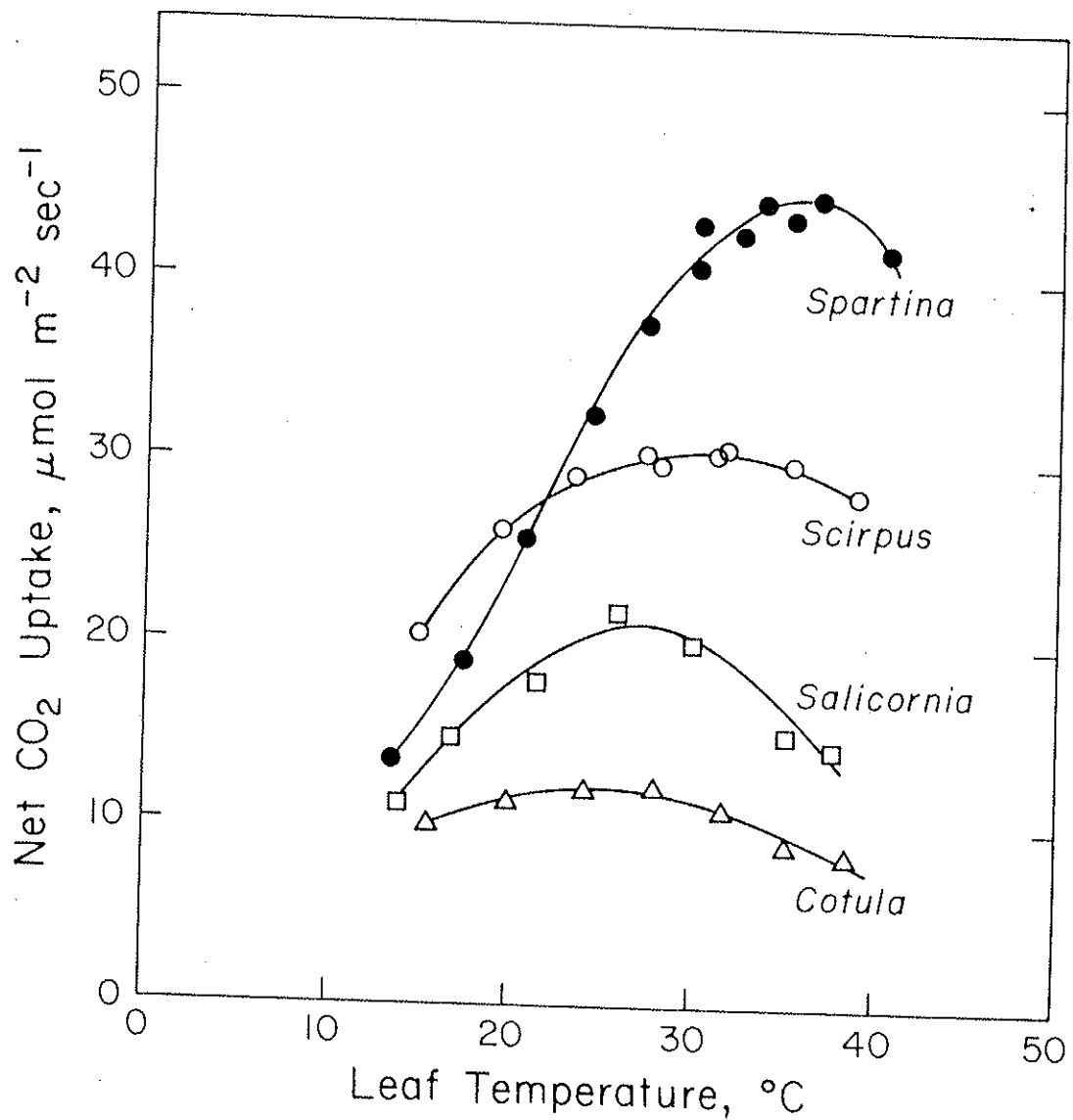
Figure 3. Photosynthetic CO_2 uptake as a function of leaf temperature for Spartina foliosa (●), Scirpus robustus (○), Salicornia virginica (□), and Cotula coronopifolia (△). Measured at high photon flux densities (1.7-2.0 mmol m^{-2} s^{-1}), 320 µbar CO_2 pressures, and a VPD of 5-10 mbar. The plants are from the same treatments as in figure 1.
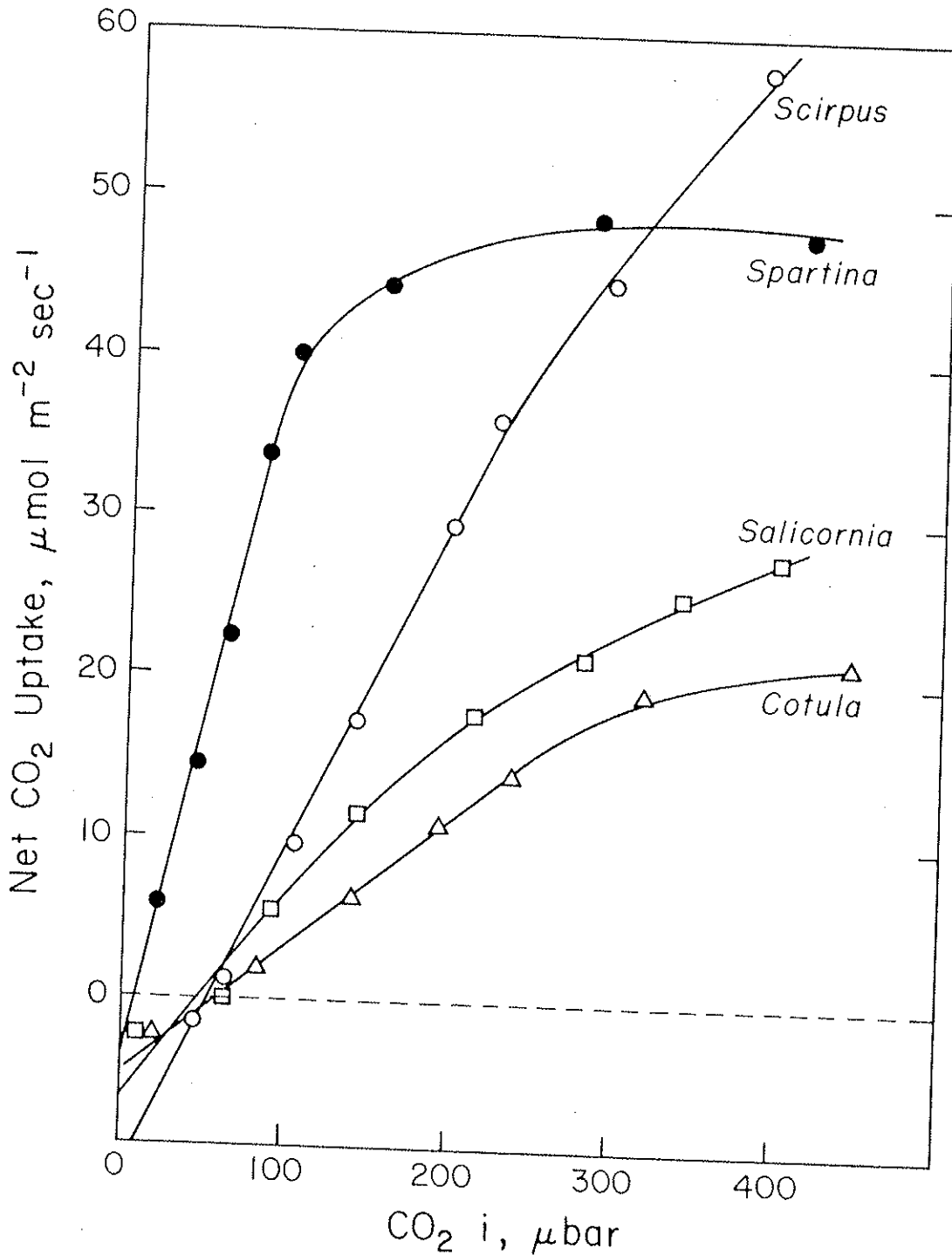
Figure 4. Photosynthetic CO_2 uptake as a function of intercellular CO_2 pressure for <u>Scirpus</u> <u>robustus</u> (⊙), <u>Spartina</u> <u>foliosa</u> (●), <u>Salicornia</u> <u>virginica</u> (□), and <u>Cotula</u> <u>coronopifolia</u> (△). Measured at high photon flux densities of 1.7-2.0 mmol m^{-2} s^{-1}, other conditions are the same as indicated in figure 1.

