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ROOT INVOLVEMENT AND PRODUCTIVITY UNDER CONDITIONS OF WATER DEFICIENCY

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ROOT INVOLVEMENT AND PRODUCTIVITY UNDER CONDITIONS OF WATER DEFICIENCY.

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C. Abstract

Sorghum genotypes with different root traits were selected to study the contribution of the root to the build-up of plant tolerance to drought. Two lines with genetic similarity were chosen for a comparative study. The SCO-233 is characterized by fast root growth, long tap and adventitious roots, and deep root system, which was a consequence of the roots length and their vertical growth. The SCO-322 had a much shallower root system which resulted from their shorter roots and their tendency to a more horizontal growth direction, as compared to SCO-233. The overall length of the 322 roots was shorter than that of the 233. The biomass of the root system, and the average number of adventitious roots per plant were greater in the 322 type. The root to shoot ratio, in dry matter, was similar in both genotypes. The above-stated differences were also expressed under water stress conditions, which were imposed by adding PEG to the roots nutrient solution medium. The dry matter production of the two genotypes was reduced by the stress, but the effect on the 233 was less pronounced. The ability to reduce transpiration rate, in response to drought, which is vital for survival in drying soils, was strongly pronounced in 233. In 322 this capability for adjustment of the stomata was much weaker, and the high transpiration levels continued after imposing the water stress.

The next stage of this research, studied under field conditions, showed the implications of the above-stated differences between the two genotypes on growth, productivity and survival as being under management of minimal

irrigation, or under dryland conditions. It was found that the 233 developed a deeper root system in the soil, as compared to 322, irrespective of the irrigation management. The angle of the root emergence from the stem in the 233 led to quicker vertical development in the soil, as compared to 322, under irrigated conditions, as well as under dry conditions. The reductions in dry matter production of vegetative tissues and grains in the 322, under drought in the field, was very considerable, and much greater than the relative reductions in 233. It was concluded that both the vegetative development and the yield production in the 322 genotype were more sensitive to dry conditions. The 233 was characterized by an early flowering and harvest. It enabled this genotype to escape the effects of the progressive drying of the soil profile later in the season. The 322 started to flower much later, and the reproductive development was exposed to a more severe dryness.

The traits of quick and deep root growth, even in drying soil and of early harvest, were used to develop a double-cropping system. Seeds of 233 were sown later in the summer following an irrigated crop. The 233 succeeded, due to its deep rooting, to exploit the remnants of deep water of the former irrigated crop and to produce in a period of less than three months, high kernel yield which was harvested before the rainy season. This system was examined for several years in the Bet-Dagan region (hamra soil) and in the Gilat region (loess-type soil) and indicated a high potential of practical benefit to agriculture in regions which suffer from shortage of water for irrigation. Under conditions of late sowing, the 322 genotype didn't produce harvestable yield before the winter. A dramatic difference between the two genotypes, which was a consequence of the difference in

rooting depth, was pronounced under extreme soil drying. The 322 reached shoot drying and death, while the 233 survived and succeeded to renew tillers development even in the absence of additional irrigation. Under conditions of rainfed agriculture, following potatoes as a former crop, the yield of 233 reached up to 5000 kg/ha and was not smaller than that of the irrigated plot. The effect of the water deficiency was much greater in the 322 type with regard to dry matter production of the shoot which also included the immature panicles.

The possibility to promote yield increase per unit field area, under conditions of water deficiency and drying of the soil profile, as a consequence of reducing spacing between adjacent rows, was studied for the two genotypes. Whether a deeper and more vertical root system will be advantageous under conditions in which adjacent rows compete on the same limited reservoir of available water in the upper soil layers was examined. The results of the field experiments supported this assumption. In non-irrigated plots, 233 gave a considerable increase in both shoot-dry matter production and kernel yield, due to the reduction in plant row spacing from 100 to 50 cm, which was accompanied by the doubling of the plant stand in the field. Cv. 322, which had a more horizontal root system didn't respond in the same way, and a much smaller addition in dry matter production per unit field area, resulted from the same changes in row spacing.

D. Objectives of the Research

1) To study the relations between the expression of root traits in sorghum and the tolerance to drought.

2) Study the implication of root morphology in sorghum on sorghum adaptation to conditions of water-deficiency in the soil profile.
3) To use the knowledge on root behavior, under conditions of nutrient solution, as significant information which might be relevant to adaptation to drought in the field.
4) To use the results of the research, in the above-stated aspects, as a basis for improving sorghum productivity under semi-arid conditions.
5) To examine the possibility of using deep remnant, water of summer crop for growth of deep-rooted sorghum with short growth season, as a second crop.

E. Research report

Introduction

Exposure of roots to drought affects their biochemical, physiological and growth activities followed by an influence on shoot development and activities. Water stress may either encourage root growth (Watts et al., 1981) or suppress it (Newman, 1966). The root:shoot biomass ratio may be altered under drought with the potential effects of such change on the sink-source interrelationships of both organs. Under cycles of drought and rewatering, root tips in the drying zones may be damaged (Russel, 1977). Since the biosynthesis in the root of cytokinins (Skene, 1975; Goodwin and Morris, 1975), N-amino compounds (Dierks-Ventling and Tonelli, 1982; Oaks et al., 1977), or ABA (Wilkins and Wain, 1974; Kundu and Audus, 1974) takes place mainly in the apices, and their translocation to the shoot may be affected by a possible change in root tips viability.

Traits which affect root function under water stress conditions play a basic role in determining plant sensitivity or tolerance to water deficiency. Sullivan and Brun (1975) reported on the importance of an extensive root system with high root surface area in maintaining high rates of leaf water potential, stomatal conductance and photosynthetic activity in soybean, under drought conditions. Nour and Weibel (1978) compared root characeristics of sorghum cultivars previously ranked for drought resistance. They found a positive correlation between root weight and volume, dry weight root:shoot ratios, and the drought tolerance. Boyer et al. (1980) proposed that the ability of modern soybean cultivars to maintain a higher midday leaf water potential than did old cultivars was due in part to larger root systems in the new lines. Quiesenberry et al. (1981) found that in exotic cotton lines the number of lateral roots was significantly correlated with both shoot dry weight and leaf area under drought conditions. Bhan et al. (1973) reported that drought resistant genotypes of sorghum had more vertically-oriented roots, higher root number and weights, and greater root:shoot dry weight ratio than susceptible lines. Genotypic variation for the degree of horizontal versus vertical orientation of nodal roots has been identified in corn (Irwin et al., 1985). Such a trait can affect the penetration of root to deeper soil layers and consequently the adaptation to water stress. Cook (1985) found that sorghum varieties with deeply placed and numerous lateral roots were characterized as drought resistant. The importance of root branching, and the proliferation of lateral roots, has been studied mainly under non-stressed conditions but may be highly significant under stress conditions. A high degree of branching and proliferation of lateral roots

has been associated with increased dry matter production (McIntosh and Miller, 1981; Quisenberry et al., 1981; Ketring et al., 1982), photosynthetic activity (Jesko and Vizarova, 1980), and nitrate reduction in roots (Pan et al., 1985). Branching determines the number of root apices and therefore may affect the overall production of materials such as growth substances, N-amino compounds and growth inhibitors biosynthesized in the root sytem. A highly-branched root system may be better able to compensate for the loss of root tips or a decrease in their biochemical activity caused by soil drying.

The recovery of root system function after a stress period is of great importance since root recovery is a precondition to the continuation of shoot activities. The recovery has two main aspects: a) Regrowth and branching of the root sytem and initiation of new lateral roots, and b) restoration of the ability to biosynthesize organic compounds vital for shoot activities and to translocate them upward.

Research in Israel

Materials and Methods

The research in Israel compared two sorghum genotypes: SCO-223 and SCO-322. The plants were grown in three different systems: a) In plastic containers filled with nutrient solution; b) In solid medium, in pots; c) In the field, in heavy and silty soil (Bet Dagan area), or in loess type soil in the Gilat region. The soil from Bet Dagan is characterized by 85% sand, 4% silt, 11% clay, 0.6% organic matter, pH 8.15 and water retention capacity of 7.9% at 1/3 atmosphere. The research

which was carried out in nutrient solutions (hereafter referred to as Exp. 1) was divided into two sections. In the first one (Exp. 1a) the plants were not exposed to water stress, and the emphasis was on studying differences in root traits. Seeds for Exp. 1 were sown in vermiculite. Seedlings of similar size and stage of developent were selected four to five days after emergence and transferred to the liquid medium which consisted of half-strength Hoagland nutrient solution supplied with a double amount of Fe. Four seedlings were grown at distances of 40 cm from each other in containers of 15-liter solution volume which was constantly aerated. The plants were grown in a greenhouse whose temperature during the day and night was kept at a range of 22-25^{o}C. Periodical measurements of seminal root length were carried out in the same plants during a period of several weeks. Differences between the two genotypes in total root biomass, number of adventitious roots and root depth were studied. In addition, analysis of dry matter production, assimilate allocation and the quantitative root to leaf ratio was also carried out. In the second section of Exp. 1 (hereafter referred to as Exp. 1b) plants were grown as in Exp. 1a, but in addition to the control non-stressed treatments, water stress was imposed on plants which were grown in separate containers. Water stress was built up gradually by the increase in PEG concentration in the root nutrient solution. A week after the seedlings transfer to the liquid medium, PEG 6000 was added in 6% concentration, and two days later the concentration was increased to 8% PEG (w/v). The effects of the water stress which was imposed through the PEG addition, on root development, growth, transpiration rate, and dry matter production, were studied. At

intervals of 7 days the nutrient solutions, with or without the PEG, were replaced by new solutions.

In the pot experiment (hereafter referred to as Exp. 2) sorghum seeds were sown in mid-May in pots which contained 11 kg of Gilat soil, fully saturated with tap water (17.6% pot capacity). After one month, the plants were divided into three groups to start different treatments of irrigation; the amount of water lost by transpiration was replaced as a percentage of the total quantity missing: 100, 80, 60 (v/w). All pots were weighed and the water was added as predetermined. Soil surface was covered with black plastic sheets to avoid evaporation. Soil samples were taken 3 times during the entire period of the experiment to determine soil moisture at two depths: 0-9 cm and 9-16 cm. Plant water status was determined by measuring leaf water potential with Scholander's pressure chamber. Plant fresh weight, leaf area and number, and leaf photosythesis were also measured.

Field experiments

The field experiments were carried out over a three-year period. In 1990, in the Experiment Station in the Bet Dagan region, and in 1991 and 1992 in the Gilat Experiment Station in the southern part of Israel. The Bet Dagan region is characterized by a typical Mediterranean climate, and that of Gilat by that of a semi-arid zone. In Bet-Dagan, two experiments were conducted: BD1 was sown in the beginning of March and BD2 in Mid-June. The plants were grown, in row spacing of 100 cm and at stand of 80,000 plants per hectare. The dryland treatments existed mainly on the water reservoir in the soil profile which remained after the winter rains, while the other treatments were irrigated by sprinklers during the growth season.

In BD2 the germination and the further supply of water were carried out by a drip irrigation system. Half of the plots of the two genotypes was irrigated during the whole season. In the others, irrigation was terminated 21 days after emergence (hereafter referred to as non-irrigated treatments). The first experiment in Gilat (G1) was sown on July 30th, 1991, following potatoes which were harvested in June. The row spacing was 100-cm apart, and the plants stand was 120,000 per hectare. The plants were germinated by sprinklers, in amounts of 50 mm H_2O. A further 30 mm were given at 5-day intervals, 10 mm each time. Later on, irrigation was given by sprinklers to half of the treatments (the irrigated treatments), and terminated in the rest (the non-irrigated treatments). The second experiment in Gilat (G2) was started on August 25th, 1992, on a field which was previously planted with potatoes. In this experiment, seeds were germinated as formerly described. The non-irrigated treatments got a total amount of 80 mm H_2O, and the irrigated plots were drip-irrigated till harvest every three to four days.

Results and Discussion

I. Experiments in nutrient solution

1. The expression of differences in root traits

A comparative study of root development in the SCO-233 and SCO-322 genotypes was carried out in Exp. 1a. During an 18-day period, following sowing, a much deeper root system was developed in the 233, in liquid medium (Table 1). The rate of root elongation was almost doubled in the 233. The ultimate length of the seminal and adventitious roots was

significantly greater in the 233. On the other hand, the initiation rate of adventitious roots, their average number per plant, and the ratio in numbers of root:leaf, were considerably greater in the 322, as shown in Table 2. An expression of the above stated differences in the field will lead to a singificant difference in root distribution between the two genotypes. The 322 is expected to be characterized by a shallower root system with denser root biomass in the upper layers of the soil profile, as compared to the 233 type. The 233 is expected to arrive more quickly to the depth and to exploit deeper reservoirs of available water. These possible changes in the model of root distribution might be very significant, ecologically, under non-irrigated conditions, especially while the distribution of water along the soil profile is not equal. A denser root system in the upper layers might expose the plant earlier to water stress, as a consequence of the progressive soil drying downward.

The distribution of dry matter between the root, stem, and leaves, of the young plant, and its effect on the quantitative ratio between the root and the foliage, are presented in Table 3. Both the total production of dry matter per plant, and the proportional allocation of assimilate to the different organs, was similar, over a 20-day period, in both genotypes (Table 3). Consequently, their dry matter ratios between the roots and the leaves were also similar in the early growth stages. It was therefore concluded, that the stated former differences in root traits between the two genotypes, did not result from the rate of assimilate allocation from the shoot to the root, but from a difference in the morphological development of the roots. If this process will exist even under dry conditions, it is expected that regardless of the effect of water stress

on the production of dry matter by the foliage, the morphological differences in root development, which are very significant in non-irrigated agriculture, will be expressed.

In the later growth period, a considerable difference in dry matter allocation to the vegetative and reproductive organs was detected (Table 6). In 61-day-old plants the root to foliage ratios in dry matter were 0.56 and 1.15 in the 322 and 233, respectively. This dramatic change might be connected to the earlier development of panicles in the 233 genotype, which was accompanied with a slowness in leaf growth and termination in leaf initiation on the main stem. This difference in root to foliage ratio might be critical under conditions of soil drying, as concerned plant productivity and survival, and will be discussed later.

2. Effects of water stress on root and shoot development

The findings which are presented and discussed in Section 1 describe the differences in root traits between the 233 and 322 genotypes under non-stressed conditions. The continuation of the research focussed on trying to study whether these traits will be similarly expressed also under conditions of water stress. It was assumed that the potential contribution of root deepening, for example, to the build-up of tolerance to drought, is primarily dependent on the way by which water deficiency promotes, or suppresses, the expression of such a trait. In Exp. 1b young 19-day-old plants were raised in nutrient solution and exposed to water stress which was imposed by adding 8% polyethelene glycol (PEG) to the root zone medium. The 322 plants responded by a temporary wilting which disappeared after a couple of days. The 233 plants showed a much less observable wilting.

Subsequent measurements (at two-day intervals) of adventitious root initiation rate, were carried out over an 8-day period, on 30-day-old plants, which were exposed formerly to 11-days of added PEG, or grown as control without PEG. The data in Table 4 did show that the PEG, in the concentration used, did not significantly slow the initiation rate of adventitious roots. The average number of roots per plant was not affected by the whole period of PEG addition (Table 4). Measurements of the additional length of adventitious roots, in cm per plant, were done in Exp. 2b. The same plants were examined, in a non-destructive procedure, at 2-day intervals, as was done for root initiation. The results, as presented in Table 4, did show that the process of root elongation was strongly slowed down in the 322 genotype, and not significantly in the 233. It means that at least under conditions of mild water stress (8% PEG) the 322 is much more sensitive than the 233, as concerns root development.

The ability to continue root initiation and elongation under water-stress conditions, is a trait of extreme importance for promoting tolerance to drought. It might enable the plant, whose root zone is in a process of drying, to penetrate to deeper and more humid soil layers, and in consequence, the plants chances of survival are increased, and the potential damage to their productivity is reduced.

A long exposure to PEG which lasted over a 24-day period to 21-day-old plants, considerbly reduced the root increase in fresh matter, as compared to non-stressed plants (Table 5). This reduction was more pronounced in the 233 genotype. Since the relative decreases in root initiation and elongation were much smaller (Table 4), it was concluded that the reduction in root biomass resulted mainly from decrease in root diameter. The

combination of a continuation in root initiation, and elongation, in the normal intensity, with a reduction in the total root biomass, is also very significant under drought. It enables expansion of the roots to deeper layers with a smaller use of assimilate for root growth. This trait is highly important in case the production of dry matter by the shoot is reduced, as expected under drought. Continuation of the experiment beyond the 3- to 4-week period, following the start of PEG supply, was not efficient, as a result of accelerated process of root degradation and the appearance of pathogens.

3. Dry matter production and allocation under water stress

Imposing water stress by adding 8% PEG to the root zone medium decreased dry matter accumulation in the whole plant. The reduction was very considerable in the 322 genotype, and very moderate in the 233 (Table 6). It showed that at least under the conditions which prevailed in Exp. 1b, the 233 was more tolerant to water stress, as expressed by dry matter production. In both genotypes the stem was the most sensitive to water stress. Its relative share in assimilate accumulation was strongly reduced by the water stress, while that of the leaves and roots was relatively enhanced (Table 6). Analysis of dry matter distribution in the plant organs indicated a trend of great significance relating to adjustment to dry conditions, which differed in the two genotypes. In the 322 the water stress increased very dramatically the relative allocation of dry matter to the leaves on behalf of the supply to the stems. In the 233, which showed an earlier reproductive development, the "excessive" assimilates, which were saved from the stem, were mainly allocated to the panicle

development. It means that while in the 322 the fraction of the organs which contribute to an enhanced transpiration (i.e. the leaves) and consequently to an increased sensitivity to drought, were promoted by the water stress. In the 233 the yield fraction was promoted under the same conditions. From the beneficial point of view of the farmers whose interest is for kernel yield, and not for dry matter production in general, the 233 is potentially more productive under dry conditions than the 322.

Another trait which has great significance is the ability of crops to be productive under non-irrigated conditions with an early flowering and harvest. These processes enable the crop to"escape" the most severe effects of the deteriorating conditions of water availability, later on in the growth period. The data presented in Table 6 indicate that both flowering timing, and dry matter accumulation in the panicles, were considerably earlier in the 233 genotype, under both stressed and non-stressed conditions.

4. Transpiration rate under water stress

The total transpiration of a plant is determined by its foliage area on the one hand, and the transpiration value per unit leaf area on the other hand. The main factor which affects transpiration rate is the extent of stomatal opening. The ability of a plant to regulate its stomatal opening, and thereby to adjust itself to the limited supply of water from its root zone is very significant ecologically in dryland agriculture, or under conditions of limited irrigation. Partial closure of stomata will slow the rate of root zone drying and will enable an elongated period of survival under drought. On the other hand, such a process might reduce

photosynthesis due to the reduction in CO_2 influx. The balance between the two contrasting effects, will detremine productivity under dry conditions. The effects of PEG addition on the total foliage area, and on the transpiration rate per unit leaf area, are presented in Table 7. The imposed water stress caused reduction in total leaf area per plant, as compared to treatments which were not exposed to the PEG. The relative decrease in leaf area was more significant in the 233 genotype. The ratio in leaf area between the control and the stressed plants was 2.7 in the 233 and just 1.6 in the 322 (Table 7). These data are in good agreement with the effects of the stress on dry matter accumulation in leaves, as discussed in Section C. It seems that under conditions of water stress, the 233 decreases the area of its transpiring leaves in greater proportions than do the 322. Measurements of transpiration rate per unit leaf area are shown in Table 7. The water stress reduced the transpiration considerably in the 233, while the values in the 322 stayed unchanged. It is possible that these results express a better ability of the 233 to efficiently control its stomatal conductance, under conditions of water deficiency.

II. Experiments in soil-filled pots.

The experiments in Section I were carried out in containers filled with nutrient solution. The water stress was not imposed by soil drying, but by decreasing the water potential of the solution due to the addition of PEG. The big advantage of using the solution medium was in establishing the ability to follow differences in root development and morphology, along time, without the use of destructive treatments. Exp. 2 was done in

soil-filled pots and the water stress was caused by soil drying and the decreased availability of water in the root zone.

5. Soil drying effects on leaf water potential

The irrigation procedure in Exp. 2, which in the water-stressed treatments replaced only partially the daily water losses by transpiration, led to soil drying. Root zone water content was distinctly divided into three groups according to the treatment applied. In all the treatments the upper soil layer was drier than the deeper one (Fig. 1). When plants were fully irrigated (treatment 1), water depletion from the soil increased with time because of extensive growth and water use. In the other two treatments (i.e. replacement of 80% and 60% of the initial water content in the pot); soil water content stayed more or less the same during the experimental period which lasted over 60 days following sowing. Replacement of 60% of the lost water (treatment 3) decreased soil moisture to values close to the wilting point, which characterize the specific used soil (i.e. around 7%). The deficiency in available water in the pots led to a remarkable drop in leaf water potential (Fig. 2). The effect was more dramatic in the 322 plants. The leaf ψ_w in treatments 1, 2 and 3 in 322 arrived at values of 1.60, 2.08 and 2.37, respectively, and in 233 at values of 1.34, 1.57 and 1.70 MPa measured 60 days after sowing. Reduction in $L\psi_w$ is a very common symptom of water deficiency in leaf tissues.

