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Carbon Balance and Water Relations of Sorghum Exposed to Salt and Water Stress[1]

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ABSTRACT

The daily (24 hour) changes in carbon balance, water loss, and leaf area of whole sorghum plants (*Sorghum bicolor* L. Moench, cv BTX616) were measured under controlled environment conditions typical of warm, humid, sunny days. Plants were either (a) irrigated frequently with nutrient solution (osmotic potential −0.08 kilojoules per kilogram = −0.8 bar), (b) not irrigated for 15 days, (c) irrigated frequently with moderately saline nutrient (80 millimoles NaCl + 20 millimoles $CaCl_2 \cdot 2H_2O$ per kilogram water, osmotic potential −0.56 kilojoules per kilogram), or (d) preirrigated with saline nutrient and then not irrigated for 22 days.

Under frequent irrigation, salt reduced leaf expansion and carbon gain, but water use efficiency was increased since the water loss rate was reduced more than the carbon gain. Water stress developed more slowly in the salinized plants and they were able to adjust osmotically by a greater amount. Leaf expansion and carbon gain continued down to lower leaf water potentials.

Some additional metabolic cost associated with salt stress was detected, but under water stress this was balanced by the reduced cost of storing photosynthate rather than converting it to new biomass. Reirrigation produced a burst of respiration associated with renewed synthesis of biomass from stored photosynthate.

It is concluded that although irrigation of sorghum with moderately saline water inhibits plant growth in comparison with irrigation with nonsaline water, it also inhibits water loss and allows a greater degree of osmotic adjustment, so that the plants are able to continue growing longer and reach lower leaf water potentials between irrigations.

Physiological studies have often dealt separately with salt and water stresses, but in the field, salt stress is usually accompanied by water stress. Soil salinity problems occur most often in arid regions where soil moisture deficits are also frequent. Irrigation of crop plants with poor quality irrigation water often results in both salt stress and water stress in the dryer parts of the irrigation cycle, yet there is very little published information about the physiological responses of plants to this common condition.

Both low soil osmotic potentials (due to dissolved salts) and low soil matric potentials (associated with reduced soil water content) cause lower water potentials in plants. In glycophytes, soil moisture deficit and soil salinity each result in reduced leaf expansion rates and lower photosynthetic rates per unit of leaf area (1, 5, 18, 21). Effects on respiratory rates seem to be more complex, since soil moisture deficits have been shown to reduce both the growth and maintenance components of respiration (23), but salinity caused an increase in maintenance respiration (20). Neither salinity nor water stress affected the yield of growth processes, which is the ratio of net carbon gain to gross carbon input after subtracting maintenance losses (20, 23). There are no data on photosynthetic or respiratory rates of plants exposed to both salt stress and water stress.

Many plant species adjust osmotically when exposed to either salt in the growth medium (3, 8) or reduced soil moisture (10). Osmotic adjustment is beneficial in that it allows photosynthesis and growth to occur at lower plant water potentials than would otherwise be possible (15). There may well be a metabolic cost of this adjustment; however, the net effect on the daily carbon balance was found to be positive in sorghum plants exposed to water stress (15).

It is known that NaCl salinity may be beneficial to the water balance and growth of halophytes, particularly under water stress conditions (6, 7, 14). Salt in the growth medium may provide some benefits even for glycophytes. Two studies of the combined effects of salt and water stresses on growth of wheat (*Triticum aestivum L.*) (21) and maize (*Zea mays* L.) (22) showed that although salinity reduced the rates of leaf expansion under well-irrigated conditions, it also allowed leaf expansion to continue down to lower leaf water potentials under water stress. Thus, the combined effects of salinity and water stress may be less detrimental to plant growth and carbon gain than the sum of the separate effects of salinity and water stress.

In a previous paper we analyzed the water relations and the daily carbon balances of vegetative sorghum plants undergoing osmotic adjustment during a cycle of water stress and reirrigation (15). In this paper we extend our studies to include the effects of salinity, both alone and in combination with water stress.

MATERIALS AND METHODS

Four treatments were studied: (a) no salt or water stress, (b) salt stress without water stress, (c) water stress without salt, and (d) both salt and water stress. All treatments were continued for several weeks, and were replicated two to four times with similar sized plants.

In all four treatments, seeds of sorghum (*Sorghum bicolor* L. Moench., cv BTX 616) were placed on moistened tissue paper for 2 d, and the germinated seeds were planted in pots containing 2.5 L of fritted clay growth medium (Absorb-N-Dry). Plants were irrigated daily with sufficient full strength nutrient solution to cause drainage (*i.e.* to excess). The osmotic potential of the solution was −0.08 $kJ \cdot kg^{-1}$ (1 $kJ \cdot kg^{-1}$ = 1 MPa = 10 bars, approximately).