Figure 5. Effect of salinity on mean CO_2 uptake for _Spartina foliosa_ (●),
Scirpus robustus (○), _Salicornia virginica_ (□), and _Cotula coronopifolia_
(△). Measured at 320 μ bars of CO_2 pressure and photon flux densities
of 1.7-2.0 mmol m^{-2} s^{-1}, leaf temperatures of 30°C and VPD of 5-10 mbar.
Each point represents the mean of 2-8 leaves at each of 4 salinity
treatments.

Figure 6. Relative photosynthetic CO_2 uptake for _Spartina foliosa_ (●),
Scirpus robustus (○), _Salicornia virginica_ (□), and _Cotula coronopifolia_
(△) as a function of salinity. For each treatment, rates are plotted
relative to the maximum rate for each species.
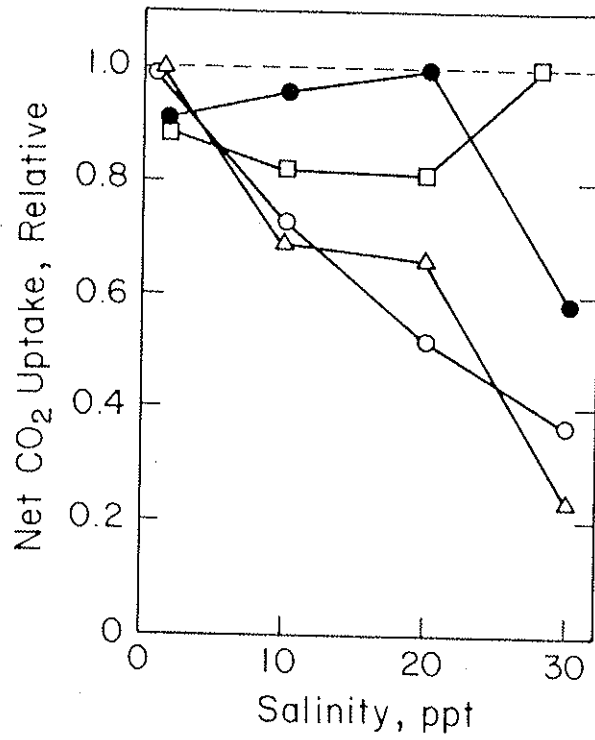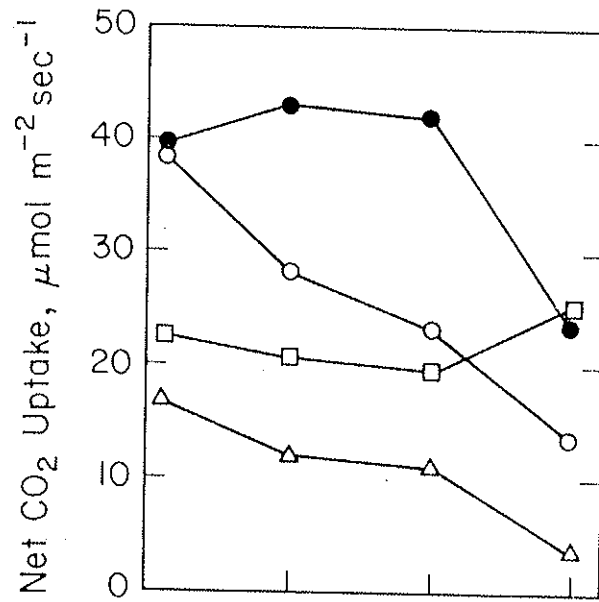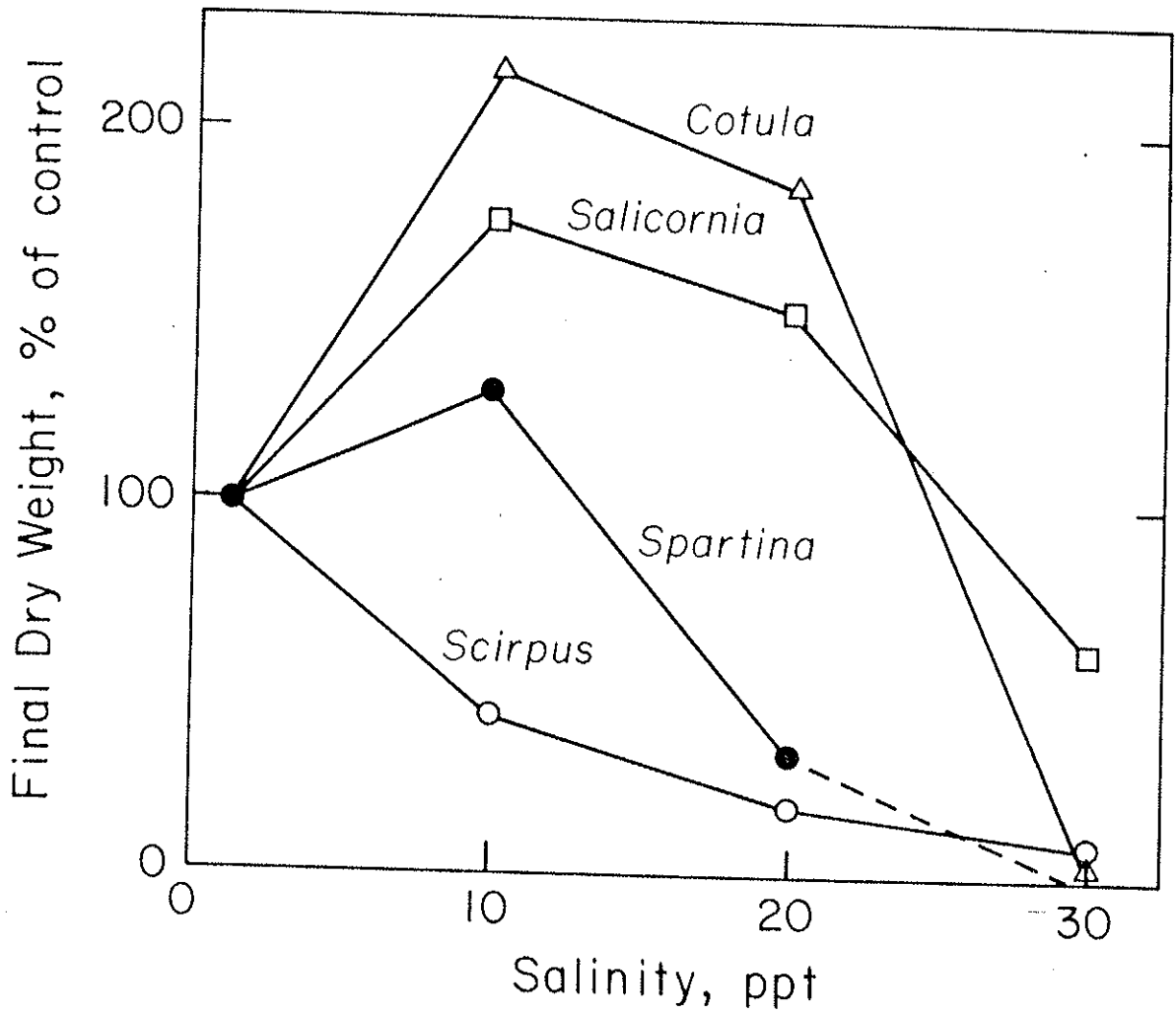
Figure 7. Mean total dry weight (n=5) as a percent of the control dry weight