The mechanism by which plants might decrease the magnitude of water losses from the leaf tissues, and consequently reduce the fall in $L\psi_w$ values, is mainly by slowing transpiration rate. It seemed, therefore, that the response detected in this section, as concerns the changes in $L\psi_w$

are in good agreement with the formerly reported findings, which indicated that the 233 succeed better to decrease the losses of water through transpiration, as compared to 322.

6. The effects of soil drying on reproductive development and photosynthesis

The data presented in Table 6 was indicated on an earlier reproductive development in the 233 genotype as compared to 322. The findings in Exp. 2 indicate that also in solid medium this difference existed. The 233 plants started to flower around 65 days after sowing, while the 322 didn't start to flower even a month later. The water stress conditions slowed the panicle development, as pronounced by their fresh weight in the 233 genotype (Fig. 3). This effect was not a consequence of a decreased activity of photosynthesis, as can be studied from Fig. 4. The data in Fig. 4 indicates that at least over a 22-day period, after the differential treatments of water supply, the imposed deficiency in available water didn't reduce photosynthesis significantly. The combination of an early panicle development, with a high photosynthetic activity under drought, are additional indications of the potential of the 233 genotype to be productive under dry conditions.

III. Experiments in the field under practical conditions

The work which was discussed in the former sections showed great differences between the two genotypes in the expression of basic root and shoot traits. These differences were pronounced under both water stress or non-stressed conditions. The root traits of the 233 which might be very

significant under dryland conditions or under non-sufficient irrigation, include: quick root elongation, long roots, vertical tendency of root development and deep root system. The 322 genotype was characterized by a tendency to more horizontal root growth and great extent of root initiation per plant. Under water stress the elongation of the 322 roots was considerably suppressed, as compared to the response of the 233. The 233 showed a better possibility to reduce its transpiration under water stress, as compared to the 322, resulting both from a decrease in foliage area and of a decrease in transpiration rate per unit leaf area. The early flowering and panicle development in the 233 might also be an advantage under conditions of progressive soil drying, in the absence of rain or irrigation. The objectives of the field experiments were to study whether the responses which were detected in plants growing in liquid medium will also be expressed in the field under practical conditions, and what the effects on growth and productivity of the two sorghum genotypes will be.

7. Root development in irrigated and dryland plots

Observations on root morphology, numbers and distribution in the soil, of the 322 and 233 genotypes, as affected by irrigation or under drought, were carried out in Exp. BD1 (see Materials and Methods), which was done in the Bet Dagan region. Photographs which were taken at the end of the season indicate that irrespective of the irrigation management, the emergence angle, and root direction of the adventitious roots was more horizontal-oriented in the 233. The root biomass in the upper soil layers was considerably more dense in the 322. It was very significant that this difference between the two genotypes existed in humid, as well as in dry

soil. Measurements of adventitious root number per unit length of plant row are presented in Table 8. The number of roots per meter row in the 233 and 322, in irrigated and dryland plots, arrived at 706, 1173, 400, and 639, respectively. It was also noted in the field that the 322 develop more roots than do the 233. In both genotypes drought reduced considerably root initiation. The relative decrease in root number arrived at 1.76 and 1.83 in the 233 and 322, respectively. This response was different from the effect in solutions, as presented in Table 4, which didn't show a significant reduction in root numbers as a result of PEG addition. It is possible that such an effect is pronounced under conditions of very lengthy and severe drought, as characterized the conditions in Exp. BD1. It is also possible that low soil moisture in the vicinity of the root initiation sites, is an inhibiting factor to root initiation. It is possible, that under field conditions the reduction in root number is ecologically adventitious. It might reduce the competition on assimilates between the individual roots, and consequently enable a relatively greater supply of photosynthate to the fewer existing roots. Such a supply is a precondition to preserving the potential of root elongation and deepening, which is critical under drought.

In concluding the experiments in the liquid medium (Exp. 1a,b) it was questioned whether the trait of root elongation, which characterized the 233 genotype, will also exist in the field and lead to the establishment of a deep root system. The findings in Table 9 approved of this possibility. The depth to which a significant fraction of these roots arrived after 105 days from emergence in irrigated and dryland plots of 322 and 233 was 51, 67, 95 and 105 cm, respectively. The root system of both

genotypes was deepened under drought. Under both irrigated and dry conditions, the 233 had a considerably deeper root system than did the 322. Under conditions in which available water in deeper soil layers are the only source of water in the drying profile, the above stated trait of the 233 is extremely important, as it might contribute to better tolerance and survival.

8. Humidity in the soil profile of irrigated and dryland plots

Measurements of moisture content in the soil profile of irrigated and dryland plots are shown in Table 10. Up to the depth of 120 cm, the humidity in the non-irrigated plots was much smaller than in the irrigated plots, and ranged between 8% to 12% water content (on dry weight basis). These values are below or a little above the wilting point of the specific soil. It shows that the non-irrigated plots were exposed to a very considerable deficiency of available water in their root zone. The data in Table 9 indicated that most of the detectable roots of both genotypes were concentrated in these dry layers, as concerns the non-irrigated treatments. The distribution of water along the profile was not significantly affected by the genotype. The values of moisture content in the different soil layers were similar to both genotypes. It seems that due to the long period of no irrigation both genotypes exploited most of the available water in these depths, and their different models of root distribution was not expressed, as pronounced by the level of water extraction from different depths.

9. Physiological responses of irrigated and dryland treatments

Measurements of leaf water potentials during the day, as measured 100 days after emergence, are presented in Table 11. The very common symptom of water stress in leaves, which is a decrease in leaf water potential, was pronounced in both genotypes. The $L\psi_w$ values in the non-irrigated plots of both genotypes were similar during the whole day, and much lower, as compared to those of the irrigated plots. There was no indication of a considerable difference between the two genotypes. Measurements of leaf water content, were done in the morning and at noon. The data in Table 12 indicate that in the transition from morning to noon the plants in the dryland plots of both genotypes arrive at a much greater water deficiency in the leaf blades, as compared to the irrigated plots. The reductions in water content (as calculated from Table 12) from 0900 to 1200 arrived in the irrigated and non-irrigated 233 and 322 genotypes at: 0,0003, 0.0, 0.0015 and 0.0022 g/cm^2, respectively. The leaves which were examined for their water status, as previously described, were also measured for changes in their photosynthetic activities during the day. The data which are presented in Table 13 indicated a considerable reduction in photosynthesis of the water-stressed plants, during the whole day. The non-irrigated plants of the 233 genotype had a relatively smaller reduction in photosynthesis as compared to the 322 type. It means that assimilate production in the leaves of the 233 was more efficient under drought than that of the 322. The measurements which are described in Table 13 were carried out late in the growth season, and it is not known whether this difference characterized the situation of earlier periods. Taking into account the findings in Tables 10 and 12 it seems that the differences in

photosynthetic activities, as studied from Table 13, were not a result of a better leaf water status in the 233 genotype. Measurements of chlorophyll and protein contents in the leaves, as presented in Table 14, do not indicate that these parameters, which might indicate differences in the photosynthetic apparatus, were differently affected by the drought in the two genotypes. A better understanding of the differences in photosynthesis between the water stressed plants of the two genotypes is not yet up-to-date.

10. Reproductive development and yield in irrigated and dryland plots

The data in Table 15 prove that the reproductive development of the 233 genotype was much earlier than that in the 322, irrespective of the irrigation management. The severe drought which prevailed in the dryland plots did not accelerate significantly the heading timing in the 233 type, but prevented it almost totally in the 322 genotype. It was concluded that this vital reproductive process is non-sensitive in the early type (the 233), but might be prevented by lengthy drought in the 322. The average weight of kernel in the 233 type was also not significantly reduced by the drought. The expression of this parameter in the 322 was impossible as a result of flowering absence in the water-stressed plots. During the 4 months of growth the 233 genotype arrived at full maturity and harvest, while the irrigated plots of the 322 just started their grain filling. The yield in the 233 was not considerably reduced by the dryland conditions and arrived at 425 and 378, at the irrigated and non-irrigated plots of the 322 genotype, respectively. The prominent symptoms of drought in the 233 genotype were an earlier foliage drying, and shorter petioles of panicles,

as compared to the irrigated plots. In the 322 a dramatic suppression of vegetative growth in the dryland plots was observed, and expressed the extreme influence of drought on the growth of this genotype.

11. Development of late-sown sorghum in Bet Dagan

The results of Exp. BD1 showed the tolerance to drought, on the one hand, and the ability to give an early yield, on the other, of the 233 genotype. In Exp. BD2 it was therefore studied whether these traits will promote the option of using the 233 as a second, late-sown crop, which will be harvested before the winter, and will use limited amounts of water. The two genotypes, which were sown on the 13th of July were drip-irrigated at 3-day intervals till the 10th of August. The plants received up till this date 250 mm H_2O. From this date on, the irrigated treatments received routine supply of water (15 mm each for 3 days), while in the other plots water supply was terminated on this date.

11.1. Soil drying by the two genotypes.

The water amounts which all the plots got by irrigation till the 10th August in Exp. BD2, were enough to wet the profile to a depth below 200 cm, as was shown be excavations below this depth at the end of the season. It is possible that some of the deeper water remained as unused water, the result of the former crop which grew earlier on the same field. The content of water, at different soil depths, at the end of the season, as measured by neutron probes are presented in Table 16. The 322 genotype extracted a lot of water from the 0 to 80-cm depth. The 233 genotype extracted relatively smaller amounts of water from these layers. A gradual increase in water content below the 80-cm depth was detected in the non-irrigated

treatments of both genotypes. It indicated the existence of a deep reservoir of water at the time of irrigation termination. In all treatments, a considerable amount of available water existed below the 100-cm depth. The irrigated treatments were exposed to a very wet soil profile, and water was readily available in all the measured depths. The existence at the end of the season of considerable amounts of deep water in the water-stressed plants indicated a limited ability to exploit them at the necessary timing. It cannot be concluded that the plants did not need this water, since in the 322 non-irrigated plots plants died from dryness.

11.2. Root spreading in the soil profile.

A deep excavation to a depth of 250 cm was carried out 120 days after sowing, along the plant rows. It made it possible to observe very clearly the location of the roots. The data are presented in Table 17. It can be seen that in both genotypes the early termination of irrigation led to deepening of the roots. The effect was much greater in the 233, whose root system was considerably deeper than that of the 322 either in the irrigated treatment or in the non-irrigated plots. A considerable amount of 233 roots appeared at a depth of 133 cm in which water was available in the non-irrigated treatment according to Table 16. The shallower root system of the 322 concentrated mainly up to 95-cm depth, and has therefore much less available water, as can be studied from Table 16. The trait of deeper root growth of the 233 genotype, which was observed first in nutrient solutions, and under dryland conditions, showed similar behavior under conditions in which the soil profile was deeply wetted at time of irrigation termination.

11.3. Effects of water stress on leaf osmotic and water potentials and on leaf water status.

Measurements of leaf water potential of irrigated and non-irrigated plants were carried out at midday on a sunny day, using a pressure chamber. The plants were 43 days after irrigation termination in the water stress treatments. The data are presented in Table 18. The leaf water potential of the non-irrigated 322 plants was much lower than that of the irrigated plants, while in the 233 genotype the decrease of $L\psi_w$ was much smaller. This indicated that the 322 genotype suffered from a much more severe stress than the 233. Measurements of osmotic potential and water deficiency in the leaves were carried out 30 days after irrigation interruption. Leaves were sampled at midday on a sunny day. Half of the blade was cut immediately and its water content was measured. The rest of the leaf was free to absorb distilled water overnight from its lower section. The water content, after overnight saturation, was measured. The difference in water content before and after saturation expressed the water deficiency of the leaf. Osmotic potential was measured on leaf sap which was taken after deep freezing. The data in Table 19 shows that in the 322 genotype the non-irrigated plants had a greater leaf water deficiency than the irrigated plants. In the 233 treatments both irrigated and non-irrigated plants had a similar water status. The measurements of the osmotic potential showed a similar trend. The osmotic potential of the non-irrigated 322 plants was much higher than that of the irrigated treatment, while in the 233 treatments such a difference was not observed.

11.4. Effects of drought on assimilate production and allocation

The effects of irrigation continuation, or termination, in early growth stages, on dry matter production, and its allocation to leaves, stems and panicles, are presented in Table 20. The effects of irrigation termination on dry matter production was not dramatic up to the 100-day period after sowing. The moderate reductions in total dry matter per plant were similar in the two genotypes. The stem was shown to be the most sensitive to drought, as concerns the suppression of dry matter accumulation. In the 322 genotype a greater suppression of leaf growth (as expressed by dry matter accumulation) was demonstrated, as compared to the decrease in the 233. A difference in the model of assimilate distribution, in response to drought, was observed. In the 233 genotype the relative distribution between the stems, leaves and panicles was not affected by the drought. In the 322 a relatively greater allocation of dry matter to the panicles was observed, on behalf of the stem. Acceleration of assimilate allocation to reproductive organs is a common result of water stress in many plants. The expression of such a tendency in the 322 genotype, in the non- irrigated treatments, and its absence in the 233, indicate a greater sensitivity of the 322 to the conditions of soil water deficiency.

11.5. Effects of drought on vegetative and reproductive development

The effects of irrigation conditions on plant height, on foliage area, and on the average number of tillers and panicles per plant, are presented in Table 21. Both genotypes responded to the drought, which was imposed by irrigation termination, by reductions in foliage area, plant height, and panicles number per plant. The effects of drought in the 322 were greater than in the 233, in most of the above stated parameters. The suppressive

effect of drought on tillering amount was considerable in the 322, and not significant in the 233. These symptoms indicate a greater sensitivity of the 322 genotype to drought under the specific conditions of Exp. BD2, as already shown either under dryland conditions (Exp. BD1) or in liquid medium with added PEG (Exp. 1b).

11.6. Effects of drought on leaf conductance

Both genotypes responded to drought by a considerable decrease in leaf conductance (Table 22). The values in the non-irrigated treatments, relative to values in the irrigated plots, appeared in the 233 and 322 at 67.8 and 52.4 percent, respectively. The greater magnitude of stomatal closure (as expressed by leaf conductance) in the 322 genotype, under drought, indicates also a greater sensitivity of this genotype to water stress conditions. The measurements which are shown in Table 22 represent old plants which were exposed to a long period of drought. These results of leaf conductance might therefore be determined by an integrated effect of leaf senescence and a worsened leaf water status.

11.7. Drought effects on survival and late tillering

The survival capability of plants, under conditions of prolonged drying of the soil profile, is primarily dependent on the root ability to spread to deeper layers and extract their water reservoirs. The manifestation of such a process will be indicated by the slowing of plant drying on the one hand, and the continuation of growth activities on the other. The effects of elongated exposure to conditions of irrigation absence, as imposed in Exp. BD2 on leaf dryness and late tiller emergence are described in Tables 23-26. The data in Table 23 did show that the 322 genotype was more sensitive to the soil moisture deficiency, as pronounced by the extent of

leaf dryness. The percentage of naturally-dried leaves, out of the total leaf biomass in 110-day-old plants, as determined by weight ratios of oven-dried leaves, arrived at: 23.6, 83.5, 45.7 and 4.1 in the irrigated and non-irrigated plots of the 322 and 223 genotypes, respectively. A similar tendency was manifested in Table 24. The late tillers which emerged during the 80- to 100-day period, after emergence, started their growth when the effects of irrigation absence became dramatic, as expressed by the accelerated process of foliage drying. Such young organs were naturally more sensitive to deficiency in water supply, and responded by quick wilting and drying, especially of the youngest expanded leaf. Table 24 demonstrated that the process of leaf drying in the young late-emerging tillers was much quicker and critical in the non-irrigated 322 plants, as compared to the 233 plants. The percent of young tillers which arrived at complete dryness was 38.9 in the 322, and just 20% in the 233. Tillers in which the youngest expanded leaf was dried consisted of 44.5% and 2.2% of the plants in the non-irrigated plants of 322 and 233, respectively. The fact that the youngest leaf was first to be dried indicated that this phenomenon was not a consequence of natural dryness of old leaves, but resulted from an insufficient supply of water. The ability to develop new tillers, at periods when deficiency of water in the soil became critical (i.e. after 90 days from emergence), is shown in Table 25.

Irrigated and non-irrigated plants of both genotypes were excised 10 cm above the soil surface and observations were made on the emergence of new tillers from the remaining organs. The non-irrigated plants of the 322 genotype failed totally in developing new tillers, while in the 233 genotype the level of tillering in non-irrigated plants came to 36% of the

level in the irrigated plants. In intact plants, during the same period (i.e. 90 to 120 days after emergence), the average number of tillers which emerged in meter lengths of rows arrived at: 25.2, 1.2, 15.8 and 7.0 in the irrigated and non-irrigated plots of 322 and 223, respectively (Table 26). The same trend was shown in cut as well as in intact plants. It indicates that the existence, or absence, of the shoot was not the dominant factor which affected the extent of tillering in non-irrigated plants. It was therefore concluded that the ability of continuous water supply over that period played the major role in enabling the continuation of growth processes. The fact that available water in considerable amounts was present in deep layers (see Table 16), supports the assumption that the basic reason for the considerable advantage of 233, as concerns survival and growth potential, resulted from its ability to spread its roots to these deep-wetted layers.

12. Late-sown sorghum as integrated in a double-cropping system with potatoes

The findings of the work, which was carried out at Bet Dagan, emphasized the existence of shoot and root traits in the 233 genotype, which might promote a productive performance of the crop under conditions of water deficiency. The prominent shoot traits were an early reproductive development and harvest, and small effect of drought on the yield, especially under conditions of mild water stress. The shoot itself demonstrated efficient functioning under water stress conditions, as pronounced by: photosynthetic activity, assimilate allocation to panicles

and roots, normal flowering, slow foliage drying, and the ability to flower and be productive when the crop is late-sown. The most significant root traits of the 233 genotype were a quick rate of root elongation, long roots, the establishment of a deep root system, continuation of quick root growth under dry conditions, and a tendency to develop roots with a prominent vertical direction of growth. The potential of the 233 genotype to survive under drought, to exploit deep water, and to give early yields from late sowing, seemed very promising. It was assumed that such a crop might grow with a minimal irrigation, and use remnants of water which leaked down to the root zone of the former crop. Raising 233 as a second crop following potato, in a double-cropping system, seemed very efficient from the point of view of water saving. Potato is a crop with a shallow root system and high sensitivity to drought. Therefore, the crop is frequently irrigated with a relatively large amount of water. A considerable amount of excessive water leaks down to the shallow root zone, together with nutrients, and may be a major source of these compounds to the deep rooted 233 genotype. Potato is generally harvested not later than mid July, especially in the southern part of Israel, which is the main source of potatoes in Israel. This period seems suitable for a productive performance of the late-sown 233 genotype.

The continuation of the research in the Gilat region of Israel focussed on studying the possibility of using the 233 genotype in a double cropping system with potatoes. It was examined whether the characters of the 233 which were expressed under the climate and soil types of the Bet Dagan region, will be similarly expressed also in the Negev region.

12.1 Moisture content in the soil profile

Measurement of water content in the soil down to the 120-cm depth were done 35 and 65 days after emergence in Exp. G1, and presented in Table 27. Measurements of the earlier date are indicated on a drier profile in the non-irrigated plot, as compared to the irrigated ones, in both genotypes. The difference was considerable down to the 60-cm depth between the irrigated (I) and moderately-stressed (MD) plots. In deeper layers the humidity was similar in these treatments. It indicated that the moderate stress didn't promote up to the 35 days after emergence a deep water extraction. The plots of the non-irrigated, extreme stress (Ex), were already in the early growth period, exposed to a very severe dryness in most of the measured layers (Table 27). The extremely stressed plants of the 322 demonstrated a deeper extraction of water, as compared to the Ex treatment of the 223 genotype in the early period. In the later period (65 days after emergence), a considerble further drying of the 0 to 120 cm depth was detected in all the non-irrigated treatments. The soil humidity in the Ex treatments was very low in all the measured depths. In the moderately stressed plants of both genotypes, the dryness after 65 days from emergence also arrived at extreme values, although it was still considerably more humid as compared to the EX plots. Technical difficulties prevented moisture measurements below the 120-cm depth and it is therefore unknown whether the two genotypes differed in water extraction from deep layers. It was assumed that the ability to survive and produce dry matter under extreme drought, as indicated in Table 27, was enabled due to water availability below the 120-cm depth.

12.2 Tillers and panicles development

The experiments in Bet Dagan indicated that drought affected, especially in the 322 genotype, both tillering and panicle emergence. The effects of the different soil moisture content, which imposed different severities of water stress, on these two parameters, are shown in Table 28. Under conditions of moderate stress the number of the emerged tillers and panicles was not affected, as compared to the irrigated treatments, at least over a period of 95 days after emergence. Under extreme drought the 322 demonstrated a much greater sensitivity of its reproductive development, which was expressed by almost a total inhibition of panicle emergence. Under similar conditions the reduction in panicle emergence in the 233 genotype was the same as in the moderate-stressed treatments, and just slightly reduced as compared to irrigated plants. These results support the conclusion that was drawn from Exp. BD2, and according to it the growth processes, after a long exposure to drought, in the 322 genotype, are more inhibited than in the 233.