Fifteen d after planting, the plants were repotted into 8 L pots. For the two saline treatments, irrigation with full strength nutrient solution was continued for 2 d after repotting, then the plants were irrigated to excess daily for 7 d with full strength nutrient solution containing 100 mmolal salt (80 mmol NaCl + 20 mmol $CaCl_2 \cdot 2H_2O$ per kg water, total osmotic potential

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−0.56 kJ·kg^{-1}). For a moderately tolerant species such as sorghum, this salt concentration should be slightly above the threshold level for a reduction in vegetative production in the field (4). In the two nonsaline treatments, irrigation was continued with full strength nutrient solution without salt.

Growth conditions were: air temperature 30°C, dewpoint temperature 10 to 15°C, CO_2 concentration 330 to 420 μl L^{-1}, windspeed 0.7 m s^{-1}, PPFD[2] 1000 μmol s^{-1} m^{-2}, daylength 12 h. Tillers and dead leaves were removed, and leaves were numbered as they emerged.

When the 8th leaf was fully expanded and the 12th leaf was emerging from the whorl (between 25 and 27 d after planting), the test plants were moved to whole-plant assimilation chambers for determination of the daily carbon balance. In the two water-stressed treatments, irrigation was stopped when the plant was placed in the assimilation chamber. The plants were reirrigated when the net carbon gain (ΔW) fell to about 0.3 gC d^{-1}. The nonsalinized plants were reirrigated to excess with 4 L full strength nutrient solution during the night of the 15th d in the chamber. The salinized plants were reirrigated the night of the 22nd d with 7 L of 100 mmolal salt in full strength nutrient solution. This was judged sufficient to leach salts accumulated since the previous irrigation. In the two treatments without water stress, plants were irrigated every other day to excess with 1 to 2 L of full strength nutrient solution, or with nutrient solution containing 100 mmolal salt.

The air temperature in the chamber was 30°C, the dewpoint temperature was 23°C, the PPFD at the top of the plant was 1400 μmol s^{-1} m^{-2} for 12 h, and the windspeed was 0.5 m s^{-1}. The CO_2 concentration was maintained in the range 320 to 350 μl L^{-1} by manual enrichment with CO_2 during the light period. As in previous experiments (15, 23), integrated CERs, per plant were used to calculate values of the three daily (24 h) carbon balance parameters:

ΔS = gross input of substrate carbon from photosynthesis (gC plant^{-1} d^{-1})
= integrated CER in 12 h of light minus integrated CER in 12h of darkness (where dark CER is negative) (it was assumed that the daytime loss was equal to the nighttime loss)

ΔW = net 24 h gain of carbon by the plant (gC plant^{-1} d^{-1})
= integrated CER in 12h of light plus integrated CER in 12 h of darkness

and

ΔR = 24 h loss of carbon due to respiration
= $\Delta S - \Delta W$

Leaf areas were calculated as length × maximum width × 0.68 (15). Leaf length was measured as the distance from the tip to the ligule on fully expanded leaves, and from the tip to the deepest visible part of the whorl on expanding leaves. Visually estimated senescent leaf area was subtracted from the calculated leaf area to give green leaf area.

To determine the water status of the plants during the stress cycle, a port in the assimilation chamber was opened briefly and 6 mm disc samples of fully exposed leaves were taken from psychrometric measurement of water and osmotic potentials (15). Pressure potentials were estimated by subtracting osmotic potentials from water potentials.

Water potential samples were taken daily (or every other day in some cases), 4 h before the end of the day. In separate experiments under identical conditions designed to quantify the degree of osmotic adjustment (15), four to eight leaf discs that had been punched from fully exposed leaves in the daytime were allowed to dry for various lengths of time (up to 3 min) before placing them in the sample chambers. The water potential at zero turgor was estimated by linear regression analysis of water potential *versus* pressure potential for these discs ($r^2 > 0.92$). In cases where the pressure potential was already zero, some of the discs were rehydrated by floating them on water and blotting the surfaces dry before placing them in the chamber.

Water loss was determined by weight change. Each potted plant was suspended from a load cell in the assimilation chamber. The pot was wrapped with aluminum foil to minimize water loss other than transpiration. A few small holes were punched in the foil to allow gas exchange and to allow entry and drainage of the irrigation solution. Load cell voltages were measured hourly and differences were converted to WERs using calibration factors obtained by adding various amounts of water to dry fritted clay in the pots. Daily (24 h) water loss rates were calculated by integrating hourly WERs.

CER and WER data were collected and analyzed hourly with a data acquisition and control unit (Hewlett-Packard model 3497A), which was controlled by a personal computer (Hewlett-Packard model 9816S). The data unit incorporated a quartz clock, a digital voltmeter, two 20 channel relay multiplexers for analog voltage and thermocouple output measurement, and an 8 channel actuator for 120 V switching.