for Cotula coronopifolia (△), Salicornia virginica (□), Spartina foliosa
(●), and Scirpus robustus (○) at four salinity treatments. Spartina
seedlings were severely inhibited by 30 ppt salinity and final dry weight
declined during the treatment period.
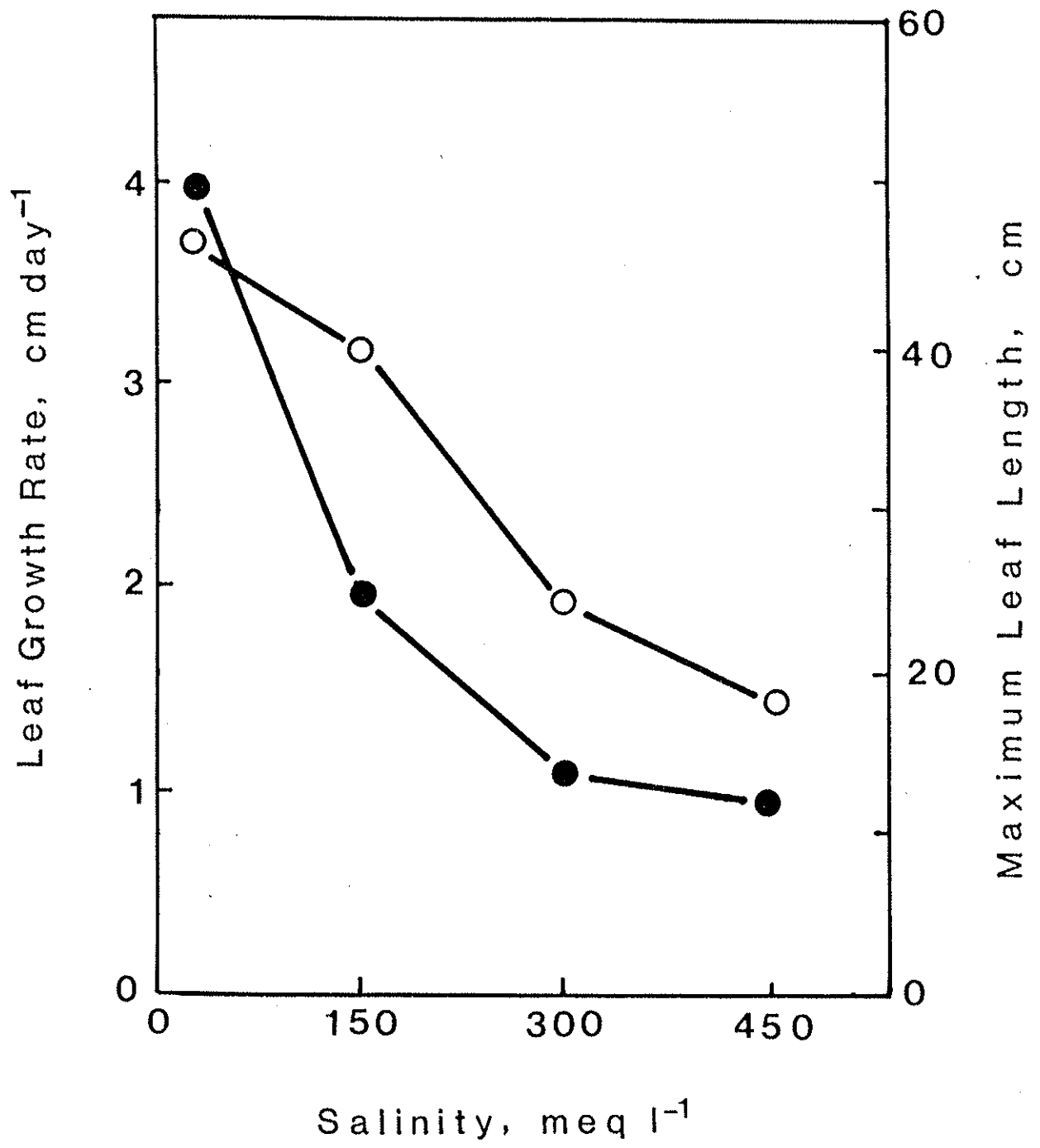
Figure 8. Leaf elongation rate (○) and maximum leaf length (●) of Scirpus
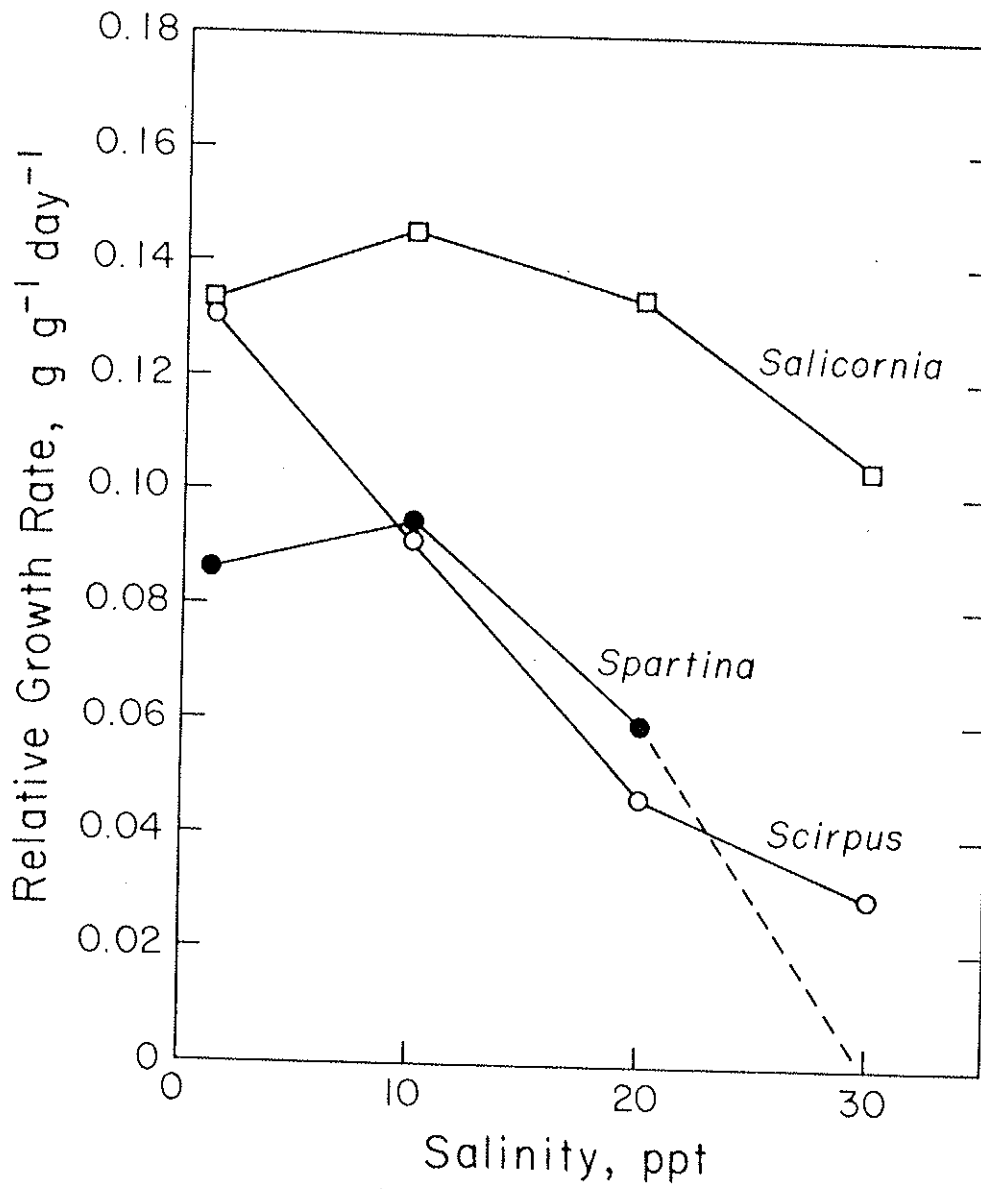robustus as a function of salinity.