12.3 Dry matter accumulation and yield

Reductions in dry matter production, both in vegetative and reproductive organs, are very common responses of many plants to water stress and drought. The data in Table 29 indicates that from this prospective, the 322 is more sensitive to drought than the 233, a trend that was found in the former experiments (Exp. 1b and BD1,2). Under the specific meteorological and soil conditions in the Gilat region, the same difference was shown. The total dry matter production in the moderate-stressed plots of 233 was not reduced in comparison to the irrigated plots. In the 322 a considerable

decrease in dry matter accumulation was detected, even under the moderate-stress conditions. This difference between the two genotypes was much more enhanced under conditions of extreme drought. While the dry matter production in the extremely-stressed plants of 322 was 7% of the accumulation in the irrigated treatment, in the 233 it arrived at 34% of the irrigated ones. The findings which are presented in Table 30 demonstrated that under moderate stress the kernels yield in the 233 genotype was not reduced by the moderate drought. The yield values (in g dry matter per m^2) came to: 205, 228, and 68, in the treatments of irrigated (I), moderate stress (MD) and extreme stress (EX), respectively. The effects of drought on the average weight of kernels, in the 233 genotype, were moderate in the MD treatment, and very considerable in the EX plots. The dry matter weight of an average kernel in the I, MD and Ex treatments of 233 came to: 16.7, 13.3 and 10.7 g per kernel (Table 30). The moderate stress which did not reduce yield in the 233 genotype was very influential as concerns the 322, and reduced its kernel yield from 246 g/m^2 in the irrigated treatment, to 159.3 g/m^2 in the moderate-stressed one. Under the stress of extreme drought the 322 did not give any yield.

The results of Exp. G1 proved the possibiity of using the 233, as a constituent in a double cropping system with potatoes in the Negev. A considerable and early yield, without a significant amount of irrigation was achieved from late sown plots. The next stage in this research was planned with the aim of increasing the productivity of such a system.

13. Effects of spacing on the performance of late-sown sorghum under drought

The experiments which were formerly carried out in Beg Dagan and Gilat, used the conventional agricultural row spacing (100 cm). The shoot and root traits of the 233 genotype make this type potentially efficient under conditions of a dense row spacing in a non-irrigated agriculture. On the one hand, the shoot is compact and tolerant to drought. On the other hand, the vertical and deep tendency of root growth might reduce the competition between adjacent rows on the limited amount of available water in the upper soil layers. The experiment in the second year in Gilat (Exp. G2) examined the effects of a very late sowing date (end of August) on the crop performance, while the row spacing was the new variable.

13.1 Moisture content in the soil profile

The effects of genotype and row spacing on the extraction of water from different depths are shown in Table 31. It was found that the potatoes which were harvested in mid July left in the 30 to 120 cm depth considerable amounts of available water. Measurements on the 58th day after sowing showed that the non-irrigated treatments of both genotypes extracted most of the available water down to the 90-cm depth. In the depth of 90 to 120 cm the 233 extracted considerably greater amounts of water than did the 322, in the non-irrigated plots. The irrigated treatments of both genotypes did not extract significant amounts of water from the 90 to 120 cm depth. Doubling the row density didn't result in greater soil drying below the rows, in both the non-irrigated genotypes, at least down to the

depth of 120 cm. This result is unexpected and it may be explained as an indication that in all the non-irrigated treatments most of the available water down to the 120 cm depth was used during the first 60 days of growth. This assumption is supported by the findings that the values of soil drying were similar to all the non-irrigated plots, irrespective of genotype or row spacing. Similar information which describes changes in soil humidity below the 120-cm depth is absent. It is therefore unknown whether a considerable reservoir of water existed in these depths, and supplied the needed water for the late growth stages of the non-irrigated plots. It is also unknown whether the two genotypes extracted different amounts of water below the lowest measured layer.

13.2 Dry matter accumulation

The effects of drought on the dry matter accumulation in the two genotypes are shown in Table 32. In the 233 genotype the non-irrigated treatments produced similar amounts of dry matter to the irrigated ones, while in the 322 a considerable decrease was shown in the non-irrigated plots. This difference between the two genotypes was expressed irrespective of the row spacing. Doubling the row density in the 233 increased considerably dry matter production, of the shoot in general, and panicles in particular. In the non-irrigated plots the effect was greater than in the irrigated ones. Shortening row spacing in the non-irrigated plots of the 233, resulted in a greater production of dry matter per unit field area, as compared to irrigated plots with greater row spacing. It indicates that this genotype is very efficient under dense plant stand, even under dry conditions. In the 322 genotype the

drought reduced considerable dry matter production. Increasing row density increased moderately dry matter production, but relatively much less than the effect in the 233 genotype. At the very late sowing date (26th August) the 233 demonstrated during a 58-day period from sowing a very considerable dry matter accumulation in the panicles. It showed between 26 to 29% of the total dry matter accumulation in the stems and leaves (calculated from Table 32). This result showed that the trend of early reproductive development existed also in very late sown plants irrespective of the transition to the autumn season. The 322, during that period, just started to flower. This response is mostly important in a double cropping system, in which the sorghum has to be harvested over a short period. The quantitative ratio in dry matter between the panicles and the remaining shoot organs (stems plus leaves) in the 233 genotype was not affected by the irrigation management. There is no indication that any morphological or growth parameter in the 233 plants was affected by the drying of the 0 to 120-cm depth. Under these specific conditions, at least over 58 days, the 233 was not water-stessed, while the 322 was strongly affected by the drought. The data in Table 33 indicate that in both genotypes the drought did not lead to different distribution of assimilates as concerns allocation between the leaves and the stems. The dry matter accumulation per unit leaf area, was also unaffected in both genotypes by the absence of irrigation.

13.3 Reproductive development

The effects of drought and row spacing on the number of panicles which emerged during the growth season are presented in Table 34. In the 233

genotype the panicles emergence was not affected by the drought in both row densities, while in the 322 a considerable reduction in panicle numbers was shown in the non-irrigated treatments. The difference between the two genotypes might result from the later reproductive development of the 322 genotype, which exposed it to the influence of a much greater soil dryness as compared to the 233 which had a much earlier flowering period. Another significant difference between the two genotypes was their response to the increase in row density. In the 233 the denser canopy had a considerably greater panicle emergence per unit field area, in the irrigated and non-irrigated treatments. In the 322 the response was different. Decreasing row spacing didn't enhance considerably the panicle production, irrespective of the irrigation management. Measurements of dry matter accumulation in kernels of the 233 genotype are shown in Table 35. Most of the dry matter content of the mature harvested kernels was produced after the 24th of October. It showed that this genotype succeeded to fill its kernels in spite of the extreme dryness of the 0 to 120 cm depth which prevailed over that period, as shown in Table 31. In the 322 genotype the kernels didn't accumulate up to the 22nd of November a considerable amount of dry matter. The average weight of the kernels was not affected considerably by the drought in the 233 plots. It again indicated that under the specific conditions in Exp. G2 significant expressions of water stress effects, were not pronounced in the 322 genotype. Data on kernel yield are shown in Table 36. A considerable yield, which ranged from 4732 to 5599 kg/h was achieved, in plants growing mostly in the autumn, while the temperatures are decreasing and the day length is shortening. The yield of the non-irrigated plots was not lower than that of the irrigated ones.

Maximum yield of 5599 kg/h was harvested in the non-irrigated treatment with row spacing of 0.5 meter. A significant addition in yield was achieved by shortening row spacing. It showed that in respect to both the reproductive and vegetative processes, the 233 genotype is very efficient in narrow-row spacing and gives an enhanced production of dry matter yield, under such conditions. The data in Table 37 show that the accumulation of dry matter in the panicles of the 322 genotype, as measured on the 22nd of November, was low, while the 233 arrived at this date to maturity and harvest. From the very late sowing date, as carried out in Exp. G2, the 322 genotype lacked the potential of producing considerable and harvestable yield before the winter rainfall. Increasing the row density resulted in a moderate increase in shoot dry matter production of the 322 genotype under conditions of irrigation or under drought (Table 37).

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References

1. Bhan, S., Singh, H.G. and Singh, A. (11973) Ind. J. Agric. Sci. 43: 828-830.

2. Boyer, J.S., Johnson, R.R. and Saupe, S.G. (1980) Agron. J. 72: 981-986.

3. Cook, G.C. (1985) M.Sc. Thesis. Texas A&M Univ. College Station, Texas.

4. Dierks-Ventling, C. and Tonelli, C. (1982) Plant Physiol. 69: 130-134.

5. Goodwin, P.B. and Morris, S.C. (1979) Aust. J. Plant Physiol. 6: 195-200.

6. Irwin, R.L., Johnson, W.C. and Elkins, C.B. (1985) Highlights of Agric. Res. 32, No. 1, Alabama Agr. Exp. Stn., Auburn Univ., Alabama.

7. Jesco, T. and Vizarova, G. (1980) Photosynthetica 14: 83-85.

8. Ketring, D.L., Jordan, W.R., Smith, O.D. and Simpson, C.E. (1982) Peanut Sci. 9: 68-72.

9. Kundu, K.K. and Audus, L.J. (1971) J. Exp. Bot. 25: 479-489.

10. McIntosh, M.S. and Miller, D.A. (1981) Crop Sci. 21: 15-18.

11. Newman, E.I. (1966) New Phytol. 65: 273-283.

12. Nour, a.M. and Weibel, D.f. (1978) Agron. J. 70: 214-218.

13. Oaks, a., Aslam, M. and Boessel. I.L. (1977) Plant Physiol. 53: 391-394.

14. Pan, W.L., Jackson, W.A. and Moll, R.H. (1985) J. Exp. Bot. 36: 1341-1351.

15. Quiesenberry, J.E., Jordan, W.r., Roark, B.a. and Fryrear, D.W. (1981) Crop Sci. 21: 889-895.

16. Russel, R.S. (1977) in "Plant root systems: their function and interaction with the soil." McGraw-Hill Book Company, U.K.

17. Skene, K.J.M. (1975) in "Development and function of roots." Eds. Torrey J.B. and Clarkson D.T. Academic Press.

18. Sullivan, T.P. and Brun, W.A. (1975) Crop Sci. 67: 319-322.

19. Watts, S., Rodriguez, J.L., Evans, S.E. and Davies, W.J. (1981) Ann. Bot. 47: 596-602.

Table 1: Elongation rate of seminal roots growing in nutrient solution (± SD).

Genotype	Seminal root length (cm) at age (days): 18	25	32
322	10.9 ± 1.6	17.7 ± 1.3	23.4 ± 2.6
233	16.3 ± 2.3	30.6 ± 4.6	38.9 ± 8.4

Exp. 1a

Table 2: Number of adventitious roots and root depth of sorghum plants growing in nutrient solution. Measurements were carried out 20 days after sowing (± SD).

Genotype	Adventitious root number / plant	Root depth (cm)
322	10.0 ± 1.4	19.7 ± 4.0
233	6.7 ± 0.9	30.2 ± 2.6

Exp. 1a

Table 3: Dry mattter production, assimilate allocation and quantitative root/leaf ratio of 20 day-old-plants (± SD).

Geonotype	Total dry wt (g/plant)	Percentage of dry matter allocated to: roots	stems	leaves	Root dry matter/ leaf area unit (g/dm^2)
322	0.447±0.087	28.1±4.4	25.7±2.7	46.2±2.0	0.12 ± 0.026
233	0.393±0.058	28.3±1.5	27.8±0.8	43.8±1.7	0.12 ± 0.014

Exp. 1a.

Table 4: The effects of 8% polyethelene glycol (PEG) given to 19-day-old plants on initiation* of adventitious roots and their total elongation. With (+) or without (-) PEG (± SD).

Age (days)	Number of adventitious roots/plant 322(+)	322(-)	233(+)	233(-)
30	2.2±1.3	4.3±1.2	2.2±0.4	2.0±1.0
32	4.7±1.3	5.2±0.4	4.0±1.4	4.0±0.9
34	5.0±1.2	7.2±1.8	4.7±1.2	5.1±1.3
36	8.3±2.2	9.5±2.5	6.8±1.4	5.8±1.4
38	12.0±3.1	13.7±2.3	12.0±3.7	10.8±2.1
Age (days)	Total length of adventitious roots (cm/plant) 322(+)	322(-)	233(+)	233(-)
30	9.4±2.8	12.1±2.6	6.1±2.7	6.4±2.5
32	17.4±5.3	30.5±8.1	20.2±8.1	17.6±4.3
34	33.4±8.6	50.7±13.2	39.6±10.0	35.3±6.5
36	50.7±13.3	102.6±24.3	61.7±12.9	69.4±10.1
38	111.6±26.4	181.1±32.1	110.9±27.8	123.6±30.2

* Observations were done on roots that were less than 5 cm length at age of 30 days, and roots that were initiated later on.

Exp. 1b

Table 5: The effects of 8% PEG, given to 21 day-old plants on the amount of root biomass and number of roots, and on the root to leaf number ratio. Plants were exposed for 24 days to the PEG. With (+) or without (-) PEG. (± SD).

Genotype	Root fresh wt (g/plant)		Number of roots/ plant		Number of roots/ leaf	
	+	-	+	-	+	-
322	35±8	57±10	34.2±5.8	39.2±4.4	1.7±0.3	2.6±0.9
233	25±8	45±11	26.6±5.7	28.6±6.7	3.8±1.0	2.8±0.7

Exp. 1b.

Table 6: The effects of 8% PEG, given to 21 day-old plants on dry matter production and assimilate allocation. Plants were harvested 40 days after PEG addition. With (+) or without (-) PEG. (± SD).

Treatment	Total dry matter (g/plant)	Percentage of dry matter allocated to:			
		Roots	Stems	Leaves	Panicles
322 (+)	16.1 ± 1.9	23.9±4.4	31.7±2.6	44.4±4.3	-
322 (-)	25.2 ± 2.4	16.1±2.2	51.6±3.7	28.8±4.6	3.4±* 2.6
233 (+)	15.2 ± 0.7	22.3±2.0	40.5±5.2	27.1±4.5	10.1±1.2
233 (-)	18.4 ± 1.7	14.7±2.7	65.9±7.2	12.6±3.9	6.6±2.5

* Just a third of the plants had panicles.

Exp. 1b.

Table 7: The effects of 8% PEG given to 21 day-old plants during a 40-day period on total foliage area and transpiration rates. With (+), or without (-) PEG (±SD).

Treatment	Total foliage area (dm^2/plant)	Transpiration rate* (g H_2O/dm^2 x day)
322 (+)	8.1 ± 1.5	70.2 ± 13.6
322 (-)	12.8 ± 2.0	69.5 ± 5.0
233 (+)	14.7 ± 2.7	93.6 ± 11.9
SCO 233 (-)	38.5 ± 6.5	131.2 ± 18.9

* Was measured over 24 hours on a sunny day.

Exp. 1b.

Table 8: The effects of drought and genotype on the number of adventitious roots which emerged in well-irrigated or water-stressed plants. Measurements were carried out 120 d after sowing (± SD).

Genotype	Irrigation	Root no./meter row
322	+	1173 ± 94
322	-	639 ± 85
233	+	706 ± 84
233	-	400 ± 37

Exp. BD1

Table 9: The lowest depth in which a significant fraction of thin roots (less than 0.5 mm diameter) was observed in soil excavation which were carried out between adjacent plants, inside the row. Measurements were taken 105-d after emergence.

Genotype	Irrigation	Root depth (cm)
322	+	51
322	-	67
233	+	95
233	-	105

Exp. BD1

Table 10: Soil moisture in the profile of irrigated and non-irrigated treatments, as measured 100-d after emergence (±SD).

Soil depth (cm)	Moisture content (%)			
	Irrigated		Non-irrigated	
	322	233	322	233
0-30	12.9	12.8	8.2	8.6
30-60	14.3	14.5	9.6	10.6
60-90	14.8	14.9	10.6	11.4
90-120	15.4	15.3	11.2	11.9

Exp. BD1

Table 11: Leaf water potentials of irrigated and non-irrigated treatments, as measured during the day, 100-d after emergence (±SD).

Genotype	Irrigation	Leaf water potential (-MPa)		
		0900-1000	1200-1300	1600-1700
233	+	0.116±0.010	0.134±0.011	0.138±0.013
233	-	0.146±0.010	0.186±0.010	0.177±0.014
322	+	0.101±0.014	0.150±0.010	0.106±0.017
322	-	0.144±0.012	0.192±0.012	0.172±0.016

Exp. BD1. The third leaf from the top of the main stem was examined.

Table 12: Changes in leaf fresh weight*, from the morning to noon in leaves of irrigated and non-irrigated plots (±SD). Measurements were taken on July 2nd.

Genotype	Irrigation	Leaf fresh weight (g/cm^2)	
		0900	1300
233	+	0.0130 ± 0.0021	0.0127 ± 0.0025
233	-	0.0144 ± 0.0022	0.0129 ± 0.0016
322	+	0.0177 ± 0.0030	0.0178 ± 0.0028
322	-	0.0158 ± 0.0017	0.0136 ± 0.0012

* Leaf disks from leaf region without main xylem elements were taken. The leaf below the flag-leaf of the main stem was examined. The disks in the morning and noon were taken from adjacent tissues.

Exp. BD1

Table 13: Changes in photosynthesis during the day in leaves of irrigated (I) and non-irrigated (NI) plots. The third leaf from the top of the main stem was examned in plants 90-d after emergence (±SD). The solar radiation (PAR) was expressed in μEm-2s-1, and photosynthesis (P_N) in $mg/dm^2/h$.

	0900-0920		1330-1400		1700-1730	
Treatment	PAR	P_N	PAR	P_N	PAR	P_N
233 I	1300±27	31.6±5.0	1702±45	40.2±2.7	1100±34	26.5±4.0
233 NI	1360±47	21.9±2.3	1680±34	32.1±3.7	1220±26	22.9±5.0
322 I	1365±39	41.8±2.1	1695±28	38.9±3.0	1150±20	21.5±4.6
322 NI	1330±57	19.2±3.3	1660±45	18.2±4.2	1250±20	14.2±4.6

Exp. BD1.

Table 14: Chlorophyll and protein content in leaves of irrigated or non-irrigated plants. The second leaf from the main stem top was analyzed in plants 100-d after emergence (±SD).

Genotype	Irrigation	Chlorophyll content (mg/cm^2)	Protein content (mg/gr F.wt)
233	+	35.9 ± 8.2	11.2 ± 2.0
233	-	41.4 ± 7.6	11.1 ± 2.4
322	+	31.9 ± 7.6	9.2 ± 1.3
322	-	35.2 ± 6.4	9.6 ± 1.0

Exp. BD1

Table 15: Reproductive development and yield parameters in irrigated and non-irrigated plots which were harvested 120-d after emergence.

Genotype	Irrig.	Days to heading	Kernel weight (mg)	Grain yield (g/m^2)
233	+	75	16.7	425
233	-	76	17.0	378
322	+	115	11.5	13
322	-	-*	-	-

Exp. BD1

* No heading

** Most of the plants did not flower.

Table 16: Soil moisture in the profile of irrigated and non-irrigated treatments as measured 100 days after sowing (± SD).

Soil depth (cm)	Moisture content (%)*			
	Irrigated		Non-irrigated	
	322	233	322	233
0-20	26.4±1.6	29.2±0.7	12.5±1.0	14.0±1.1
20-40	24.4±0.7	27.8±0.6	17.0±1.2	19.0±1.2
40-60	21.4±1.2	23.8±1.5	18.0±0.5	19.0±1.0
60-80	21.8±0.6	22.6±0.8	18.1±0.6	20.0±0.6
80-100	22.3±1.2	23.3±0.5	18.7±0.4	20.5±0.4
100-120	23.4±1.8	24.5±0.9	20.2±1.1	21.2±0.9
120-140	23.8±2.2	24.6±1.2	21.7±1.3	22.3±1.5

Exp. BD2

* Field capacity of the soil is 28-29%.

Table 17: The depth in which a significant density of roots was observed along the plant row in irrigated (I) and non-irrigated (NI) plots 120-d after sowing (±SD).

Treatment	Root depth (cm)
322 I	70 ± 14
322 NI	95 ± 8
233 I	93 ± 3
233 NI	133 ± 19

Exp. BD2

Table 18: Leaf water potentials in irrigated (I) and non-irrigated (NI) treatments as measured 43-d after irrigation stopped (± SD).

Treatment	Leaf water potential (MPa)
322 I	0.120+0.013
322 NI	0.185±0.012
233 I	0.106±0.008
233 NI	0.123±0.011

Exp. BD2

Table 19: Osmotic potentials of leaves in irrigated (I) and non-irrigated (NI) treatments, and the effects of overnight supply of water to cut leaves, on leaf water content. Measurements were carried out 30-d after irrigation termination (± SD).