The actuator was used to control the sequence of lighting and gas sampling for the two assimilation chambers. The multiplexers were used to switch the digital voltmeter in sequence to thermocouples in the chambers, to an IRGA (Binos model 4a.1) measuring CO_2 concentration in incoming and exiting gas streams, to mass flowmeters for measurement of CO_2 injection rate (Tylan model FM 360), and to load cells for plant water loss measurement (Alphatron model SL 50). The microcomputer controlled the data unit, accepted the voltage data from it, and calculated and plotted all the CO_2 and water exchange parameters from these data, using the calibration factors for each instrument.

RESULTS AND DISCUSSION

Water Status (Fig. 1). During the first few days of the water stress cycle, leaf osmotic potentials of the plants that had been preirrigated with saline nutrient solution were about 0.4 kJ·kg^{-1} lower than the respective values for the plants that had been preirrigated with nonsaline nutrient solution (Fig. 1c). However, pressure potentials were about equal, showing that the salinized plants had fully adjusted to the salt before the experiment was begun (Fig. 1a).

Water stress developed gradually in both treatments up to d 12. In the nonsalinized plants, water potentials (Fig. 1b) and osmotic potentials (Fig. 1c) then dropped rapidly. Water and osmotic potentials decreased much more slowly in the salinized plants; positive (although reduced) turgor was maintained for 2 additional days. During d 13 through 15, water, osmotic, and pressure potentials were higher in the salinized plants.

Plants were reirrigated (with saline or nonsaline nutrient solution) when net carbon gain dropped to 0.25 to 0.35 gC d^{-1}. This occurred 7 d later in the salinized plants. Upon reirrigation, water potentials increased more rapidly than osmotic potentials, so that pressure potentials were higher immediately after reirrigation than they were in the initial well-irrigated phase of the experiments. Pressure potentials had returned to near prewater-stress values by 4 d after reirrigation. Salinized plants still had water and osmotic potentials about 0.4 kJ·kg^{-1} lower than their original values.

The data for the water potential at zero turgor (Fig. 1d) indicated that the salinized plants adjusted over a longer period of time and reached lower values.

Time Trends of Leaf Area and Carbon Balance (Fig. 2). Com-

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[2] Abbreviations: PPFD, Photosynthetic photon flux density; CER, CO_2 exchange rate; WER, water exchange rate; WUE, water use efficiency; LA, leaf area.

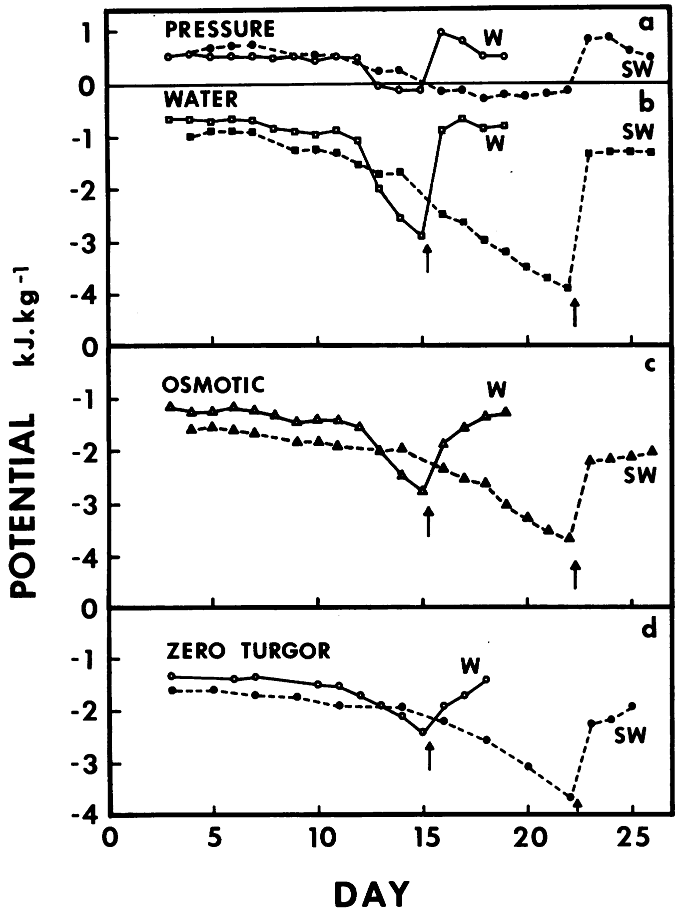

FIG. 1. Pressure potential, water potential, osmotic potential, and water potential at zero turgor, of sorghum plants exposed to water stress (treatment W) or salinized and then exposed to water stress (treatment SW). Data were determined psychrometrically on discs punched from fully exposed attached leaves, 4 h before the end of the day. The zero turgor potential was estimated from a linear regression of pressure potential on water potential. Arrows indicate times of reirrigation.