Figure 9. Mean relative growth rates (n=4 or 5) of <u>Salicornia</u> <u>virginica</u> (▫),

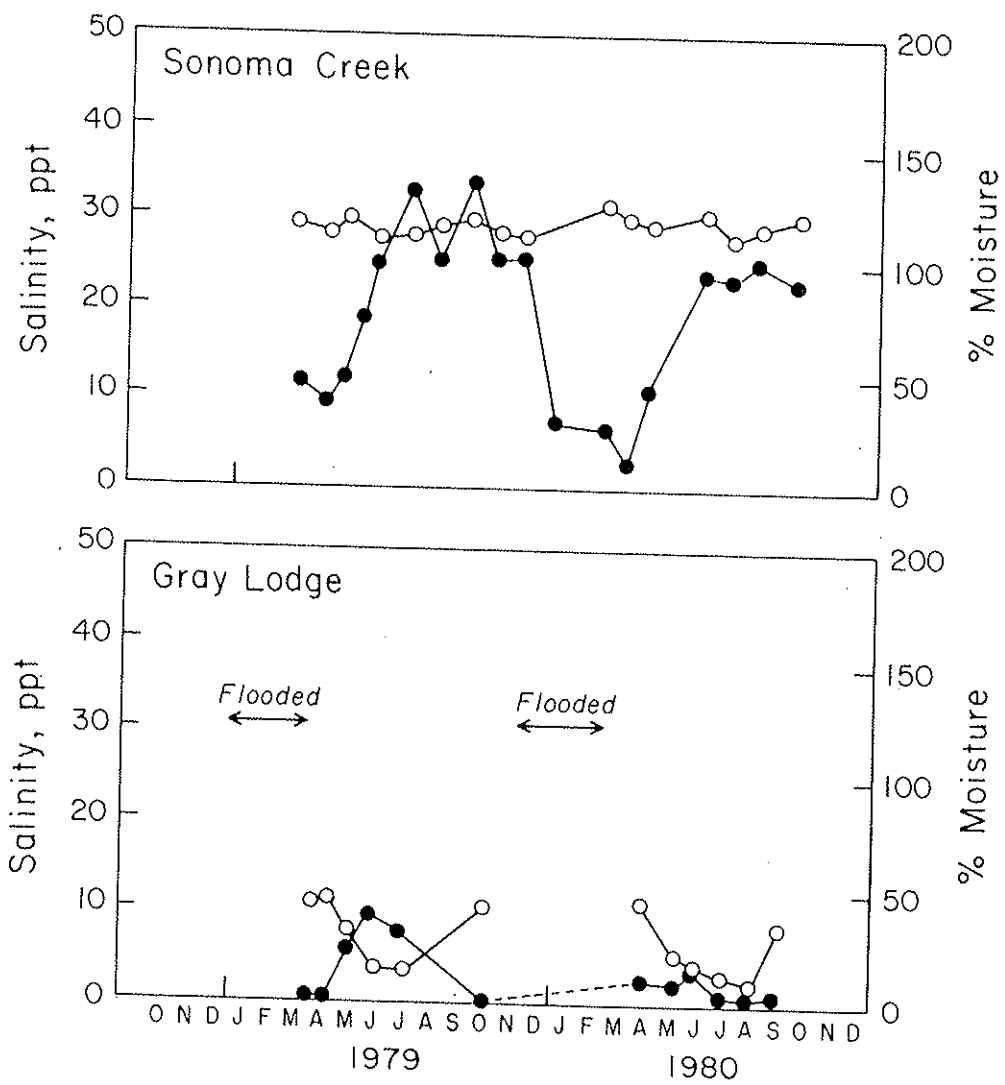<u>Spartina</u> <u>foliosa</u> (●), and <u>Scirpus</u> <u>robustus</u> (O) as a function of salinity.
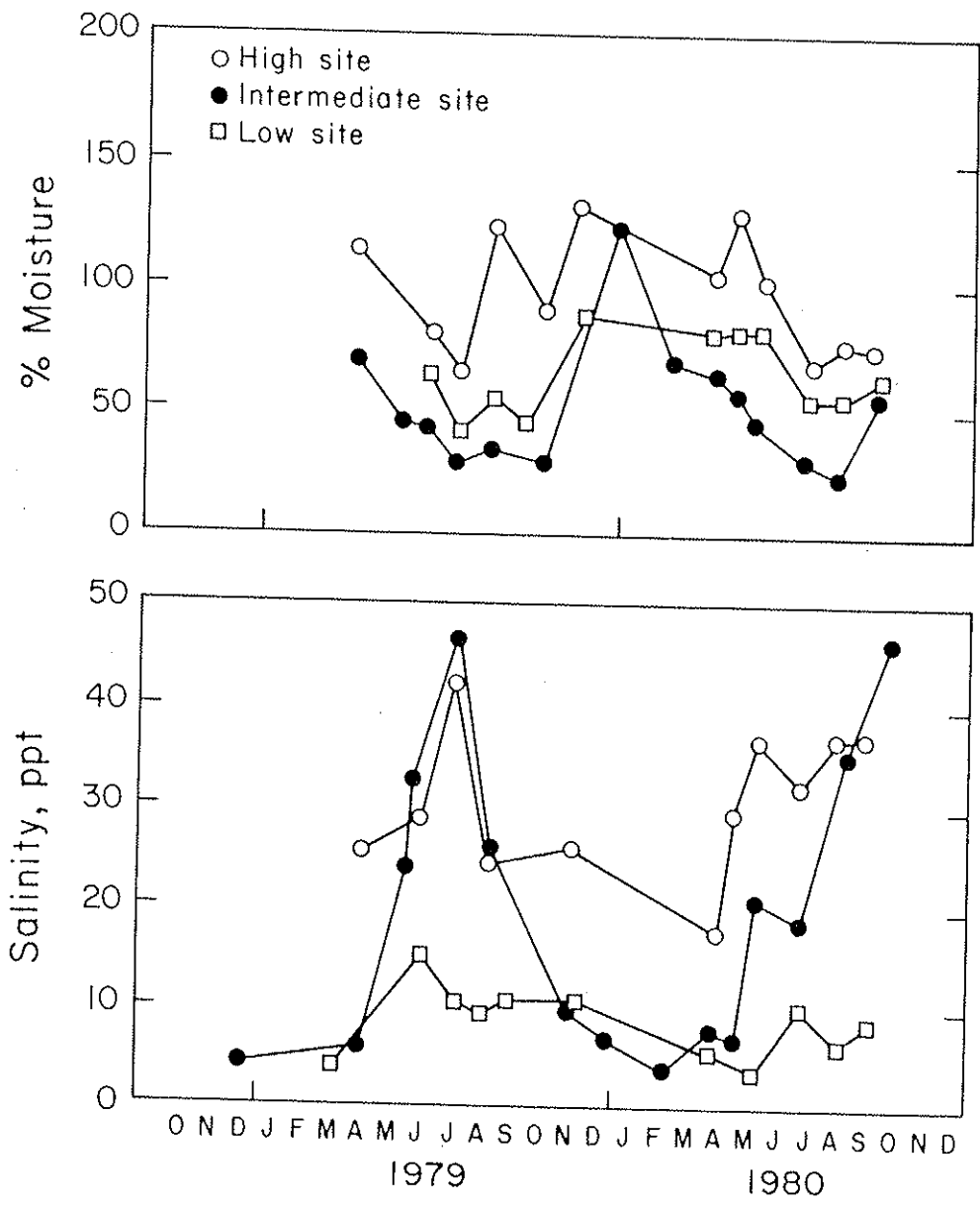
Figure 10. Seasonal progression in percent soil moisture and apparent soil
salinity during the years 1979, 1980 at Suisun marsh. Data is from three
sites within the marsh which differed in soil salinity characteristics.