Treatment	Leaf Ψ_s (mOsmol)	Leaf water content (g H_2O/mg dry wt)	
		Before saturation*	After saturation**
322 I	380 ± 57	2.29 ± 0.22	2.31 ± 0.26
322 NI	487 ± 37	2.17 ± 0.18	2.51 ± 0.17
233 I	448 ± 34	2.15 ± 0.30	2.49 ± 0.35
233 NI	459 ± 30	2.10 ± 0.32	2.44 ± 0.19

* The water content at mid-day.

** Water content after overnight supply of water to cut blades.

Table 20: Dry matter accumulation and its proportional allocation to the different organs in irrigated and nonirrigated treatments, as measured 100-d after sowing (± SD).

Geno-type	Irri-gation	Dry matter (g/plant)				Dry matter (in % of total) allocated to:		
		Leaves	Stems	Panicles	Total	Leaves	Stems	Panicles
322	+	49.9±9.2	99.0±15.1	90.9±27.1	239.8	21.3±3.1	41.3±6.9	37.4±8.1
322	-	36.9±6.3	67.5± 8.6	95.3±20.8	206.5	17.9±1.5	32.4±4.8	49.5±5.2
233	+	24.1±3.9	81.8±20.3	103.4±20.1	209.2	11.8±1.7	38.3±3.2	49.9±2.4
233	-	21.9±4.5	71.7± 2.1	93.3±17.4	187.0	11.8±1.3	38.0±5.5	50.5±6.1

Exp. BD2

Table 21: Morphological and reproductive development in irrigated and non-irrigated treatments, as measured 70-d after emergence (± SD).

Geno-type	Irri-gation	Plant height (cm)	Foliage area (dm^2 per plant)	Average number per plant		Quantitative ratio in number of Panicles/Tillers
				Tillers	Panicles	
322	+	107.6±11.2	75.4±14.9	3.7±1.5	3.3±1.2	0.8±0.1
322	-	76.6± 6.5	59.2± 7.6	2.8±0.7	2.5±1.0	0.9±0.2
233	+	103.2±13.4	57.2± 8.6	6.7±1.1	6.3±1.6	1.1±0.3
233	-	88.8±14.5	46.2± 7.6	6.5±2.3	5.6±2.1	1.0±0.1

Exp. BD2

Table 22: The decrease in leaf conductance of non-irrigated treatments, as pronounced by the relative decrease (in percent) as compared to the irrigated plot of the same genotype. Leaves were measured at noon, 110-d after emergence (± SD).

Genotype	Irrigation	*Leaf conductance (percent)
322	+	100 ± 4.7
322	-	52.4 ± 3.4
233	+	100 ± 7.2
233	-	67.8 ± 5.1

Exp.BD2

* Average solar radiation in leaf surface during the measurements ranged from 1410 to 1466 $\mu E\ m^{-2}s^{-1}$.

Table 23: Percentage of dry leaves* out of the total leaf fraction as measured in irrigated and non-irrigated plots 110-d after emergence (±SD).

Genotype	Irrigation	Percentage of dry leaves
322	+	23.6± 3.3
322	-	83.5±37.2
233	+	45.7± 9.3
233	-	54.1±17.3

Exp. BD2

* Both the dry and green leaves were dried in an oven and the proportional fraction of the original dry leaves was calculated.

Table 24: Drought damage to young tillers* as observed 110-d after emergence. Tillers were divided to stages of dryness as follows: a) All leaves green, b) Only the youngest leaf dry; c) All leaves dry (±SD).

Genotype	Irrigation	Percent of tillers in stage of dryness		
		a	b	c
322	+	100.0	-	-
322	-	16.6±2.7	44.5±7.8	38.9±5.1
233	+	95.0±4.2	-	5.0±4.3
233	-	77.7±9.4	2.2±0.8	20.0±5.3

Exp. BD2.

* Tillers which emerged in the period of 80 to 100-d after emergence. The tillers were without panicles.

Table 25: Renewal of tillers emergence* following shoot cutting which was carried out 90-d after emergence. New tillers were counted over a 3-week period (± SD).

Genotype	Irrigation	New tillers per plant
322	+	7.5±1.5
322	-	None
233	+	12.8±3.1
233	-	4.6±1.8

Exp. BD2

* Tillers were emerged below the soil surface.

Table 26: Number of young tillers which emerged in the period of 90 to 120-d after emergence, in intact plants (± SD).

Genotype	Irrigation	Tillers no. per meter^2
322	+	25.2 ± 4.2
322	-	1.2 ± 0.9
233	+	15.8 ± 4.6
233	-	7.0 ± 2.8

Exp. BD2

Table 27:. Moisture content in the soil profile in irrigated (I), and non-irrigated plots which were exposed to moderate (MD) and extreme (Ex) soil drying. Measurements were carried out 35 and 65 d after emergence.

Depth (cm)	Water content (%)					
	322			233		
	I	MD	Ex	I	MD	Ex
			35-d			
0- 30	12.0	7.0	5.8	15.0	8.3	6.7
30- 60	12.7	8.6	7.4	13.8	10.7	6.7
60- 90	11.7	11.0	8.7	12.8	11.9	9.2
90-120	13.1	14.4	10.0	13.2	15.2	12.2
			65-d			
0- 30	14.2	6.7	5.1	15.7	7.0	5.7
30- 60	13.6	8.6	7.1	14.6	9.1	7.0
60- 90	14.2	10.0	7.4	13.8	10.1	8.1
90-120	13.9	11.6	8.6	13.3	12.1	10.3

Exp.G1

Table 28: Number of tillers and panicles that emerged during the 95-d period after emergence, in irrigated (I), and non-irrigated plots which were exposed to moderate (MD) and extreme (EX) soil drying.

Genotype	Treatment	Number per m^2	
		Tillers	Panicles
322	I	17.1	16.5
322	MD	19.2	15.6
322	EX	17.6	3.9
233	I	20.0	19.3
233	MD	19.2	17.5
233	EX	18.1	16.0

Exp. G1

Table 29: Dry matter production and distribution, in irrigated (I), and non-irrigated plots which were exposed to moderate (MD) and extreme (EX) soil drying. Plants were sampled 95-d after emergence.

Genotype	Treatment	Dry matter (g/m^2)			
		Leaves	Stems	Panicles	Total
322	I	121.0	292.6	336.4	750.0
322	MD	50.5	217.3	262.2	530.0
322	EX	25.3	24.8	3.1	53.2
233	I	64.2	112.8	272.9	449.9
233	MD	53.1	145.0	316.9	515.0
233	EX	22.6	36.0	96.7	155.3

Exp. G1

Table 30: Kernels yield and weight in irrigated (I), and non-irrigated plots which were exposed to moderate (MD) and extreme (EX) soil dryness. Plants were sampled 95-d after emergence.

Genotpe	Treatment	Kernels		
		Yield* (g/m^2)	Dry matter (mg/kernel)	Humidity content (%)
322	I	246.0	11.3	2.0
322	MD	159.3	10.9	2.3
322	EX	None	-	-
233	I	205.0	16.7	4.5
233	MD	228.0	13.3	2.5
233	EX	68.0	10.7	2.0

* Dry matter
Exp. G1

Table 31: Effects of row spacing and genotype on changes in soil moisture content in treatments with (I) or without (NI) irrigation. Sorghum, was sown following irrigated potatoes*. Row spacing was 1 or 0.5 m.

Treatment	Soil moisture (%)** at depth cm: 0-30	30-60	60-90	90-120
		31.8.92		
a*	6.7	13.4	16.0	15.8
b	18.1	17.8	17.6	17.6
		25.10.92		
233(I) 1-m	14.8	17.0	17.7	19.2
" " 0.5-m	13.5	15.2	15.8	15.5
233(NI) 1-m	6.5	9.9	11.5	9.8
" " 0.5-m	7.7	9.1	10.6	9.8
322(I) 1-m	13.3	15.4	16.5	16.5
" " 0.5-m	14.8	14.6	15.8	17.2
322(NI) 1-m	7.5	10.0	12.4	12.7
" " 0.5-m	6.4	10.6	11.3	11.9

Exp. G2

* a = without irrigation for germination, b = after 50-mm irrigation for germination.

** Measurements were carried out inside the plant rows.

Table 32: Effects of row spacing and genotype on dry matter accumulation in treatments with (I) or without (NI) irrigation, of late sown sorghum, which were sown following irrigated potatoes. Row spacing was 1 or 0.5 meter. Plants were sampled 58-d after sowing.

Treatment		Dry matter ($g/meter^2$)			Quantitative ratio in dry matter
		Shoot*	Panicles	Total	Panicles/shoot
233(I)	1-m	821	295	1116	0.36
" "	0.5-m	1154	400	1554	0.34
233(NI)	1-m	654	270	924	0.41
" "	0.5-m	1106	426	1532	0.38
322(I)	1-m	1118	-**	1118	-
" "	0.5-m	1445	-	1445	-
322(NI)	1-m	844	-	844	-
" "	0.5-m	1192	-	1192	-

Exp. G2

* Included stems + leaves

** Plants of the 322 genotype did not yet start their panicles emergence.

Table 33: Effects of row spacing and genotype on dry matter distribution in the vegetative organs, in treatments with (I) or without (NI) irrigation, of late sown sorghum, which were sown following irrigated potatoes. Row spacing was 1 or 0.5 meter plants were sampled 58-d after sowing.

Treatment		Dry matter allocation to: (% of the total) shoot		Content of leaf dry matter
		Leaves	Stems	(g/dm^2)
233(I)	1-m	25.7	74.3	5.8
" "	0.5-m	26.1	73.9	5.7
233(NI)	1-m	28.8	71.1	5.9
" "	0.5-m	24.3	75.7	6.1
322(I)	1-m	46.6	53.4	4.3
" "	0.5-m	41.8	58.2	4.1
322(NI)	1-m	42.7	57.3	4.7
" "	0.5-m	47.1	52.9	4.6

Exp. G2

Table 34: Effects of row spacing and genotype on emergence of panicles in treatments with (I) or without (NI) irrigation, of late sown sorghum, which were sown following irrigated potatoes. Row spacing was 1 and 0.5 m. Plants were examined 86-d after sowing.

Treatment		Panicles number (per meter^2)
233(I)	1-m	34.5
" "	0.5-m	44.0
233 (NI)	1-m	32.0
" "	0.5-m	41.0
322 (I)	1-m	31.6
" "	0.5-m	36.5
322 (NI)	1-m	23.0
" "	0.5-m	25.5

Exp. G2

Table 35: Accumulation of dry matter in kernels of the 33 genotype in treatments with (I) or without (NI) irrigation. Row spacing was 1 or 0.5-m, plants were sowed on 26th August.

Treatment	Average dry matter per kernel (mg)	
	24.10	22.11
233 (I) 1-m	3.5	14.7
" " 0.5-m	2.8	15.0
233 (NI) 1-m	3.8	14.5
" " 0-5-m	1.3	13.2

Exp. G2

Table 36: Kernels yield * in the 233 genotype in treatments with (I) or without (NI) irrigation, of late sown sorghum, which was sown following irrigated potatoes. Row spacing was 1 or 0.5 meter. Yield was harvested 88-d after sowing.

Treatment		Kernels yield (kg/hectare)
233(I)	1-m	5132
" "	0.5-m	5399
233 (NI)	1-m	4732
" "	0.5-m	5599

Exp. G2

* Mature yield which was ready to harvest.

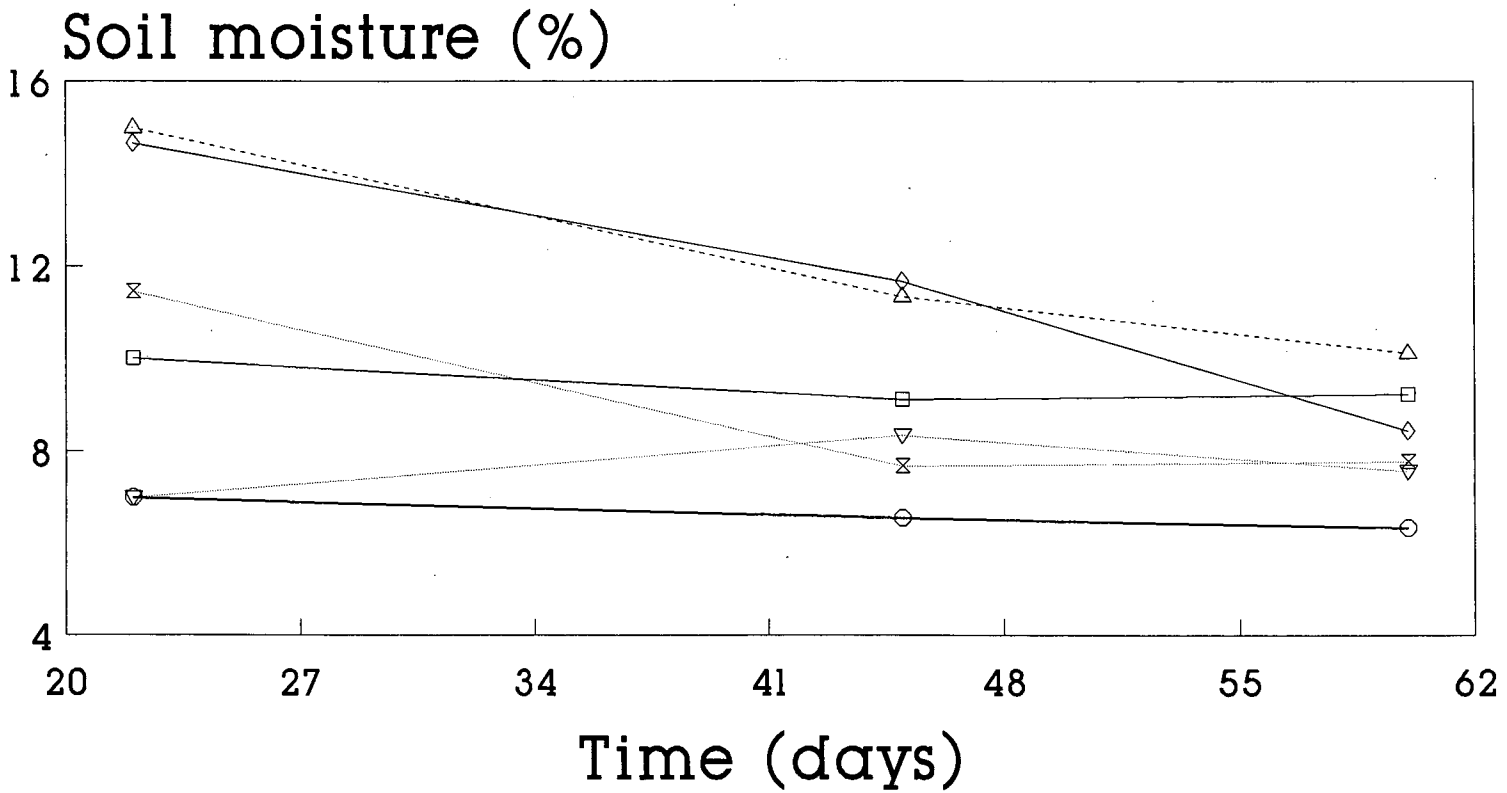
Table 37: Dry matter accumulation in the 322 genotype in treatments with (I) or without (NI) irrigation, of late sown sorghum, which was sowed following irrigated potatoes. Row spacing was 1 or 0.5 meter. Plants were harvested 88-d after sowing.

Treatment	Dry matter (kg/hectare)		
	Shoot*	Panicles	Total
322 (I) 1-m	1119.6	155.5	1275.1
" " 0.5-m	1400.0	155.3	1555.3
233 (NI) 1-m	808.6	171.0	979.6
" " 0.5-m	1010.7	139.9	1150.6

Exp. G2

* Leaves and stems.