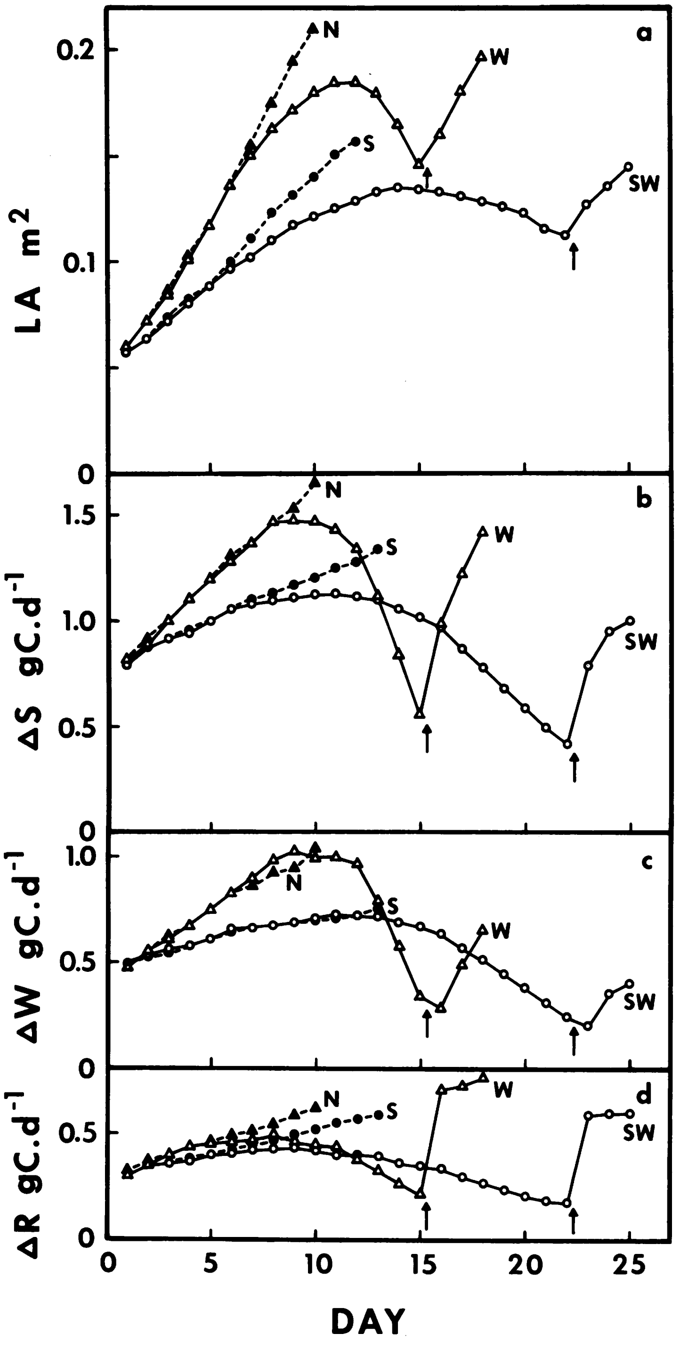

FIG. 2. Total leaf area (LA), daily (24 h) gross photosynthetic carbon input (ΔS), daily net carbon gain (ΔW), and daily carbon loss due to respiration (ΔR), of sorghum plants irrigated on alternate days with nutrient solution (nonstressed plants, treatment N), irrigated on alternate days with nutrient solution plus −0.48 kJ·kg^{-1}salt (salt-stressed plants, treatment S), exposed to water stress (treatment W), or salinized and then exposed to water stress (treatment SW). ΔS, ΔW, and ΔR were determined by integration of CO_2 exchange rates. Arrows indicate times of reirrigation of W and SW treatments.

parison of the nonstressed and salt-stressed treatments shows that salt lowered the rate of increase of green LA and caused reductions in all of the carbon balance parameters: gross photosynthetic input of substrate carbon (ΔS), net carbon gain (ΔW), and carbon loss due to respiration (ΔR).

In both of the water-stressed treatments, inhibition of leaf area increase did not become evident until d 7 (Fig. 2a). LA of the nonsalinized water stressed plants peaked on d 12 and decreased rapidly thereafter. The salinized plants continued to increase in leaf area for 2 d longer, and the rate of senescence (decrease in green leaf area) was much slower. Upon reirrigation, leaf areas resumed rates of increase similar to early in the cycle in both treatments.