Figure 11.   Seasonal progression in percent soil moisture (O) and apparent
soil salinity (●) during the years 1979, 1980 at Sonoma Creek and Gray
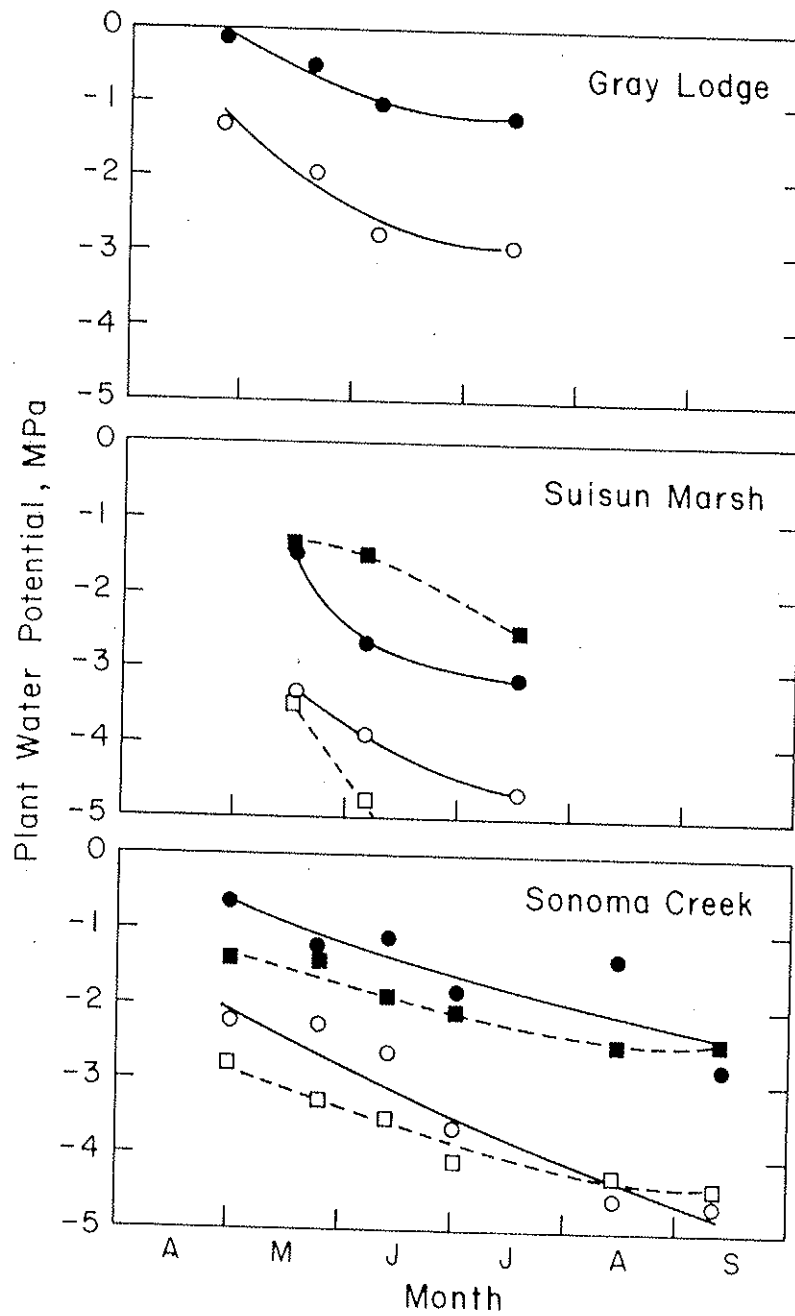Lodge.