List of Figures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100,16cm
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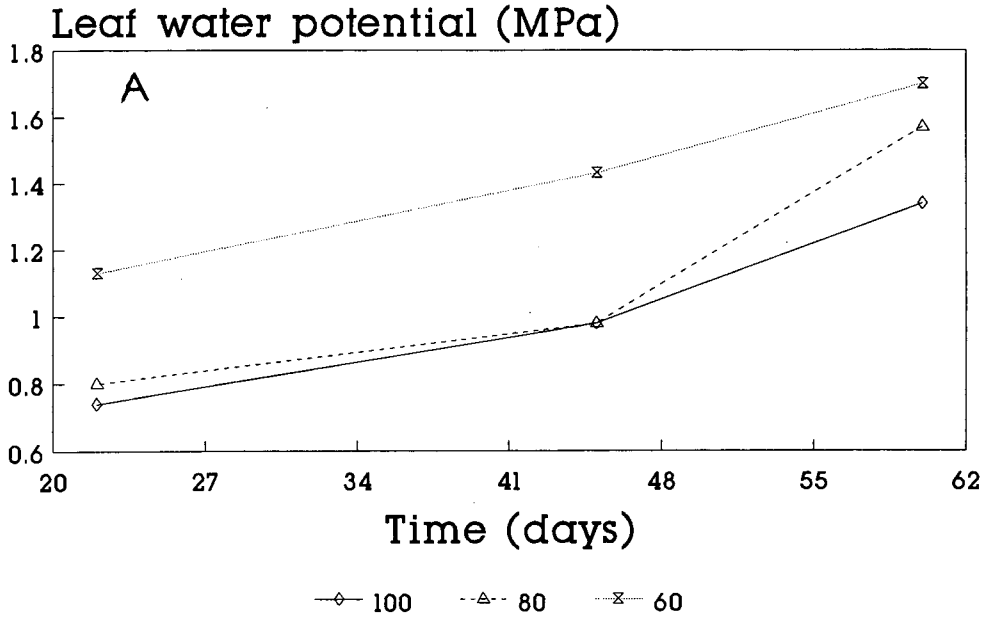
60,8cm
60,16cm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Time (days)
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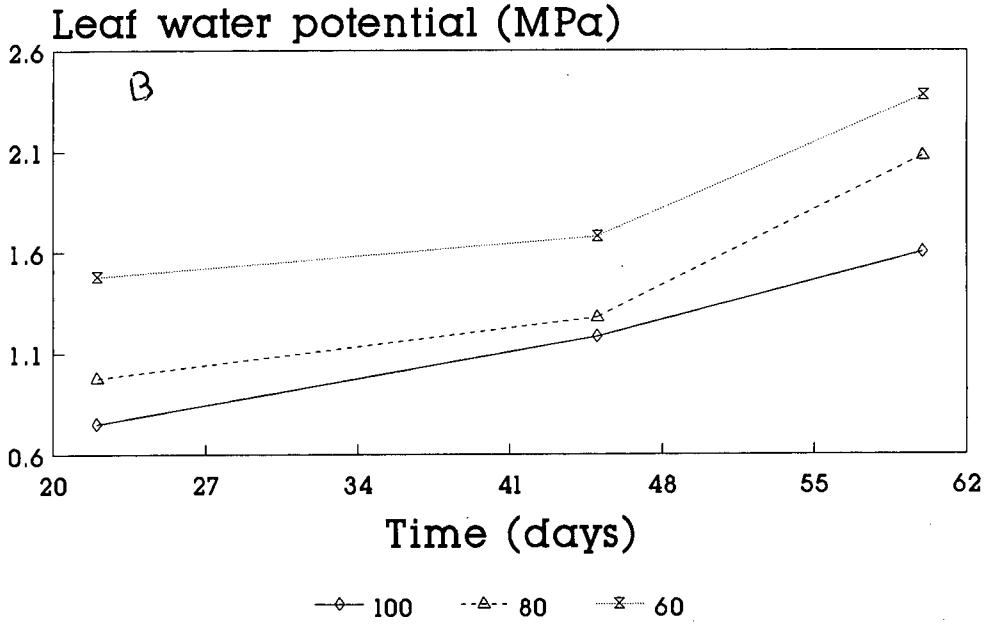
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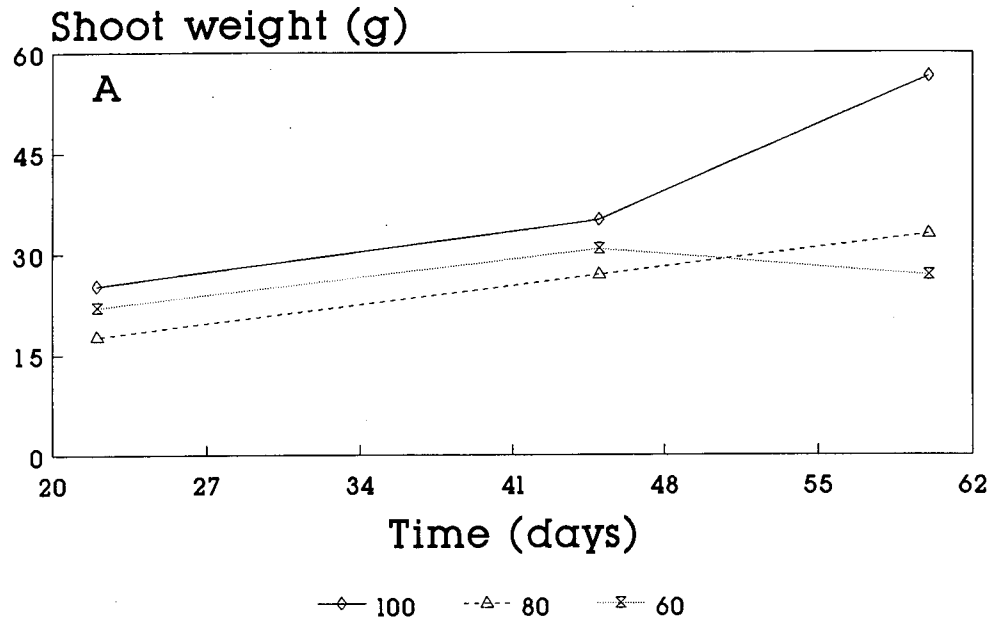
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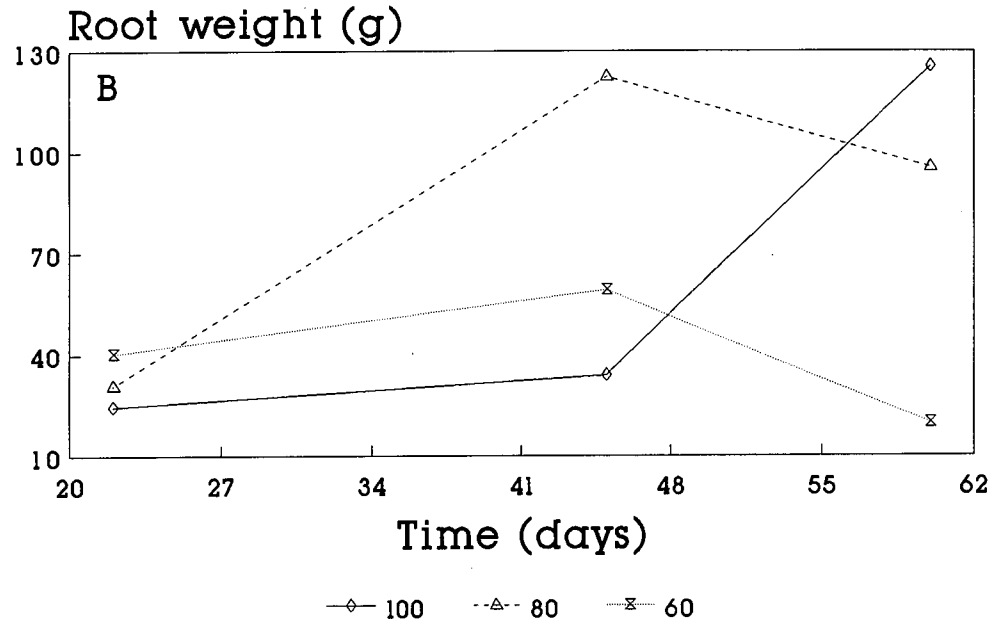
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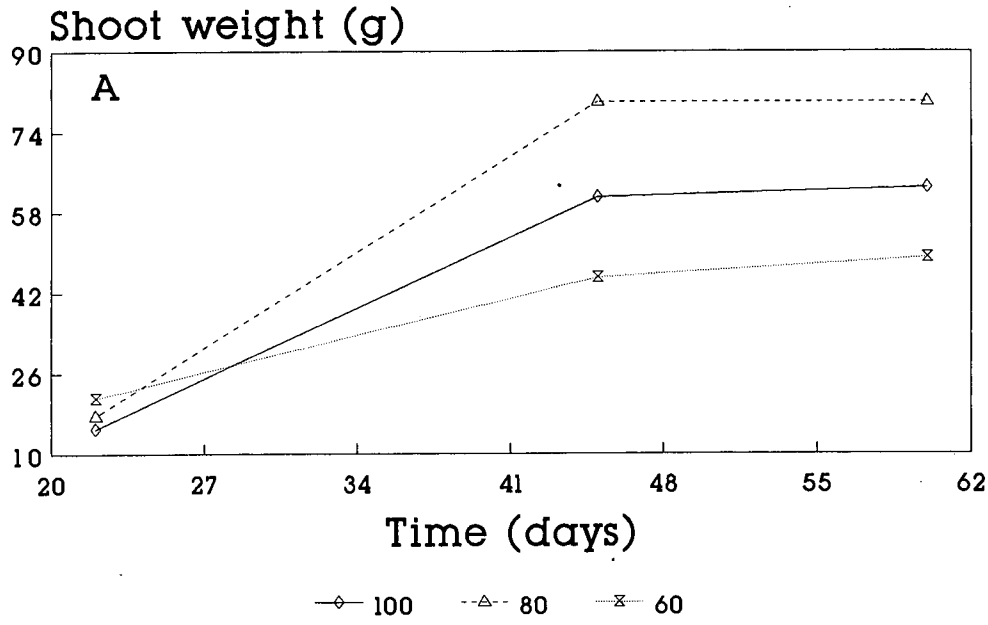
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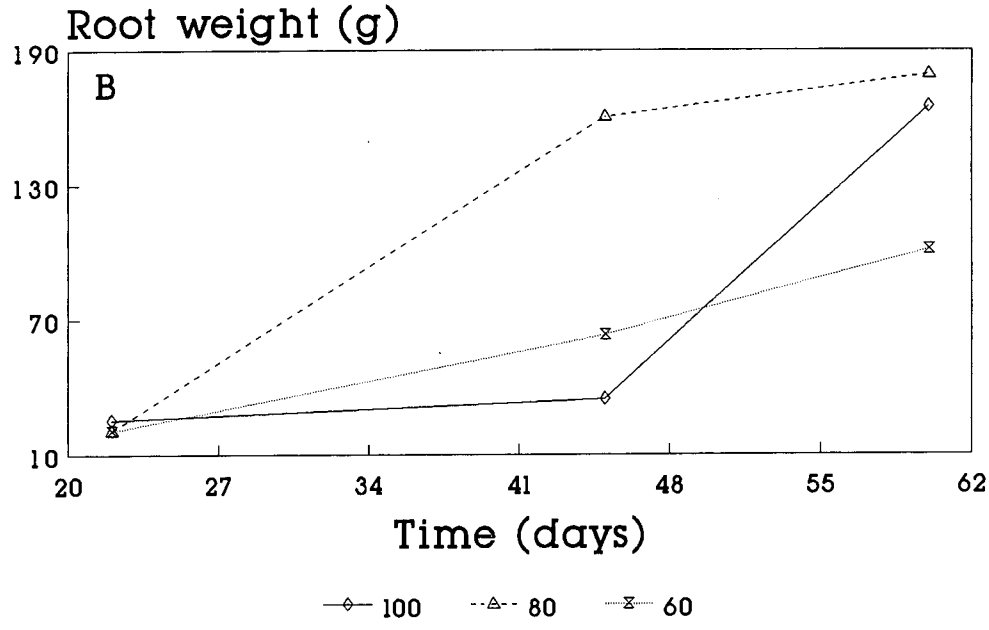
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55
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Time (days)
100
80
60

The research by the U.S. team

Research by the U.S. team addressed implications of root function in dry near-surface soil. Two aspects were studied. The first was differences between two genotypes in water absorption by and loss from roots in near-surface drying soil. The second aspect studied was the importance of duration of drying and availability of subsurface moisture on resumption of water uptake by roots following rewetting.

The U.S. team's contribution to the genotype comparison is described in the attached manuscript, REVERSE FLOW IN SORGHUM ROOTS, by X. Xu and W.L. Bland (accepted for publication in Agronomy Journal). The two genotypes studied in common with the Israeli team were SC-322-14E and SC-233-14E, hereafter referred to as 322 and 233; they were selected from the Texas Agricultural Experiment Station germplasm collection. As described in the manuscript, a glasshouse experiment was conducted, then the results were interpreted using a computer simulation model of water flow into and out of roots. The model served as a hypothesis about how a number of factors might interact to explain the observed behavior of the genotypes.

Genotype 322 showed greater drying of near-surface soil than did 233, and greater amplitude in water content cycling due to alternating water outflow and uptake. The simulation model mimicked this behavior when run with a lower critical water potential for stomatal closure for 322 and/or lower root length density for 233. These results are in keeping with observations from the Israeli team showing that 322, compared to 233, is more densely-rooted in the near-surface and that it allowed its leaves to dry to a lower water potential.

An additional finding presented in this manuscript is the first observation of water outflow from roots during the day. The simulation model provided theoretical support that the observations were correct. This has important implications for studies of outflow, because it is now clear that measurements must be made on a time interval of hours, rather than twice daily.

The lineal density of fine roots was measured for the two genotypes on 14 plants of each, grown in mist chambers. The mist chambers provided another physical environment, in addition to the field soil and hydroponics used by the Israeli team, in which to observe expression of root system morphology. Additionally, root systems grown in mist are easily measured for density of fine roots. Plants were harvested 15 days after planting for measurements. The number of laterals was counted on the basal 5 cm of the oldest nodal root. Additional parameters measured were: number of nodal roots, total length of the nodals, and leaf area. Results are presented in Table 1. There was no difference in the number of lateral roots per length of nodal root, or in leaf area at the time of harvest. The number of nodal roots in 322 was clearly greater than in 233, in agreement with observations of the Israeli team. Total length of nodal roots was larger in 233, also in agreement with data of our cooperators. Consistent expression of differences in root morphology in a range of environments indicates strong genotypic determination of the traits.

Table 1: Results of morphology study on 14 plants of each genotype, grown in mist.

	Fine root density	Number nodal roots	Length longest nodal root	Leaf area
	--No./5 cm --		----- cm -----	--cm^2--
SC-322-14E	83.4±18.7	6.9±3.3	55.5±3.3	160.0±18.1
SC-233-14E	74.0±16.3	5.6±0.6	69.8±6.8	175.0±18.1
t-test level of significance	ns	<0.002	0.2	ns

The second line of research on root function during and after drought addressed resumption of water uptake by roots following rewetting. A third genotype, RTx2817, was used in these experiments, selected because it was representative of common Texas cultivars.

Results of the experiments are described in a manuscirpt, RESUMPTION OF WATER UPTAKE BY SORGHUM AFTER WATER STRESS (accepted for publication in Agronomy Journal). The experiment demonstrated that the rate at which roots resume water uptake is influenced by the duration of their exposure to dry soil and by the availability of subsurface soil moisture. These factors must be considered when studying and attempting to predict resumption of water uptake. Procedures for comparisons of other genotypes for this characteristic were demonstrated in the research.

Reverse Water Flow in Sorghum Roots

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ABSTRACT

Efflux of water from plant roots has implications for nutrient uptake in dry soil, effectiveness of collection of water from deep in the soil, water parasitism among plants, and ability of roots to resume water uptake after exposure to dry soil. We measured the minimum soil water potential required for reverse flow in sorghum [Sorghum bicolor (L.)], the diurnal time-course of the efflux, and differences between sorghum genotypes in reverse flow. A split-root system was used in which near-surface roots were subjected to drying and deeper roots were in free water. Efflux of water to the dry soil could first be detected at a soil water potential of about -0.55 MPa, or across a soil water potential gradient of 0.55 MPa, a smaller value than previously reported to induce reverse flow. Outflow was 5 to 6% of daily transpiration during the periods of highest water use. Differences between the genotypes in the amount of water emitted and recaptured and the mean water content of the soil were mimicked by a computer simulation of water uptake and release by plant roots. Plant parameters contributing to simulation of the observed behavior were the relationship of leaf water potential to stomatal closure, and root length density. Water efflux from roots into the pot soil began at 1430 h, with the peak rate occurring near the end of the daytime period (1900 h) and cessation of outflow by 2400 h. Initiation of outflow during daytime is both physically reasonable and simulated in computer models. The time-course of outflow, however, was not correctly simulated. Measurements should be made at one hour time resolution to capture all reverse flow.

Transfer of water from zones of wet soil to dry soil through the root system has implications for nutrient uptake, the effectiveness of collection of water from deep in the soil, water parasitism among plants, and ability of roots to resume water uptake after exposure to dry soil. Referred to as negative transport, reverse flow, or hydraulic lift, it has been studied for more than half a century (Muller-Stoll, 1965; Passioura, 1988). Although it is not always observed (Dirksen and Raats, 1985; Nobel and Sanderson, 1984), evidence demonstrating its existence and magnitude is accumulating (Caldwell and Richards, 1989; Baker and van Bavel, 1988, 1986; Richards and Caldwell, 1987; Corak et al., 1987; Kirkham, 1980).

The split-root system is often applied to study of reverse flow (Baker and van Bavel, 1988, 1986; Kirkham, 1980). Most commonly the root systems is split vertically and the reverse flow is from one side to the other, but horizontally-split systems have been described (Corak, et al. 1987). In this study, use was made of a split-root system in which the top layer of soil could dry while roots below had access to free water. Advantages of this system were the high precision of measurements of water exchanges between layers, the high temporal resolution possible, and low cost for a large number of plants. Objectives of our study were to: (i) determine the water potential gradient required to induce reverse flow in sorghum, (ii) test for differences in reverse flow exhibited by two sorghum varieties, and (iii) determine the diurnal time course of water efflux from roots and subsequent use in transpiration.

MATERIALS AND METHODS

The experiments were conducted in July-November, 1990 in a greenhouse at the Blackland Research Center, Temple, Texas. Air temperature in the greenhouse had daytime maximums of 30 to 35°C, and nighttime minimums of 22 to 24°C. Sorghum was grown in 2.65-L (15 by 17.5 cm) plastic pots fitted with a water reservoir at the bottom (Fig. 1).

Reservoirs were 1000-mL plastic pet watering dishes. A 6-mm thick polyvinyl chloride ring was cemented to the bottom of the pot and the pot/ring assembly placed on top of the reservoir. The ring and pot assembly completely covered and sat inside a lip on the dish, preventing evaporation directly from the water reservoir (Fig. 1). Twenty-four 6-mm diameter holes were cut in the bottom of the pots and covered with a piece of plastic window screen. Roots grew through the holes, across a 15-mm air gap, and into the water reservoir. Water in the reservoir (a body about 6 cm deep and 15 cm in diameter) was aerated only by diffusion from the surface. No provisions were made to prevent capillary rise of water on the surface of the roots, because we do not believe that it occurs. If the outer surface of roots is non-wetting (large wetting angle, like a plastic straw), no capillary rise is expected. If the root is wettable (small wetting angle, like cotton thread), water on the outside of the root would likely be in equilibrium with that inside and upward flow on the surface is not distinctly different from flow in the root. Vapor-phase movement of water from the reservoir to the pot was found to be insignificant (data not shown).

By lifting the pot from the reservoir and weighing each separately with an electronic scale (Model PM 34, Mettler Inst., Switzerland), contributions of near-surface (pot) and deeper (reservoir) roots to transpiration could be calculated. During periods of experiments

in which weighings were made, tops of the pots were covered with 2-mm thick polyethylene foam to prevent evaporation from soil. To make a weighing, the pot and ring assembly was lifted from the dish and placed on a stand that allowed water to drip from the reservoir roots back into the dish. To protect the roots and reservoir water from evaporation during this step, the reservoir was placed in a plastic bag and the bag sides were pulled up and attached to the stand. The time required for free water to drip from the root systems increased throughout the experiment, from about one to 10 minutes; the same time was allowed for all plants on a given day.

Pots were filled with calcined clay. The water retention characteristic of the material was determined using Tempe pressure cells (Model 1400A, Soilmoisture Equipment Corp., Santa Barbara, CA) and a thermocouple psychrometer (Model SC-14A, Decagon Devices Inc., Pullman, WA) and results were in excellent agreement with van Bavel et al. (1978). Water potential of the pot medium was estimated throughout the experiment from its mass and the water retention curve. This approach assumes that water content is uniform throughout the pot. We believe this assumption was met because the pots were covered throughout the measurement period, preventing evaporation at the soil surface, and thorough and nearly uniform rooting was observed in the pots at periodic harvests (described below). Estimates of root length density from the mass of pot roots (Table 1) and the length/weight ratio observed in other experiments with this system (5 to 10 mg/m, unpublished data) yield values > 300 cm^{-2}, indicating that rooting was very thorough.

Experiment 1

Two lines of sorghum ('SC-322-14E' and 'SC-233-14E') were selected for the experiment from the Texas Agricultural Experiment Station sorghum germplasm collection, based on their similarity of agronomic nature but differing origins (Jordan et al., 1979), which may confer differences in root system behavior. Seeds were germinated in culture dishes, transferred into 50 pots (25/variety) fitted with reservoirs, and thinned to one plant per pot in a few days. Initially, all pots were irrigated to excess daily with nutrient solution (Peters 20-20-20, 0.2% w/v, Fogelsville PA) and the reservoirs were kept full of nutrient solution. When at least 100 mm of roots had grown into the reservoir (14 days after germination, 6th leaf still expanding), the gravimetric water content of pots was adjusted to 43.5% (pot capacity) in a final irrigation and the tops of the pots covered. Nutrient solution in the reservoirs was replaced with distilled water and this water level was maintained by daily additions. After 18 days of drying, a set of ten pot/reservoir systems of each cultivar was weighed twice daily (0800 h and 1630 h) on most of the next 10 ('322') or 25 ('233') days. Measurements on '322' were terminated after 28 days of drying because root volume in the reservoir had become too large to return to the dish without damage after weighing. Twenty plants of each variety were harvested over the course of the experiment (five plants on four occasions) to determine shoot fresh weight, pot and reservoir root fresh weight, and plant water content (Table 1); plants in the final harvest were from the weighed set.

To test for the effect of time of measurement on estimation of water efflux into the pot, a diurnal cycle of water exchange was measured on three pots of 'SC-322-14E' at 20 days after soil drying was imposed. Mass measurements were made at 2-h intervals from

0730 h of one day until 0930 h of the next. Selection of '322' was based on its greater reverse flow (discussed below).

Experiment 2

Because reverse flow had started by the time measurements were initiated in Experiment 1, an additional set of plants were grown to determine the time of first outflow. The device and procedures described above were used, except that 50 pots of one sorghum line ('SC-233-14E') were grown and the twice-daily weighings made from the onset of drying until the onset of outflow from the roots. Ten plants were weighed throughout the experiment and 40 plants were harvested for growth measurements as above (5 when treatments were imposed and 5 every 3-5 days thereafter; data not shown).

Water Exchange Calculations

Raw data for the water flux calculations consisted of masses of the pot/soil/plant and the reservoir water. Changes in the water content of the pot soil were taken simply as the total mass changes in the case of the diurnal measurements. With the twice-daily measurements, however, corrections were needed for changes in tissue hydration and plant growth. Water stored in the leaf, stem and root decreased due to transpiration in daytime and increased during the night. Under the conditions of our experiments decrease in water content (fresh weight w/w) of the shoot from 0800 h to 1630 h was about 1.4% (data not shown). Hydration of the roots in the pots was assumed to change in the same way as the shoots; this could not be measured directly because of the technical problem of separating

root and soil without changing root hydration.

Daily increases in total plant weight were estimated from the time-course of vegetative growth, which was determined from the periodic destructive samples. About 45% of vegetative growth, as estimated by plant height increase, occurred during the daytime and 55% at night under the conditions of our experiments (Table 2). Thus water flux (plant extraction is positive) in the pot soil was calculated as:

Water flux = (- Change of pot weight + Change of plant hydration + 0.9 x Change of plant weight). The 0.9 is the water content of plant tissues. For example, on day 15 after treatments were imposed in Exp. 2, pot weight increased 2.2 g during the night, total plant weight was 56.5 g, and the increase of plant weight during day 15 was 5.3 g. Therefore, Water flux = -2.2 + 56.5 x 1.4% + 0.9 x 5.3 x 55% = +1.2 g, indicating that reverse flow did not occur during this night, even though pot weight increased.

Simulation

To gain insight into the physics of water exchanges in our system, we ran a number of simulations using the model described by Campbell (1985, 1991). The example input parameters discussed in Campbell (1991) were used as described, and with changes in the critical leaf water potential for stomatal closure (increased to 2500 J/kg) and the root length density (decreased by one-half in layers 2 and 3). For some simulations the water content of layer 5 was reset to 0.1 m m^{-1} after each timestep to better mimic our pot and reservoir system.

RESULTS AND DISCUSSION

Minimum Water Potential Gradient for Reverse Flow

During the first six days after treatments were imposed in Exp. 2 the majority of transpiration (92-81%) was absorbed from the pot soil. With depletion of water in the soil, absorption shifted to the reservoir, consistent with theory and many observations. Reverse flow (negative flux) first occurred after 20 days of drying, when the soil water potential was about -0.55$\pm$0.03 MPa (data not shown). The resulting gradient of water potential between soil compartments was also 0.55 MPa (from free water to the -0.55 MPa soil). At the time measurements started in Exp. 1, the gradient was about 0.55 MPa for '233' and 0.60 MPa for '322,' and reverse flow was occurring. The apparent minimum potential gradient for water exchange between soil volumes required to induce reverse flow in our experiments was smaller than the 1.0 MPa reported by Baker and van Bavel (1988). This parameter is likely a function of a number of diverse factors, including plant water potential components, the limit of detection of efflux, species, and experimental conditions.