Gross carbon input ΔS (Fig. 2b) tended to follow LA, but it peaked and began to decline 2 to 3 d before LA peaked, and the declines in ΔS were more drastic than the decreases in LA. This shows that the decline in ΔS with increasing water stress was due both to decreasing LA and to decreasing gross carbon input per unit of LA.

Net carbon gain ΔW (Fig. 2c) was generally less affected by water stress than was gross carbon input (ΔS). For example, the salinized water-stressed plants maintained ΔW values virtually identical to those of the salt-stressed plants through d 12, even though differences in ΔS values had occurred by d 7. Comparing the nonsalinized water stressed plants with the nonstressed plants, ΔS values were identical through d 8, but on d 7, 8, and 9 the water stressed plants actually had greater ΔW values than the nonstressed plants.

The smaller effects on ΔW than on ΔS over this period can be attributed to compensatory changes in the respiratory loss ΔR; when leaf expansion is inhibited but photosynthesis is continuing at a high rate, the plants can store photosynthate. This is metabolically less expensive than using it to produce new leaf tissue, and hence ΔR is decreased and ΔW is increased over the value for a nonstressed plant (15). In the case of the salt-treated plants, this cost reduction evidently was balanced by an additional metabolic cost associated with the salt, so that ΔW was the same for the salinized and nonsalinized plants under water stress.

LA, ΔS, and ΔR of both the water-stressed and the salinized water-stressed plants increased dramatically on the 1st d after reirrigation, but, because of the great increase in ΔR associated with the postirrigation burst of leaf growth, ΔW did not show an increase until 2 d after reirrigation (15).

Net Gain/Gross Input (Fig. 3). A plot of ΔW *versus* ΔS shows trends in the overall efficiency of utilization of photosynthetic carbon by the plant. The salt-stressed and nonstressed plants initially tracked close together in this respect but began to diverge at higher ΔS values (Fig. 3a). The lower amount of ΔW for a given ΔS value in the salt treatment shows that there was a metabolic cost associated with increased salinity.

The ΔW *versus* ΔS plot of the salinized plants exposed to water stress (Fig. 3b) followed a general pattern similar to that of the nonsalinized water-stressed plants (Fig. 3c). ΔW increased linearly with ΔS during the first several days after the irrigation on d 0. As water stress increased and leaf expansion began to be inhibited, ΔW for a given ΔS increased. This was presumably because the plants were storing photosynthate rather than using it for synthesis of new leaves (15).

As water stress became more severe, leaves began to senesce, stomates began to close, and ΔW decreased linearly with ΔS. Plants were reirrigated when ΔW fell to about 0.3 gC d^{-1}. On the day following reirrigation ΔW did not increase even though there was a large increase in ΔS. This was attributable to the large respiratory cost of rapid synthesis of new leaves from stored photosynthate (15). On succeeding days both ΔW and ΔS increased rapidly in a linear fashion and approached the original trend line.

The ΔW *versus* ΔS plot for the salinized plants differed from that of the nonsalinized plants primarily in the slower rate of increase or decrease in ΔS with time (the points are closer together) and in the lower maximum value of ΔS achieved.

Leaf Area and Carbon Balance *versus* Water Potential (Fig.