Figure 12. Seasonal course of dawn (maximum) (open symbols) and midday (minimum) (closed symbols) water potential for Scirpus fluviatilis (O ●) from Gray Lodge and Scirpus robustus (O ●) and Salicornia virginica (□ ■) from Suisun marsh and Sonoma Creek for 1979. Each point represents the mean of 5-7 leaves.
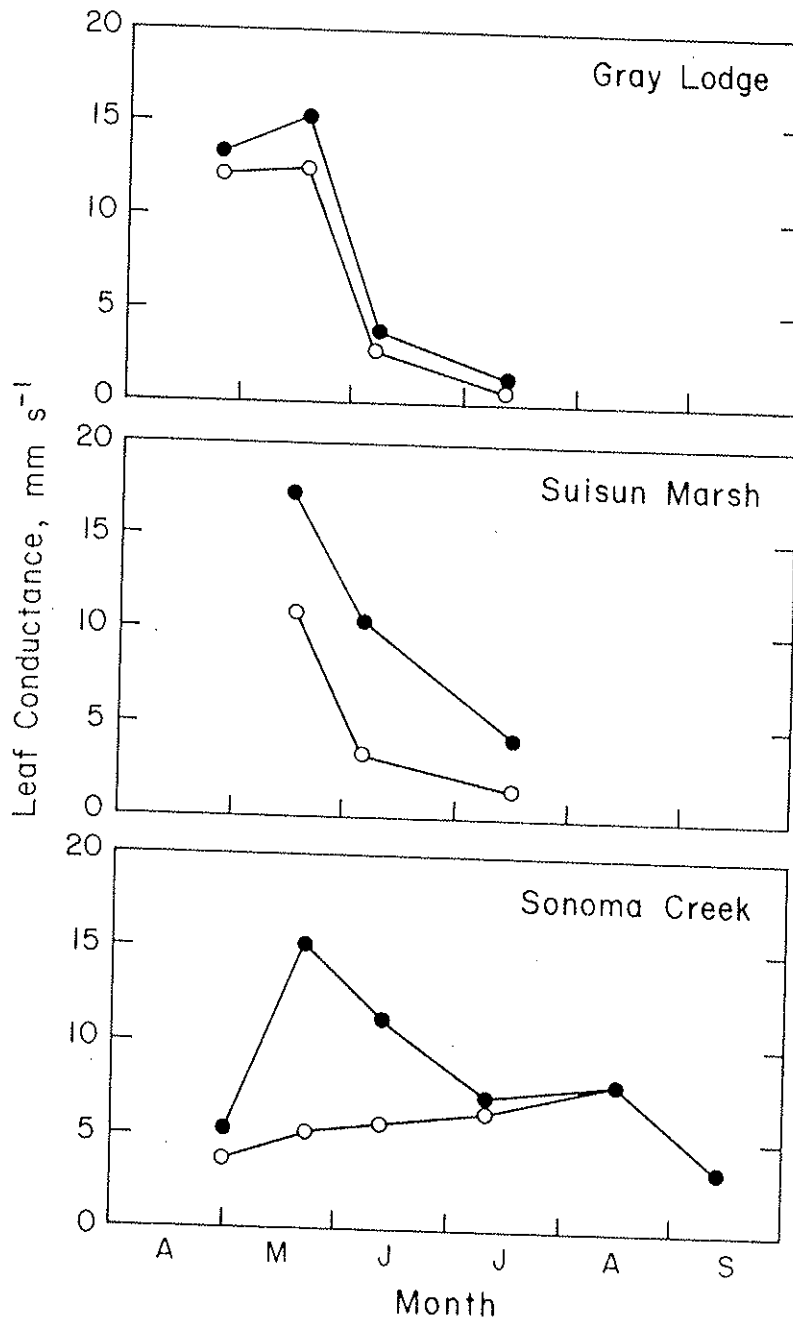
Figure 13. Seasonal course of morning (maximum) (●) and mean midday (○) leaf conductance in 1979 for *Scirpus fluviatiles* from Gray Lodge and *Scirpus robustus* from Suisun marsh and Sonoma Creek in 1979. Each point represents the mean total leaf conductance (abaxial and adaxial surfaces) determined from 5-7 leaves.
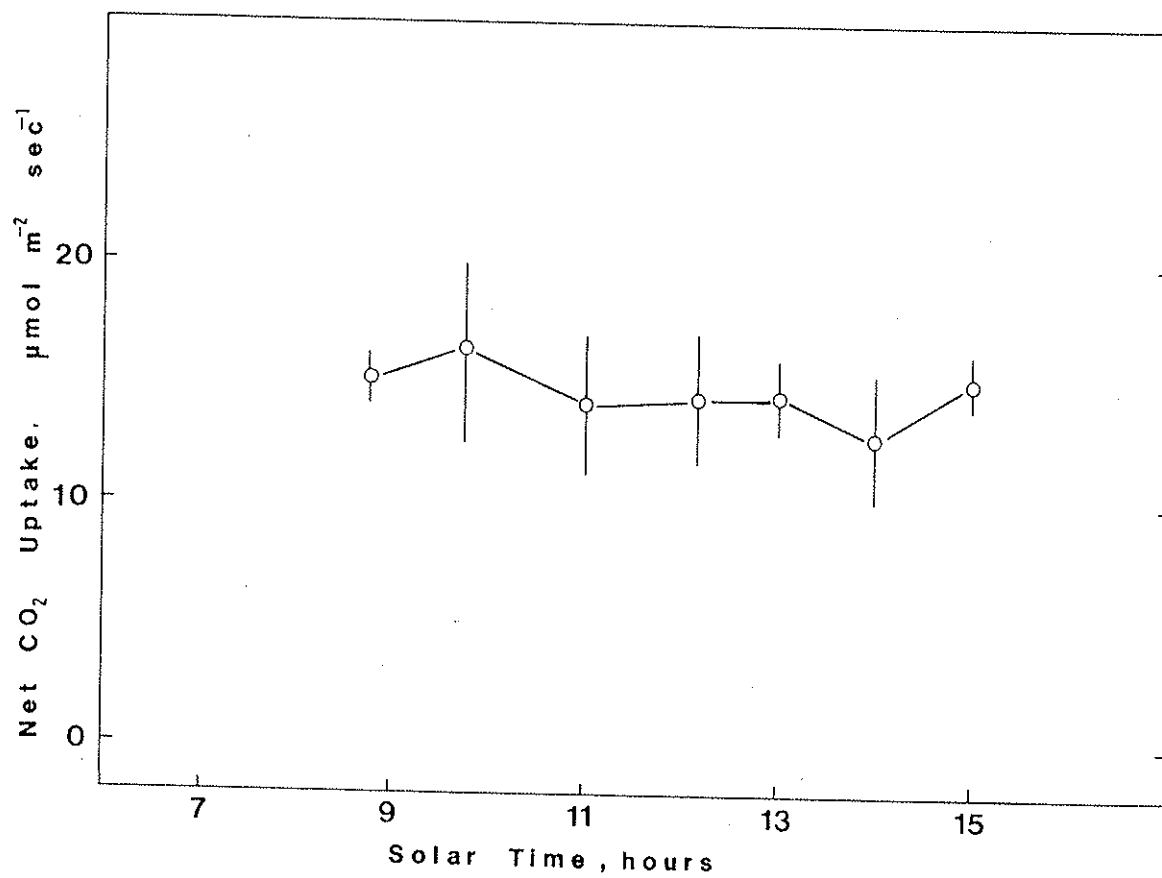
Figure 14. Daily course of photosynthetic CO_2 uptake of _Scirpus_ leaves measured at Sonoma Creek on July 12, 1980.

Figure 15.   Dry weight yields of <u>Scirpus</u> <u>robustus</u>, <u>Salicornia</u> <u>virginica</u> and

<u>Spartina</u> <u>foliosa</u> in replacement series experiments at 3 salinity levels.

The upper set of three figures (across) are the control treatment, the

middle set across, 10 ppt, and the lower set across, the 20 ppt salinity

treatments.   Note that the ordinate scale changes with salinity treat-

ment.   Down the left set of figures are the <u>Scirpus-Salicornia</u> pair, down

the middle set, the <u>Scirpus-Spartina</u> pair and down the right set are the

<u>Spartina-Salicornia</u> pair.   The symbols used for each species are the same

as in previous figures and are indicated below each figure.   The dashed

lines indicate the predicted dry weight if weight changed proportionately

with planting frequency and were independent of all interspecific com-

petitive interactions.   The initial seedling planting density was 10 with

each species alternately planted in 0, 3, 5, 7, 10 seedling combinations.