Magnitude of Reverse Flow and Genotype Differences

Between 18 and 29 d after the start of drying, reverse flow amounted to 5 to 11% of daytime transpiration from '322' and 2 to 7% from '233'(Fig. 2A & 2C). Maximum daytime transpiration from '322' in Exp. 1 (about 345 g) occurred from 20 to 22 days after treatments were imposed (Fig. 2A), coinciding with relatively large nighttime inflows of water to the pot (about 20 g, Fig. 2C), or about 6% of the peak transpiration. Similarly

'233' had its largest daytime transpiration 20 to 22 days after treatments were imposed and inflow to the pot was about 5% of this amount (Fig. 2C; later measurements on '233' were similar to those of days 25 and 28). Thus in this experiment reverse flow was an appreciable fraction of even the largest transpiration rates measured. Larger values of this fraction (25 to 50%) are observed in experiments in which plant transpiration is likely small relative to what it might have been in a well-watered control (Baker and van Bavel, 1986; Caldwell and Richards, 1989). In our experiment the artificial condition of free water available in close proximity to dry soil contributed to the large outflow at high transpiration observed here.

Generally, larger quantities of water flowed outward from the roots (negative flux, Fig. 2C) of '322' than from '233' and this outflow constituted a larger fraction of the previous day's extraction from the pot. The mean water contents of the pots at each weighing decreased with time, as did the amplitudes of the fluctuations (Fig. 2B). Patterns of soil water content similar to those in Fig. 2 were recreated by the modified (water content of layer 5 reset to 0.1 each timestep) Campbell (1991) model. Compared to Campbell's (1991) example dataset (Run C, Fig. 3), lowering the critical leaf water potential to 2500 J kg^{-1} (Run A, Fig. 3) resulted in drying of the soil to a lower potential and a larger amplitude on any day, similar to '322' compared to '233'. Root length density was decreased from the example input set (Run C) in Run B, to simulate differences in rooting observed between the genotypes (Table 1). This resulted in decreased amplitude of the fluctuations, but had little effect on final water content (Run B compared to Run C, Fig. 3). Thus differences between genotypes observed (Fig. 2) may have been due to both the tendency by '322' to allow its leaf water potential (not measured in this experiment) to become lower than that of '233' and

the greater root length of the '322' pots. Genetic differences in reverse flow likely will be related to these two traits.

Diurnal Cycle of Efflux and Influx

Soil water potential was -0.84 MPa at the beginning of the measured diurnal cycle and daily transpiration was at the maximum rate observed during the experiment. Most of the transpiration between 0730 and 0900 h came from the soil, after which its contribution decreased, reaching zero at 1430 h (Fig. 4). Reverse flow from roots then began to contribute water to the pot, reaching a maximum rate of 13.4 g h^{-1} at 1830 h, then decreasing to near zero at 2400 h. Most previous reports lacked the temporal resolution needed to demonstrate the time-course of efflux (e.g., Baker and van Bavel, 1988). However, soil water potential as measured by psychrometers apparently increased only at night in the measurements reported by Richards and Caldwell (1987) and Caldwell and Richards (1989).

The simulation exercise also indicated that outflow of water could begin in the afternoon. The example described by Campbell (1991) was run without modification to the model. Figure 5 shows the fluxes in and out of roots in several soil layers on day 7 and part of day 8 of the example. Outflow from the roots in layer 2 begins at 1500 h and from those in layer 3 at about 1800 h. Changes in model parameters would alter these results.

The simulation indicated that outflow rate was essentially symmetrical with the diurnal cycle, however, in contrast to our measurements. Radial flow from a cylindrical source is known to be initially rapid, then to decrease to a lower, steady flow (Jury et al. 1991).

Incorrect behavior of the model occurs, at least in part, because it does not iterate to find the water potential at the root surface at each timestep. This is a time-consuming calculation and soil resistance is often small relative to root resistance, so the bulk soil potential was used to find the soil resistance (Campbell, 1991). Soil resistance is comparable to root resistance during reverse flow, however, so it must be carefully estimated for accurate predictions of this phenomenon.

Results of the diurnal timecourse and the simulation demonstrate that frequent measurements are required to fully document reverse flow. Important near-surface reverse flow can occur as soon as leaf water potential begins to increase following decreasing evaporative load or stomatal closure.

In summary, efflux of water from roots occurred at a water potential gradient of about 0.6 MPa between near-surface dry soil and underlying free water. Sorghum genotypes were observed to differ in the magnitude of reverse flow, possibly due to differences in root length density and/or stomatal regulation. Finally, significant efflux can occur during daytime hours, indicating that reverse flow measurements must be made at an hourly time resolution.

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REFERENCES

Baker, J.M., and C.H.M. van Bavel. 1988. Water transfer through cotton plants connecting soil regions of differing water potential. Agron. J. 80:993-997.

Baker, J.M., and C.H.M. van Bavel. 1986. Resistance of plant roots to water loss. Agron. J. 78:641-644.

Campbell, G. S. 1985. Soil physics with BASIC: Transport models for soil-plant systems. Elsevier, Amsterdam.

Campbell, G. S. 1991. Simulation of water uptake by plant roots. In: J. Hanks and J. T. Ritchie (ed.) Modeling plant and soil systems. Agronomy 31:273-285.

Caldwell, M.M., and J.H. Richards. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. Oecologia 79:1-5.

Corak, S.J., D.G. Blevins, and S.G. Pallardy. 1987. Water transfer in an alfalfa/maize association. Plant Physiol. 84:582-586.

Dirksen, C., and P.A.C. Raats. 1985. Water uptake and release by alfalfa roots. Agron. J. 77:621-626.

Kirkham, M.B. 1980. Movement of cadmium and water in split-root wheat plants. Soil Sci. 129:339-344.

Jordan, W.R., F.R. Miller, and D.E. Morris. 1979. Genetic variation in root and shoot growth of sorghum in hydroponics. Crop Sci. 19:468-472.

Jury, W. A., W. R. Gardner, and W. H. Gardner. 1991. Soil physics. 5th ed., Wiley & Sons, New York, NY.

Molz, F.J., and C.M. Peterson. 1976. Water transport from roots to soil. Agron. J. 68:902-904.

Muller-Stoll, W.R. 1965. The problem of water outflow from roots. p. 21-29. In B. Slavik (ed.) Water stress in plants. Dr. W. Junk, The Hague.

Nobel, P.S., and J. Sanderson. 1984. Rectifier-like activities of roots of two desert succulents. J. Exp. Bot. 35:727-737.

Passioura, J.B. 1988. Water transport in and to roots. Ann. Rev. Plant Physiol. 39:245-265.

Richards, J.H., and M.M. Caldwell. 1987. Hydraulic lift: Substantial nocturnal water transport between soil layers by Artemisia tridentata roots. Oecologia 73:486-489.

Van Bavel, C.H.M., R. Lascano, and D.R. Wilson. 1978. Water relations of fritted clay. Soil Sci. Soc. Am. J. 42:657-659.

Table 1. Freshweight measurements during Experiment 1.

Days of Drying	Shoot	Pot Roots	Reservoir Roots	Total
		g		
		'SC233-14E'		
19	89.9±24.8[1]	48.8±16.4	44.1±14.6	182.6
24	120.8±19.1	66.7±11.3	82.3±34.7	269.8
29	124.5±14.8	70.8±12.3	76.9±9.9	272.2
43	160.0±19.0	56.4±8.3	63.6±7.0	280.6
		'SC322-14E'		
15	117.6±13.1	70.5±3.7	59.0±19.5	247.1
20	144.6±22.8	130.5±20.8	128.4±33.6	403.4
26	185.8±10.8	145.2±22.3	202.1±29.3	533.1
33	237.2±14.4	153.8±13.0	249.9±30.3	640.9

[1]Mean ± SD, n=5

Table 2. Sorghum height increase during day and night periods

	Days after emergence	
	11-13	20-22
	cm	
Night†	3.95±0.20*	3.44±0.15
Daytime	3.01±0.13	3.20±0.09
Night	4.42±0.13	3.81±0.24

†Three successive periods, where night was 1600 h to 0800h and daytime was 0800 h to 1600.

*Sorghum height is length from soil surface to leaf tip held erect; average of 5 replications ± S.D.

Figure Captions

Fig. 1. Pot and reservoir system to allow drying of near-surface soil with water available below.

Fig. 2. A: Daytime (0800 to 1630 h) transpiration of sorghum genotypes '322' and '233' during drying of the pot soil; water was always available in the reservoir below. B: Mean water content of the soil during the drying cycle. C: Water fluxes between roots and soil in the pots (positive is from soil to plant). All data are the mean of 10 pots, and error bars are 1 SD (C) or $\pm$ 1 SD (A); ticks on x-axis indicate start (0800 h) of each day.

Fig. 3. Computer simulations of soil water content during a drying cycle. Compared to the example run (Run C), as in Campbell (1991), Run A had stomatal regulation parameters permitting a lower leaf water potential before stomates closed, and Run B had a lower root length density.

Fig. 4. Diurnal time-course of water fluxes in/out of soil-filled pot and water-filled reservoir below. Positive water flux is from soil to root. Values are mean of 3 plants and error bars are $\pm$1 SD.

Fig. 5. Computer simulation of water exchange between roots and soil, using the example in Campbell (1991). Positive water flux is from soil to root. Outflow begins in the afternoon in near-surface layers. (Layer 1 has no root length in the example.)

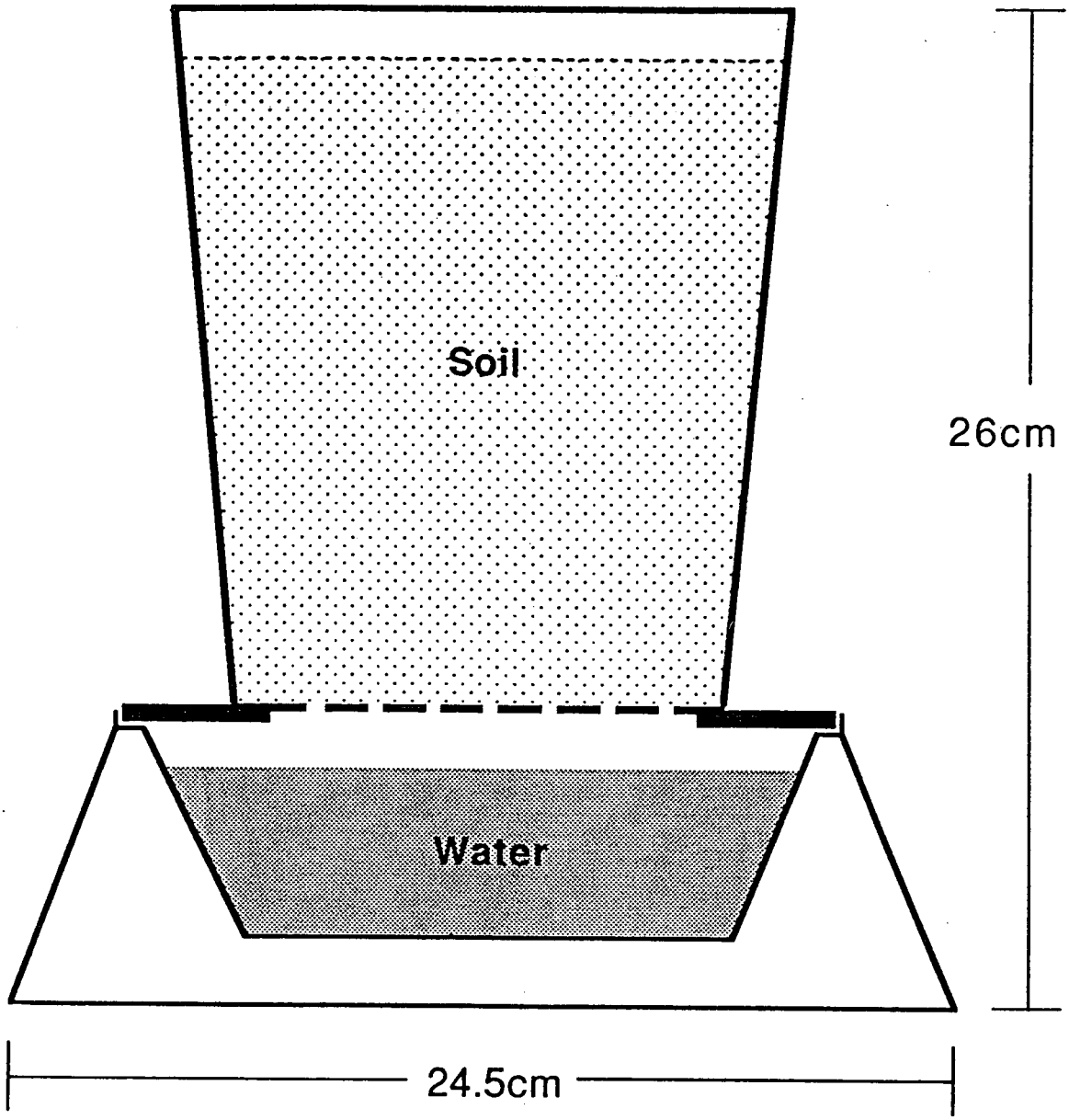
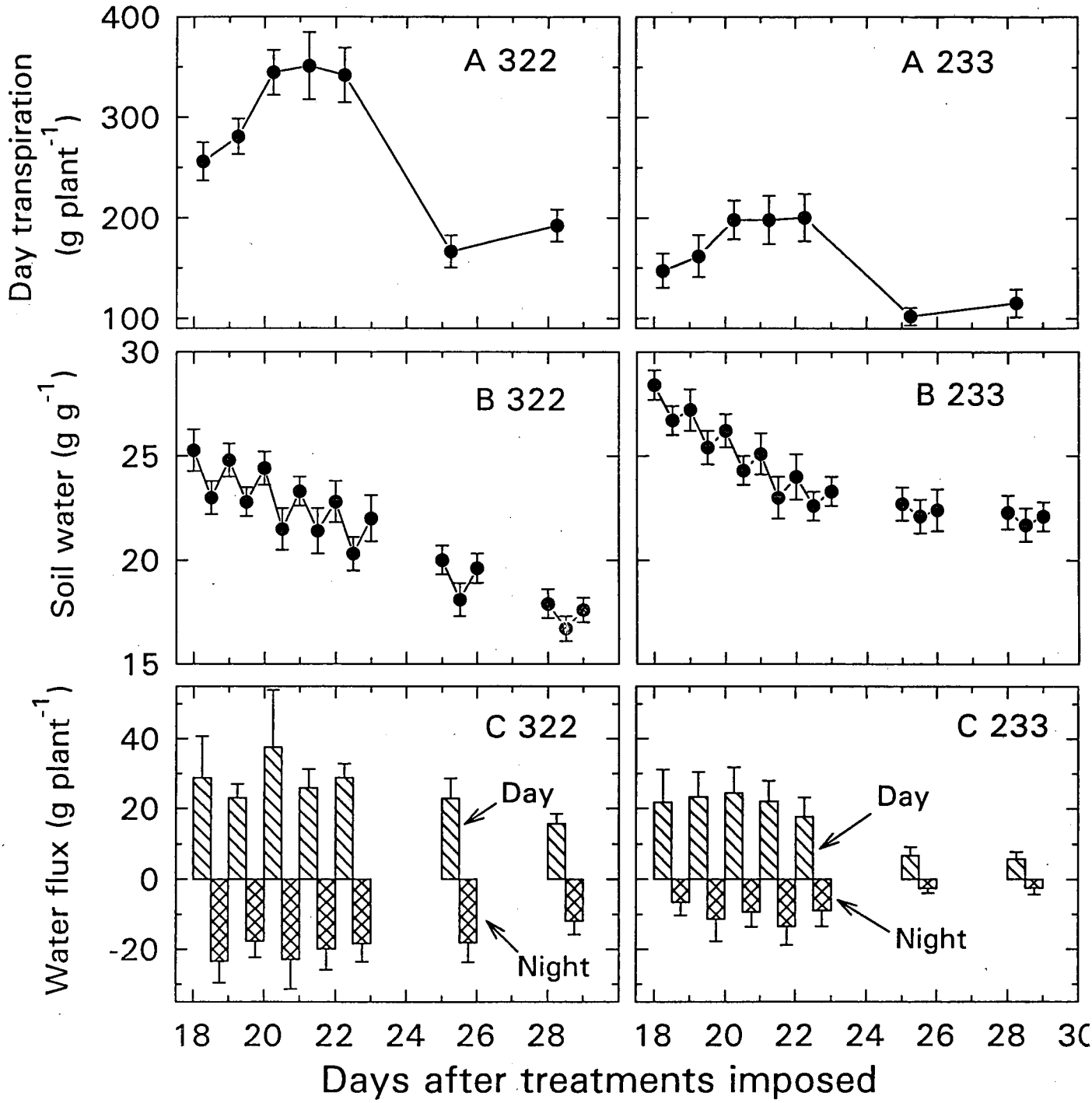
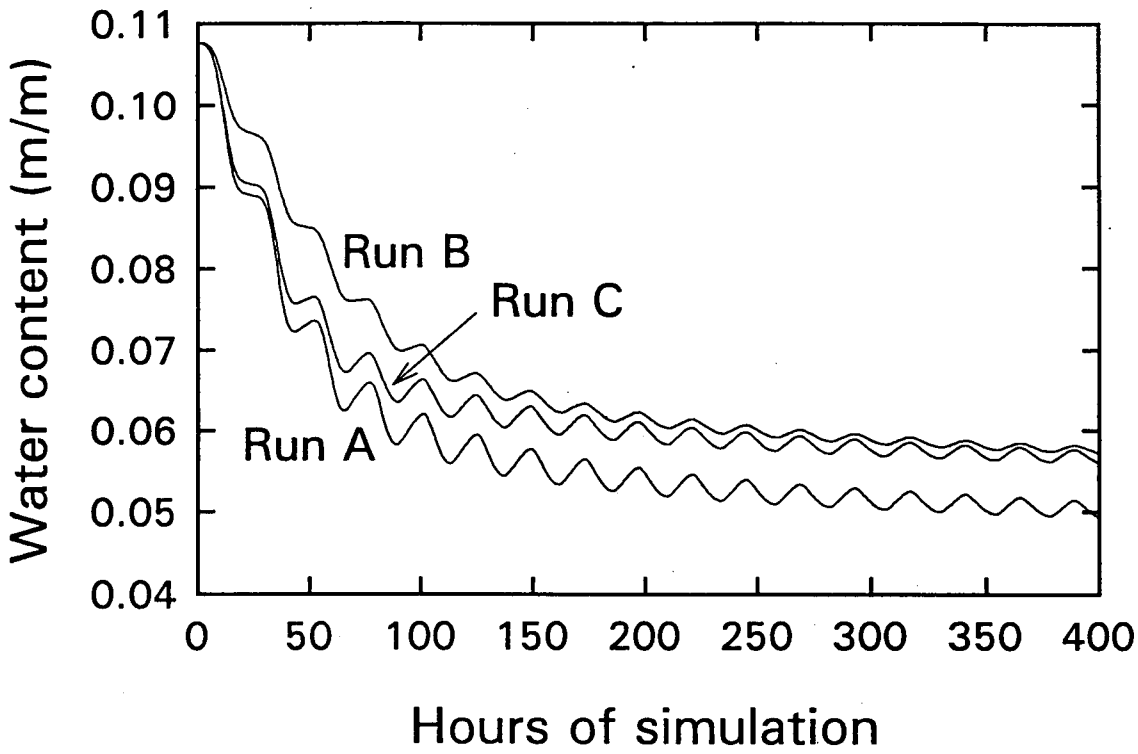


Fig. 1 Xu/Bland


A 322
A 233
B 322
B 233
C 322
C 233
Day
Night
Day transpiration (g plant^{-1})
Soil water (g g^{-1})
Water flux (g plant^{-1})
Days after treatments imposed
400
300
200
100
30
25
20
15
40
20
0
-20
18
20
22
24
26
28
30


0.11
0.10
0.09
0.08
0.07
0.06
0.05
0.04
Water content (m/m)
Run B
Run C
Run A
0
50
100
150
200
250
300
350
400
Hours of simulation

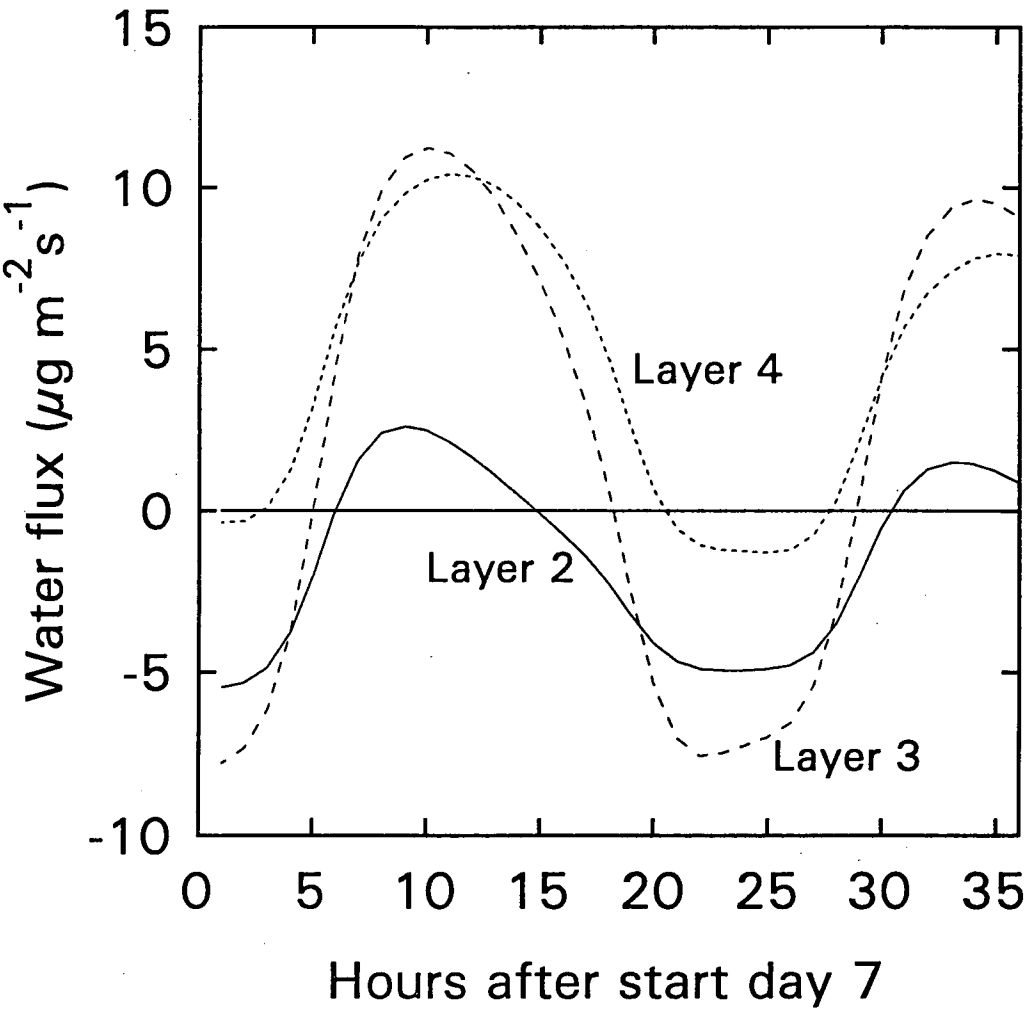


Fig. 5\Xu & Bland

Resumption of Water Uptake by Sorghum after Water Stress

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ABSTRACT

Exposure of roots to dry soil may reduce their ability to absorb water when the soil is rewet. We sought to quantify the effects of duration of exposure to dry soil and availability of water in deeper soil layers on resumption of water uptake by roots of Sorghum bicolor (L) Moench following rewetting of the soil. Plants were grown in a greenhouse in pots, half of which were fitted with a water-filled reservoir below the pot bottom. Soil was allowed to dry for either 26 or 39 d before rewetting. Reservoir roots were excised at rewatering to limit uptake to roots previously exposed to soil drying. Time courses of plant transpiration and leaf water potential prior to and after rewatering were measured. Longer exposure to dry soil slowed resumption of uptake. After 26 d of drying, plants without reservoirs transpired 63.5% of that of well-watered controls without reservoirs on the first day following rewatering, compared to 29.4% following 39 d of drying. Water available below the dry soil enabled roots to resume water absorption immediately after rewatering. On the first day after rewatering following 39 d of drying, transpiration relative to well-watered controls (with and without reservoirs) was 2.6-fold greater in plants with access to a reservoir than those without. Water-stressed sorghum showed larger root/shoot and root weight/length ratios than controls.