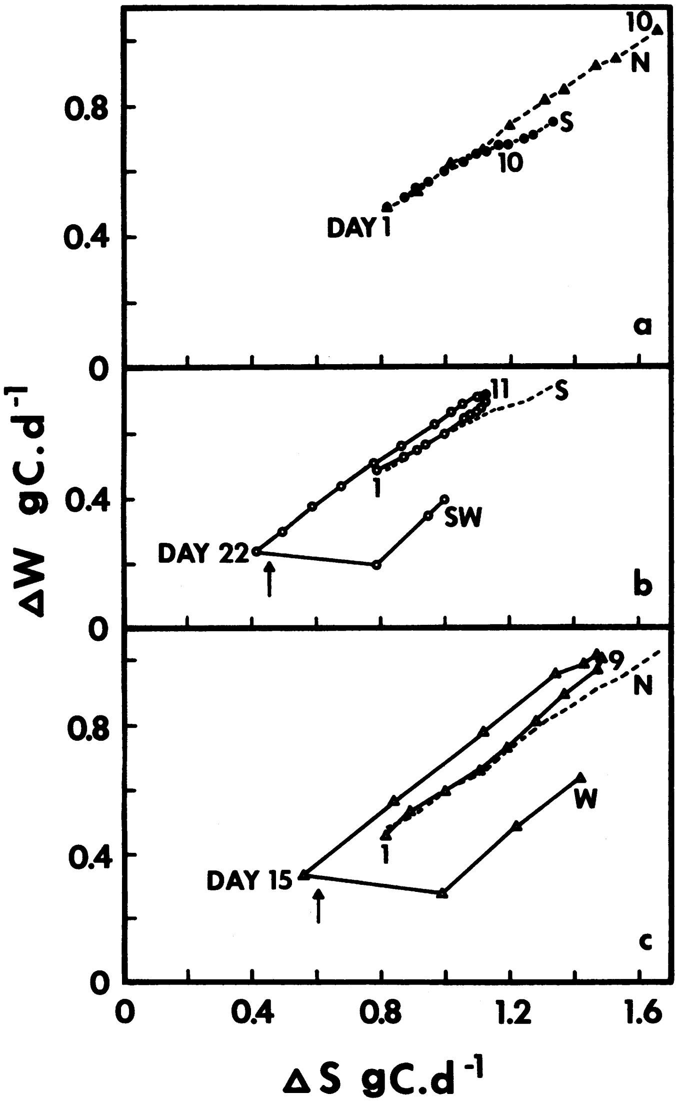

FIG. 3. Net carbon gain (ΔW) *versus* gross photosynthetic carbon input (ΔS). See Figure 2 caption for explanation of treatments.

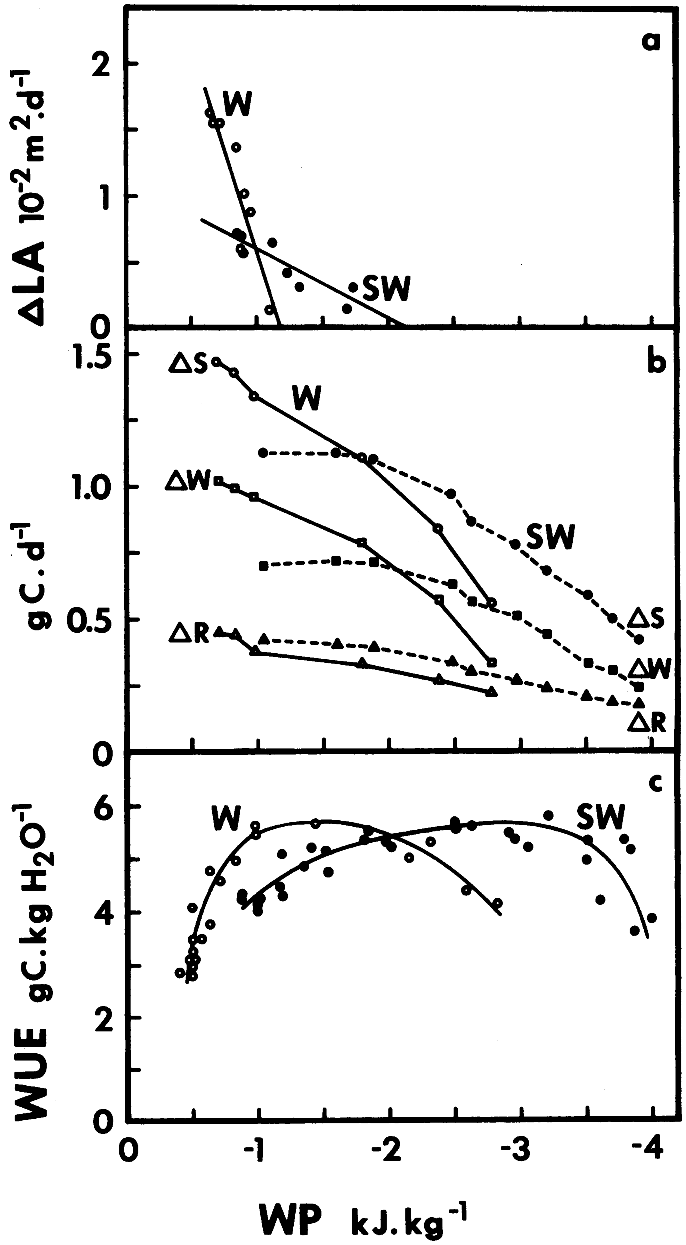

FIG. 4. Daily (24 h) increment of leaf area (ΔLA), carbon balance parameters (ΔS, ΔW, ΔR), and water use efficiency (WUE = net carbon gain ΔW per unit of water lost) plotted *versus* leaf water potential (WP) during the drying phase of the water stress cycles. See Figure 2 caption for explanation of treatments and carbon balance parameters.

4). Daily changes in leaf area (ΔLA) and carbon balance parameters of the water-stressed and salinized water-stressed treatments are plotted against leaf water potential in Figure 4. The plots are restricted to the phase when leaf water potentials were falling. At high water potentials, ΔLA was smaller in the salinized plants, but the plants were able to maintain some leaf expansion down to lower water potentials (Fig. 4a). ΔLA became zero at a water potential of -2.1 kJ·kg^{-1}, compared with -1.2 kJ·kg^{-1} in the nonsalinized plants.