INTRODUCTION

Plants growing under natural conditions are frequently exposed to cycles of soil drying and rewetting. Periods of drying shift water uptake from shallow to deeper roots, sometimes reducing near-surface uptake to zero. Rain and irrigation rewet near-surface soil first and roots there can resume water uptake. The rate at which roots exposed to dry soil resume uptake following watering has important implications, yet is little understood (Passioura, 1983, 1988). Knowledge of root water uptake following soil rewetting is needed to predict partitioning of rainfall and irrigation among evaporation from soil, transpiration, and downward movement. Recovery of plant growth after water stress may depend in part upon the rate of water uptake by rewetted roots.

Slatyer (1967) proposed that recovery from water stress was delayed by reduced water absorption caused by death of root hairs or roots, and by increased suberization of roots. Root systems subjected to severe water stress often show decreased permeability that may persist several days after rewatering. As a result, leaf water potential and processes such as photosynthesis may not return to their pre-stress rate for a few days (Kramer, 1983). Gregory et al. (1978) suggested that wheat roots retained the ability to take up water even after severe soil drying. Their uptake observations had a time resolution of 1 wk, however. Dirksen and Raats (1985) concluded that near-surface roots of alfalfa subjected to soil drying and nearly inactive for more than 24 d took up water at a high rate immediately after rewetting. Their data referred only to uptake between 2 and 5 d after rewatering and partitioning of water absorption between near-surface and deeper roots was not clear (Passioura, 1988). Finally,

Passioura (1988) concluded that resumption of water uptake by roots exposed to very dry soil may be significantly retarded.

We conducted an experiment to study resumption of water uptake by sorghum plants on rewatering following water stress. Our objective was to assess the effects of duration of soil dryness and presence of roots with access to water below the dry surface soil. To do this, we developed a system to create near-surface dry soil conditions with and without sub-surface water supplies. Measurements of water uptake by near- and sub-surface roots were made during water stress, and by near-surface roots only after rewatering.

MATERIALS AND METHODS

The experiment was conducted during winter months in 1989 in a greenhouse at the Blackland Research Center, Temple, TX. Air temperature in the greenhouse had daytime maximums of 27 to 34°C, and nighttime minimums of 21 to 34°C. Day length decreased from 10.5 h at the beginning of the experiment to 10.1 at the end. Integrated daily solar radiation flux was 6 MJ $m^{-2}d^{-1}$ on average and ranged from 10 to 1 MJ $m^{-2}d^{-1}$.

Plastic pots (2.65 L, 15 by 17.5 cm) were used as plant containers, half of which were equipped with a water reservoir. Reservoirs were 1000-mL plastic pet watering dishes. A 6-mm thick polyvinyl chloride ring (i.d. 1 cm less than the pot base diameter, o.d. equal to the water dish rim) was cemented to the bottom of the pot and the pot/ring assembly placed on top of the reservoir. Plant roots penetrated through drainage holes in the bottom of the pot, through a 15-mm air gap, and into the reservoir. By lifting the pot from the reservoir and weighing each separately with an electronic scale (Model PM34, Mettler Instr., Switzerland)[1], water loss from each compartment was measured. The pot and ring completely covered the reservoir, and the soil surface was covered during the measurement period (discussed below), so the total water loss was the plant transpiration. Water was allowed to drain from the reservoir roots before the pot was weighed; repeated weighing did not damage roots.

Pots were filled with calcined clay (Balcones Minerals Corp., Flatonia, TX), selected because of its relatively low dry bulk density, rapid drainage, large

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[1] Mention of company and/or product name does not constitute endorsement by Texas A&M Univ. System or the Univ. of Wisconsin-Madison.

quantity of plant-available water and ease with which it washed off roots. The relationship between water content and potential of the calcined clay was determined using Tempe pressure cells (Model 1400A, Soilmoisture Equipment Corp., Santa Barbara, CA) and a thermocouple psychrometer (Model SC-14A, Decagon Devices Inc., Pullman, WA). The results were in excellent agreement with those of van Bavel et al. (1978).

In the experiment presented here, sorghum (Sorghum bicolor L. Moench cv RTx2817) seeds were germinated on paper towel for 1 d, transferred into the pots, and thinned to one plant per pot in a few days. Initially, pots were irrigated to excess daily with nutrient solution (Peters 20-20-20, 0.2% w/v, Fogelsville, PA) and the reservoirs maintained full of nutrient solution. When at least 10 cm of roots had grown into the reservoirs (32 d after germination, seventh leaf collar visible), three plants with and without reservoirs were sampled for root length, root weight, leaf area, and shoot weight. Water content of the remaining pots was adjusted to 0.44 g/g (pot capacity). The top of all pots were sealed with 2-mm thick polyethylene foam to prevent evaporation, and drainage holes on pots without reservoirs were sealed with tape.

Four water-availability treatments were then imposed, each maintained for 26 and 39 d, producing a total of eight treatments. To expose plants to the situation of near-surface drying but water available deeper, a set of pots with reservoirs were allowed to dry, with the reservoirs kept full (D+R); for comparison, the pot soil was watered to capacity each day in another set of pots with reservoirs (W+R). The situation of the entire root system subjected to drying was created in pots without reservoirs. One set of these plants was allowed to dry (D-R) and another rewatered daily (W-R).

At the end of each time interval, a set of drying pots was rewatered and, in the case of +R plants, the reservoirs and roots therein were removed. Excising the reservoir roots forced subsequent water uptake to be via roots exposed to soil drying. After 26 d of drying, five pots of each water regime were sampled; after 39 d, four D–R, four W–R, five D+R, and five W+R plants were sampled. Prior to rewetting, all pots and reservoirs were weighed daily; after rewetting, the selected pots were weighed at 2–h intervals during daytime hours for 3 to 5 d.

Leaf water potential was measured prior to and following rewatering on 5–cm long pieces of leaf near the tip of the sixth and seventh leaves (covered with a small plastic bag just before excision) using a pressure chamber (Model 3005, Soilmoisture Equipment Corp., Santa Barbara, CA). When plants were harvested, roots were washed free of clay and their length measured with a root length scanner (Hawker–Dahavilland Victoria, Ltd., Melbourne, Australia). Leaf area at harvest was determined with an area meter (Model LI–3100, LICOR, Lincoln, NE). Area of individual leaves of growing plants was estimated as: Leaf Area = 0.71 x Leaf Length x Leaf Width, based on earlier calibrations.

In an ancillary experiment, effect of the presence of roots on recovery after rewatering was studied after 39 d of drying by excising roots of four D–R plants under water and leaving the cut end of the shoot in water. Transpiration was measured daily by weight loss.

RESULTS AND DISCUSSION

Transpiration and Water Absorption

Transpiration rate (per unit leaf area) from D+R pots was equal to that of W+R pots for about 8 d after treatments were imposed, then decreased to 80 to 85% and remained at this level (based on Fig. 1A and Fig. 2). Reservoirs supplied only 10 to 15% of W+R transpiration throughout the experiment, but their contribution to D+R increased to 100% by day 30 of drying (Fig. 1A), indicating that pot roots had almost ceased water uptake by the time plants were rewatered at 26 d. Transpiration rate (per unit leaf area) of D–R relative to W–R pots decreased gradually to about 20% (based on Fig. 1B and Fig. 2). Temporary wilting of D–R plants occurred on the day 19 and plants remained wilted after day 29. At the end of the experiment, soil water potential in the D–R pots was –1.7 MPa (Fig. 1C).

Insert Fig. 1 & 2

Plant Growth

The first four leaves had completed growth in all pots when treatments were imposed. Drying of the pots neither delayed appearance of subsequent leaves nor affected areas of leaves 5 to 7 on D+R plants. Growth of leaves 8 to 11 was inhibited in the D+R pots, however, resulting in significantly less leaf area relative to W+R plants after about 28 d of drying (Fig. 2).

Water stress reduced leaf growth in D–R plants relative to the W–R treatment after 15 to 20 d of drying (Fig. 2), when soil water potential had decreased only to –0.1 MPa (Fig. 1C). Appearance of new leaves was delayed and some defoliation occurred such that at the end of the experiment, leaf area of D–R plants was about 27% of W–R and W+R plants.

Drying of the soil had complex effects on both root weight and length (Table 1). On day 26, root weight of D+R pots was 1.3 times that of W+R; root length in D+R pots, however, was only 0.7 of W+R. By day 39, root weights in +R pots were equal, but root length of D+R pots was about one-half that in W+R pots. Soil drying increased both length and weight of roots in the reservoir. After 26 d without irrigation, root weight was slightly larger in D-R than in its control (W-R), but length was only 65%; at 39 d, weight and length were greater in W-R.

Thus we observed a net increase of root weight with moderate stress (D+R at 26 d) (Sharp and Davies, 1979). However, for both +R and -R treatments, root length was less for water-stressed sorghum plants than the controls, resulting in larger weight/length ratios in stressed plants (Table 1).

Insert Table 1

Preferential root growth under water stress is thought to enable plants to explore new soil volumes and, therefore, access more water (Hsiao et al., 1976; Begg, 1980; Ludlow, 1980; Sharp and Davies, 1985). Models of water uptake by roots indicate that increased root diameter is not an effective way to allocate resources for water collection, however. Measurements of root length, rather than mass, are necessary to test hypotheses about improved exploration of soil by water-stressed plants.

Root/shoot ratios decreased with plant age as expected (Aung, 1974) in well-watered treatments (W+R and W-R). Greater root growth and inhibition of shoot growth significantly increased root/shoot ratios for both D+R and D-R plants (Table 2) as is frequently reported (Pearson, 1966; El Nadi et al., 1969; Hoffman et al., 1971; Sharp and Davies, 1979).

Insert Table 2

Effect of Duration of Soil Drying

After 26 d of soil drying, pot roots were contributing less than 10% of D+R transpiration (Fig. 1A). When five of the D+R pots were rewatered and their reservoir roots removed, hourly transpiration time courses indicated the pot roots were immediately capable of meeting demand for water (Fig. 3A). The day before rewatering, total daily transpiration (integral of rate curves in Fig. 3) from D+R plants was 84% of that from W+R, but became 89 and 97% during the first and second 24-h periods after rewatering (day 1 and 2 of recovery). Leaf-water potential of the D+R plants was equal to the W+R controls by 7 h after rewatering of the pots (Table 3).

The day 39, pot roots of the D+R plants had been inactive at water absorption for 8 d (Fig. 1A). Recovery of water absorption by these roots following rewatering was slower than after 26 d drying (Fig. 4A). During the 24 h following rewatering the pots and excision of reservoir roots, total transpiration of D+R was 76% of W+R, compared with 87% on the day before. Low irradiance on the second and third days made it difficult to judge supply ability of the roots. By day 4, total transpiration was 84% of W+R, suggesting that complete recovery of transpiration still had not been obtained. Recovery of leaf water potential was faster than transpiration, equaling the unstressed plants only 30 h after rewatering (Table 3).

The five D-R pots rewatered after 26 d of drying exhibited temporary wilting for 8 or 9 d preceding watering and leaf water potentials at rewatering were about -1.9 MPa, compared to the -0.6 MPa for W-R (Table 3). Two hours after rewatering, there was visual improvement in leaf turgor and by 4 h, D-R leaves appeared similar to W-R leaves. Leaf water potentials 7 h after rewatering were

nearly equal for D–R and W–R plants (Table 3). Total transpiration by D–R plants the day before rewatering was 24% of W–R, but increased to 63.5 and 74.7% in the first and second day after rewatering (Fig. 3B). After 39 d without irrigation, D–R plants had remained wilted for 11 d. By that time, leaf water potentials were −3.7 MPa (Table 3) and total transpiration rate was 5.5% of that of the W–R (Fig. 4B). On rewatering, leaf water potential increased to −1.72 MPa within 5 h and reached the W–R level in 3 d. Total transpiration increased to 29.4, 66.0, 74.2, and 72.3% of that of W–R in the 4 d following rewatering. Thus, in the most severe treatment of our experiment, transpiration on the first day after rewatering was five-fold that of the previous day and transpiration relative to control doubled between the first and second days after rewatering.

Role of Subsurface Water Supply

Resumption of water uptake also depended on the availability of water to deeper roots. Water absorption by roots in the D+R pots decreased with soil drying and ceased when soil water potential fell to −0.45 MPa. In contrast, the D–R plants dried the pot soil to −1.7 MPa (Fig. 1C). Roots in the D+R pots had not absorbed water for 8 d by the end of the 39-d drying period, but resumed water uptake immediately after rewatering. During the first day after rewatering, D+R transpiration was 76.5% of W+R (control), 2.6 times that of rewatered plants that did not have reservoirs during soil drying.

Underlying water supply tends to reduce stress on roots in near-surface drying soil by two related means. Water uptake models (Taylor and Klepper, 1978) indicate soil water potential at a depth should be between the water potential in the xylem at the soil surface and that of underlying soil layers (in the absence of direct evaporation of soil water). Thus, drying of a layer is reduced

if deeper water is available. Additionally, release of water from sub-surface soil layers to overlying dry layers through plant roots may occur (e.g., Baker and van Bavel, 1988; Xu and Bland, 1991), preventing root desiccation.

Reopening of stomata and resumption of photosynthesis are known to be delayed after rewatering, even though leaf water potential has recovered to that of the control (Glover, 1959; Fischer, 1970). These phenomena were observed in this experiment (data not shown). Our experiment does not allow determination of whether inhibited water uptake at the root or some unknown determinant of stomatal opening limited transpiration. Measurements of reduced transpiration following rewatering may reflect decreased permeability of the root system or inhibition of stomatal opening due to lack of a chemical signal from the roots (Xu and Lou, 1980; Turner, 1986; Davies et al., 1990).

Effect of Roots on Recovery of Transpiration

Plants placed in water without roots became visibly turgid in several hours and transpiration rate increased slightly, but never to the level of rewatered D-R plants with roots (Fig. 5). Rapid regrowth of the D-R shoots resulted in leaf area increasing about 40% during the 4 d after rewatering but leaf growth was not observed on plants without roots. Roots were clearly necessary for resumption of transpiration by sorghum. Absence of leaf growth in our sorghum plants without roots may have been caused by a lack of cytokinin (Skene, 1975). In contrast, Brix (1960, 1962) observed that water absorption by loblolly pine (Pinus taeda) seedlings following a period of wilting was severely restricted by the root system. Full recovery of photosynthesis was attained in 8 h by loblolly seedlings from which the roots were excised, but intact plants did not reach the normal rate until 50 h after rewatering.

Insert Fig. 5

SUMMARY

Results indicated that duration of soil dryness and availability of water from sub-surface layers significantly affect resumption of water uptake by rewet roots. Appreciable (30% of control) uptake occurred during the first day after rewatering in the most severe treatment of the experiment, however. The significance of reduced uptake immediately after rewetting can only be judged by comparing plant extraction to other pathways of water loss from soil. Root function will have little impact on drainage losses following a rain large enough to saturate previously-dry soil. Evaporation from plants and from soils are the two competing loss mechanisms operating after small rains, so impacts of root recovery should be judged relative to soil evaporation. Improved estimates of evaporation of light rains and analysis of rainfall patterns are needed to assess the importance of impaired root function.

REFERENCES

1. Aung, L.H. 1974. Root-shoot relationships. p. 29-61. In E.W. Carson (ed.) The plant root and its environment. University Press of Virginia, Charlottesville, VA.

2. Baker, J.M., and C.H.M. van Bavel. 1988. Water transfer through cotton plants connecting soil regions of differing water potential. Agron. J. 80: 993-997.

3. Begg, J.E. 1980. Morphological adaptation of leaves to water stress. p. 33-42. In N.C. Turner and P.J. Kramer (ed.) Adaptation of plants to water and high temperature stress. John Wiley & Sons, New York.

4. Brix, H. 1960. Determination of viability of loblolly pine seedlings after wilting. Bot. Gaz. 121:220-226.

5. Brix, H. 1962. The effect of water stress on the rates of photosynthesis and transpiratin in tomato plants and loblolly pine seedlings. Physiol. Plant. 15:10-20.

6. Davies, W.J., T.A. Mansfield, and A.M. Hetherington. 1990. Sensing of soil water status and the regulation of plant growth and development. Plant, Cell Environ. 13:709-719.

7. Dirksen, C., and P.A.C. Raats. 1985. Water uptake and release by alfalfa roots. Agron. J. 77:621-626.

8. El Nadi, A.H., R. Brouwer, and J. Locker. 1969. Some responses of the root and the shoot of Vicia faba plants to water stress. Neth. J. Agric. Sci. 17:133-142.

9. Fischer, R.A. 1970. After-effect of water stress on stomatal opening potential. J. Exp. Bot. 21:386-404.

10. Glover, J. 1959. The apparent behavior of maize and sorghum stomata during and after drought. J. Agric. Res. 53:412–416.

11. Gregory, P.J., M. McGowan, and P.V. Biscoe. 1978. Water relations of winter wheat. 2. Soil water relations. J. Agric. Sci. Camb. 91:103–111.

12. Hoffman, G.J., S.L. Rawlins, M.J. Garber, and E.M. Cullen. 1971. Water relations and growth of cotton as influenced by salinity and relative humidity. Agron. J. 63:822–826.

13. Hsiao, T.C., E. Fereres, E. Acevedo, and D.W. Henderson. 1976. Water stress and dynamics of growth and yield of crop plants. p. 281–305. In O.L. Lange et al. (ed.) Water and plant life: problems and modern approaches. Springer–Verlag, New York.

14. Kramer, P.J. 1983. Water relations of plants. Academic Press, New York.

15. Ludlow, M.M. 1980. Adaptive significance of stomatal responses to water stress. p. 33–42. In N.C. Turner and P.J. Kramer (ed.) Adaptation of plants to water and high temperature stress. John Wiley & Sons, New York.

16. Passioura, J.B. 1983. Roots and drought resistance. Agric. Water Mgmt. 7:265–280.

17. Passioura, J.B. 1988. Water transport in and to roots. Ann. Rev. Plant Physiol. 39:245–265.

18. Pearson, R.W. 1966. Soil environment and root development. p. 95–126. In W.H. Peirre et al. (ed.) Plant environment and efficient water use. ASA and SSSA, Madison, WI.