Stark and Jarrell (22) found a similar response to salt in maize, but the water potentials at which leaf expansion ceased apparently were higher than in sorghum. In terms of midday leaf water potentials, we estimate that the threshold potentials for leaf expansion in the maize were -0.8 kJ·kg^{-1} in nonsalinized plants, and -1.5 kJ·kg^{-1} in plants that were salinized to levels similar to ours. These potentials are 0.4 to 0.6 kJ·kg^{-1} higher than we found in sorghum plants. Although these may represent real species differences, it is also possible that the differences are related to the rate of development of water stress (12). The rate was about twice as great in Stark and Jarrell's maize experiments as it was in our sorghum experiments. This would be consistent with a smaller amount of osmotic adjustment (12), and hence a higher threshold potential.

Our carbon balance data (Fig. 4b) followed similar trends to the leaf area data. At high water potential, both ΔS and ΔW were lower in the salinized plants, but the decreases with decreasing water potential were less rapid. Below -2 kJ·kg^{-1}, ΔS and ΔW were higher in the salinized plants.

Water Loss and Water Use Efficiency. Both salinity and water stress tended to reduce the rates of water loss per day (24 h) per plant (Fig. 5a). On d 1, when leaf areas were similar in all treatments, the water losses of all the salt-treated plants were smaller than those of the plants that had not been treated, indicating that salt caused a reduction in water loss per unit of leaf area. This effect of salt on transpiration has been found in several other species (6). Under frequent irrigation, water loss per plant of the salt-treated and untreated plants diverged further as time progressed, due to the smaller LA production with salt. Under water stress, the water loss decreased less rapidly in the salinized plants because of the less rapid decrease in water potential (Fig. 1), and the greater volume of water remaining in the growth medium.

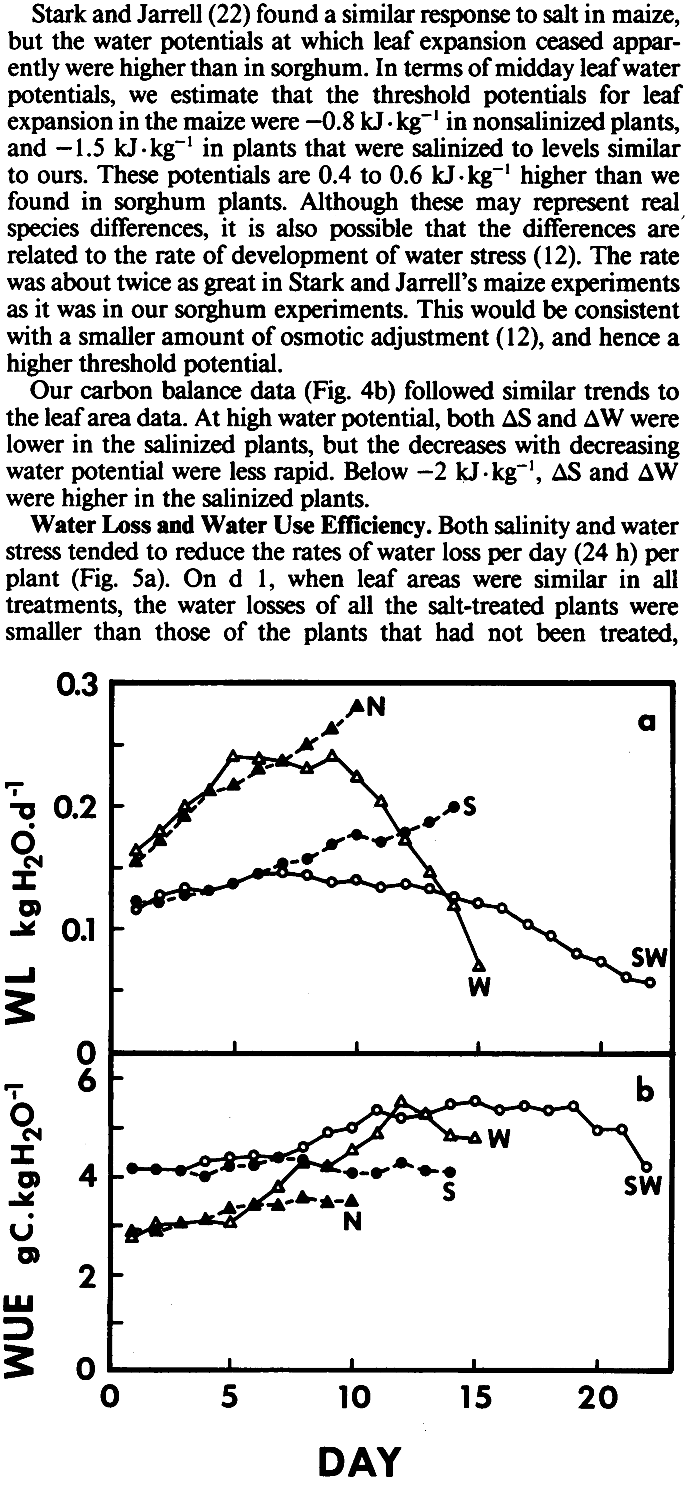

FIG. 5. Daily (24 h) water loss (WL) and water use efficiency (WUE) of sorghum plants in four treatments. See Figure 2 caption for explanation of treatments.

The WUE was calculated as daily carbon gain (ΔW) per unit of water loss. The WUE of plants irrigated regularly with salinized nutrient solution was higher than that of the plants irrigated with nutrient solution without salt (Fig. 5b). This was because salinity reduced the water loss more than it reduced the carbon gain.

This increase in water use efficiency of sorghum with a salinity increase of about -0.48 kJ·kg^{-1} compares well with data of Hoffman and Jobes (9) showing increases in yield per unit of water used by wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) salinized to similar levels. Higher salinities resulted in lower water use efficiencies in that study, and would likely have similar effects on sorghum. Maize, a more salt sensitive species, exhibited decreased water use efficiency with a salinity increase to -0.50 kJ·kg^{-1} (9). Leaf photosynthetic rate per unit of transpiration of more salt tolerant species such as saltbush (*Atriplex* species) is often enhanced even at much higher salinity levels (14, 17).

Under water stress, WUE increased gradually with time, then decreased (Fig. 5b). The time scale was somewhat more expanded in the salinized plants, but peak values of WUE were similar in both treatment.

In Figure 4c, WUE is plotted *versus* leaf water potential for the water-stressed plants. In both treatments WUE increased initially as water potentials began to drop and then declined with further decreases in water potential. The curves for the two treatments differ in that the curve for the salinized plants is offset to lower leaf water potentials. WUE values of the salinized plants were higher at the highest measured water potential (which was different in the two treatments). They also increased more gradually, and remained high over a greater range of declining water potentials.

The initial increases in WUE are consistent with other observations of increases in water use efficiency at the single leaf level (net photosynthesis/stomatal conductance, P/C_s; or net photosynthesis/transpiration, P/T) in several other species (2, 16, 17). Sawada and Sugai (19) also found that P/T of four *Plantago* species increased initially as soil water potential decreased but then declined with further decreases in soil water potential.

The decline in WUE at lower water potentials may be a function of the rate of development of stress. Jones and Rawson (12) found in water stressed sorghum that P/T of leaves decreased with decreasing water potential at a stress development rate of -0.70 kJ·kg^{-1} d^{-1}, while a stress development rate of -0.15 kJ·kg^{-1} d^{-1} resulted in a nearly constant P/T over a range of leaf water potentials from about -1.2 to -3.0 kJ·kg^{-1}. In our study, nonsalinized plants experienced a stress development rate of about -0.13 kJ·kg^{-1} d^{-1} from d 6 through d 12, and during this period WUE increased as leaf water potentials decreased from -0.6 to -1.3 kJ·kg^{-1}. After d 12 the stress development rate increased to about -0.53 kJ·kg^{-1} d^{-1} as leaf water potentials decreased to -3.0 kJ·kg^{-1} and there was a decrease in WUE. Jones and Rawson (12) presented no P/T data for leaf water potentials higher than -1.2 kJ·kg^{-1}, which is the region where our plants exhibited increases in WUE with decreasing leaf water potential.

CONCLUSIONS

Under well irrigated conditions, salt reduced the net carbon gain per day in sorghum plants. Leaf area expansion, water loss, and carbon gain per unit leaf area were inhibited. Water use efficiency was increased by salt, since water use was decreased more than carbon gain.

Salt enhanced the ability of sorghum to continue to gain carbon under water stress conditions. The plants were able to continue leaf expansion and photosynthesis down to lower leaf water potentials, and the rate of leaf senescence was less, in comparison with nonsalinized plants.

We believe the greater ability of salinized plants to continue leaf expansion and carbon gain under water stress can be attributed primarily to a slower development of water stress, which prolonged the osmotic adjustment. The slower water stress development in the salinized plants was due to a lower water loss rate per plant, which in turn was due to both smaller leaf area and reduced water loss per unit of leaf area. There may also have been some prior osmotic adjustment stimulated by the applied salt. Similar effects of prior osmotic adjustment have been observed in nonsalinized plants exposed to water stress (11–13).

Our data indicate that irrigation of sorghum with moderately saline water should reduce the growth rate, but at the same time it should reduce the water use rate and enhance osmotic adjustment, so that the plants should be able to survive and continue some growth for a longer time between irrigations than would be the case with high quality irrigation water. These physiological adjustments should mitigate the effects of using poor quality irrigation water in the field.

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