19. Sharp, R.E., and W.J. Davies. 1979. Solute regulation and growth by roots and shoots of water stressed maize plants. Planta 147:43–49.

20. Sharp, R.E., and W.J. Davies. 1985. Root growth and water uptake by maize plants in drying soil. J. Exp. Bot. 36:1441-1456.

21. Skene, K.G.M. 1975. Cytokinin production by roots as a factor in the control of plant grwoth. p. 365-396. In J.G. Torrey and D.T. Clarkson (ed.) The development and function of roots. Academic Press, New York.

22. Slatyer, R.O. 1967. Plant-water relationships. Academic Press, New York.

23. Taylor, H.M., and B. Klepper. 1978. The role of rooting characteristics in the supply of water to plants. Adv. Agron. 30:99-128.

24. Turner, N.C. 1986. Crop water deficits: A decade of progress. Adv. Agron. 39:1-51.

25. van Bavel, C.H.M., R. Lascano, and D.R. Wilson. 1978. Water relation of fritted clay. Soil Sci. Soc. Am. J. 42:657-659.

26. Xu, X., and C. Lou. 1980. Presence of roots- A prerequisite for normal function of stomata on sweet potato leaves. Acta Agric. Univ. Pekinensis 1:37-46. (In Chinese with English abstract).

27. Xu, X., and W.L. Bland. 1991. Reverse flow in sorghum plants. Agron. J. (Check @ Headquarters re: status).

LIST OF FIGURES

Table 1. Root growth as affected by water stress

Treatment		Days of drying							
		Root weight			Root length			Root weight/length	
		0	26	39	0	26	39	26	39
		mg			m			mg m^{-1}	
W+R	P†	313	1520	3102	32.3	161.6*	411.8**	9.41	7.53
D+R	P	313	1935*	2974	32.3	118.4	193.2	16.34**	15.40**
W+R	R	0.9	199	237	0.15	32.9	32.6		
D+R	R	0.9	254	741**	0.15	52.8*	143.5**		
W-R		313	1305	2967**	32.3	168.0*	395.1**	7.77	7.51
D-R		313	1365	1418	32.3	108.4	123.6	12.59**	11.47**

*, ** Significantly different from adjacent value in same column at the 0.05 and 0.01 levels by t-test, respectively.
† P=pot, R=reservoir.

Table 2. Root/shoot ratio as affected by water stress.

Treatment	Days of drying		
	0	26	39
W+R	0.155	0.142	0.103
D+R		0.201**	0.167**
W-R	0.155	0.148	0.132
D-R		0.221**	0.241**

** Significantly different from adjacent value in each column at the 0.01 level by t-test.

Table 3. Recovery of leaf water potential after rewatering.

Treatment	Days of drying					
	26		39			
	1 d ~~after~~ before rewatering	7 hr after rewatering	1 d before rewatering	After rewatering 5 h	30 h	3 d
	MPa		MPa	MPa		
W-R	-0.62†	-0.64	-0.68	-0.64	-0.70	-0.66
	-0.62	-0.68	-0.68	-0.66	-0.66	-0.66
D-R	-1.78	-0.74	-3.52	-1.72	-0.80	-0.68
	-2.00	-0.66	-3.82	-1.72	-0.90	-0.68
W+R	-0.65	-0.66	-0.66	-0.68	-0.62	-0.64
	-0.63	-0.66	-0.66	-0.66	-0.66	-0.64
D+R	-0.76	-0.70	-0.88	-0.82	-0.66	-0.62
	-0.92	-0.66	-0.92	-0.78	-0.66	-0.66

† Duplicate determinations on different plants shown.

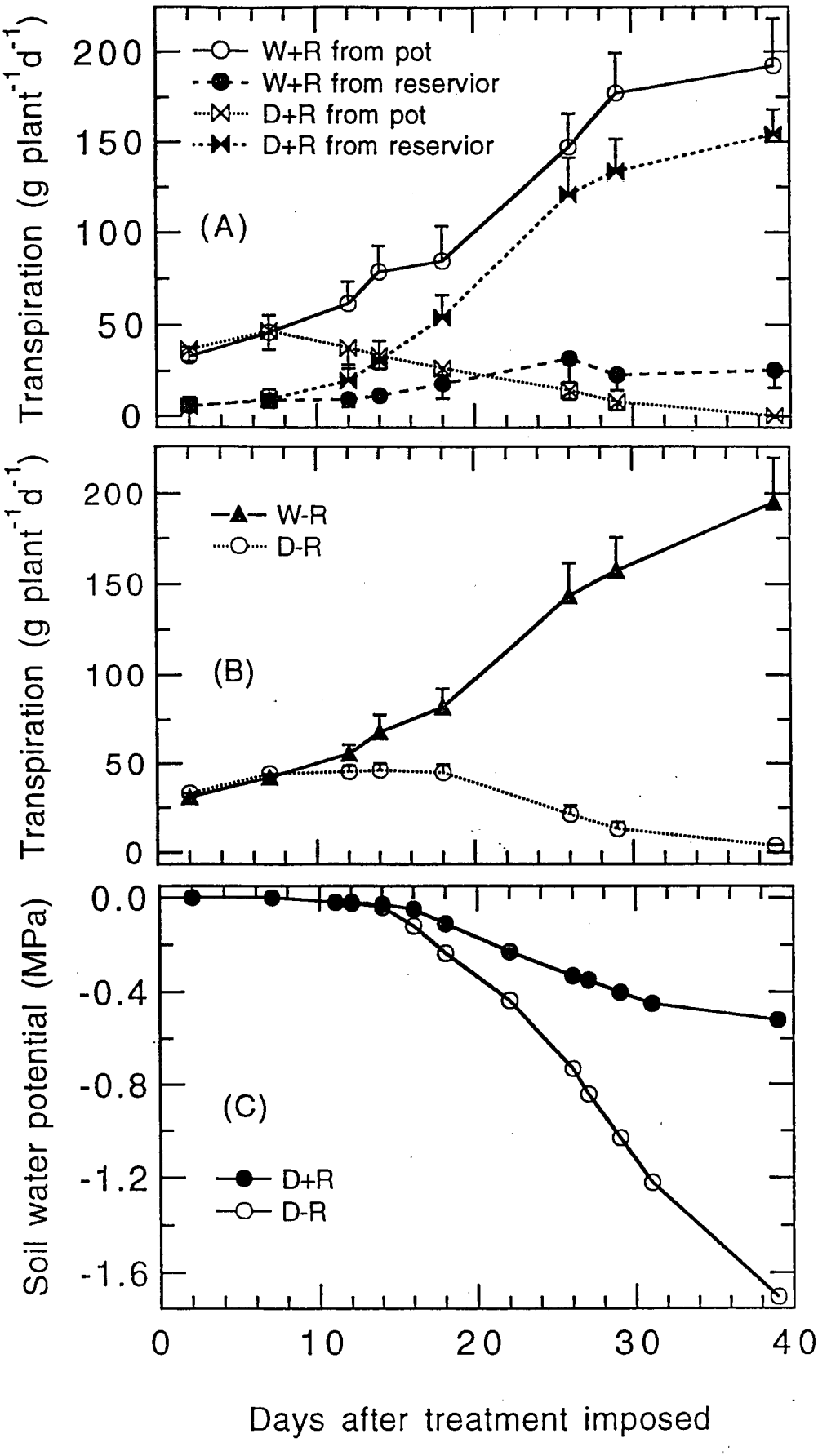
Transpiration (g plant^{-1}d^{-1})
200
150
100
50
0
W+R from pot
W+R from reservior
D+R from pot
D+R from reservior
(A)
Transpiration (g plant^{-1}d^{-1})
200
150
100
50
0
W-R
D-R
(B)
Soil water potential (MPa)
0.0
-0.4
-0.8
-1.2
-1.6
(C)
D+R
D-R
0
10
20
30
40
Days after treatment imposed

Fig. 1

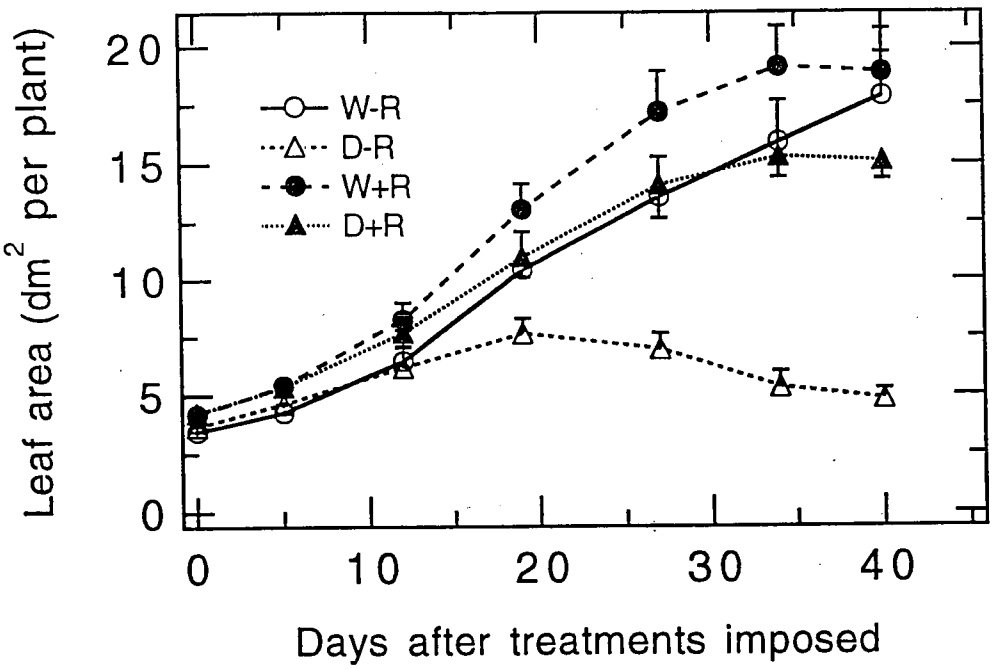
Leaf area (dm^2 per plant)
20
15
10
5
0
W-R
D-R
W+R
D+R
0
10
20
30
40
Days after treatments imposed

Fig. 2

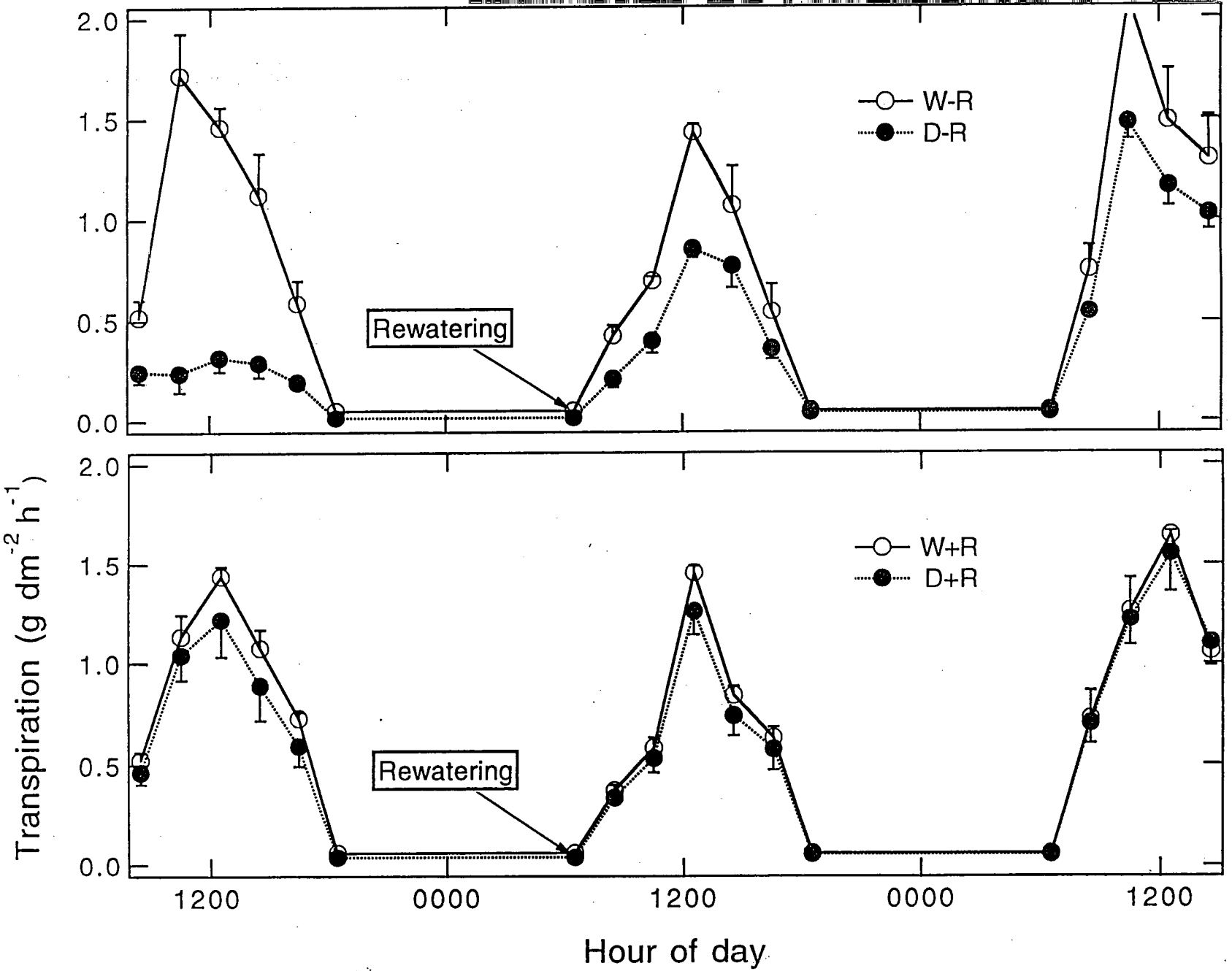
2.0
1.5
1.0
0.5
0.0
W-R
D-R
Rewatering
W+R
D+R
Rewatering
Transpiration (g dm-2 h-1)
1200
0000
1200
0000
1200
Hour of day

Fig 3

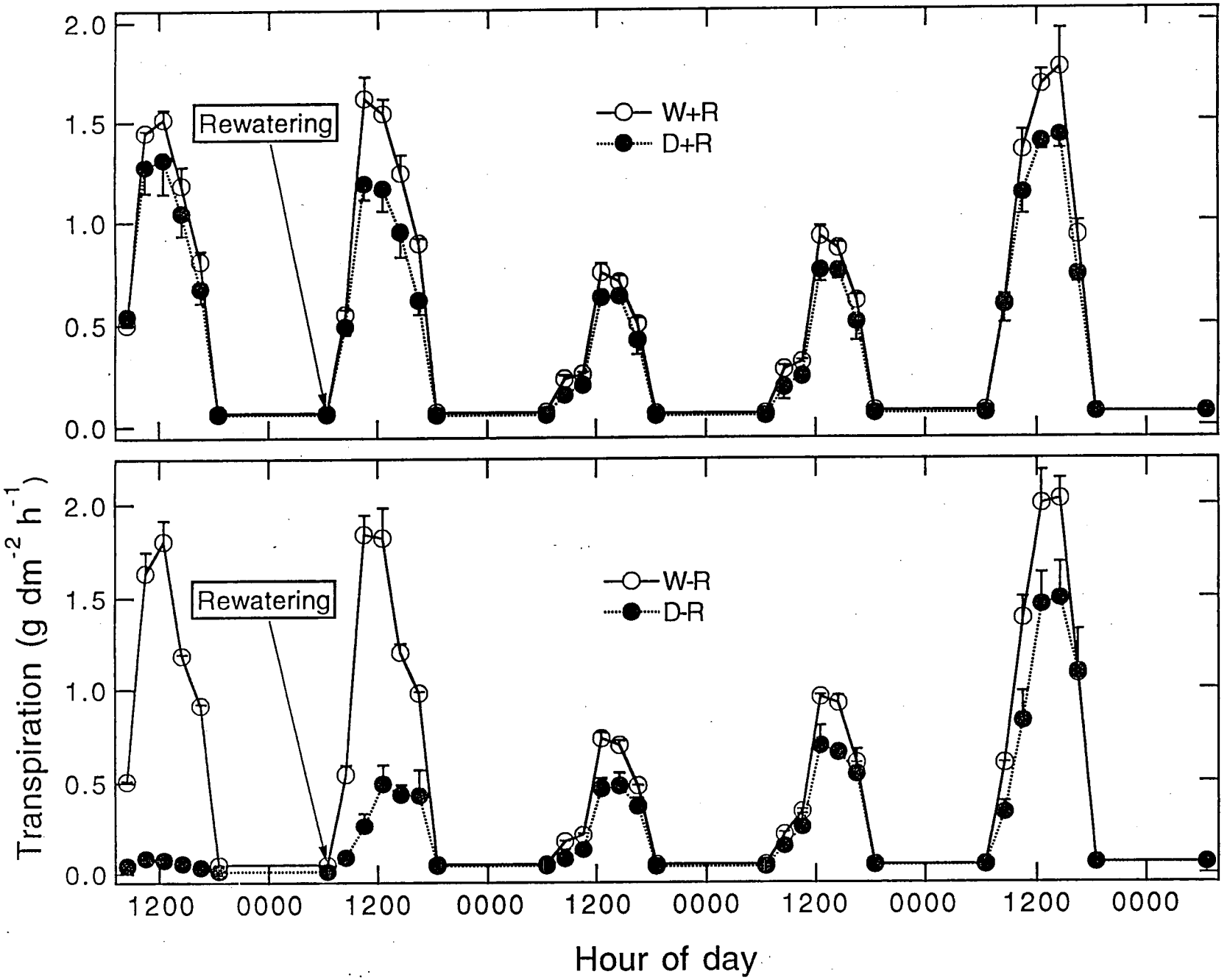
2.0
1.5
1.0
0.5
0.0
Rewatering
W+R
D+R
2.0
1.5
1.0
0.5
0.0
Rewatering
W-R
D-R
Transpiration (g dm-2 h-1)
1200
0000
1200
0000
1200
0000
1200
0000
1200
0000
Hour of day

Fig. 1

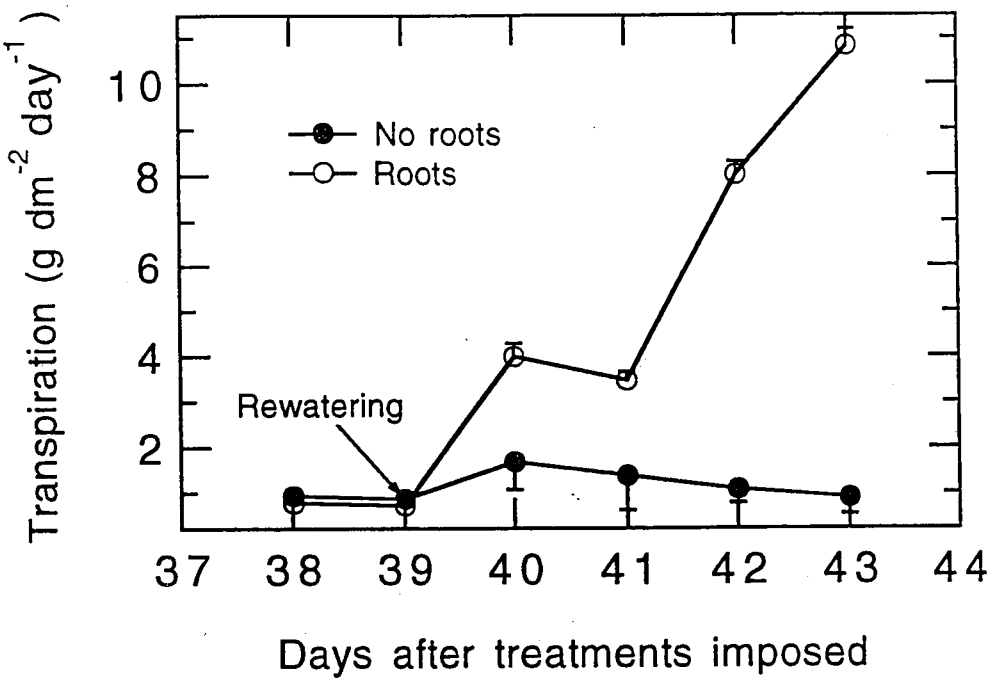
Transpiration (g dm^{-2} day^{-1})
10
8
6
4
2
No roots
Roots
Rewatering
37
38
39
40
41
42
43
44
Days after treatments imposed

Fig. 5

F. Cooperation

The cooperation between the two research groups was based on continous exchanges of views and ideas. Each group carried out an independent research, according to the general plan. The two groups worked on the same genotypes and consequently a comprehensive overlook on the general activity became possible. The activity in the USA concentrated mainly in greenhouse studies, while in Israel the focus was given to field epxeriments. At the end of the project Dr. Carmi visited the American team and the two teams summarized together the whole research.

G. Benefit to Agriculture

The increased periods and regions of drought throughout the entire world imply urgent solutions for survival. This is mainly crucial in the Third World, where food is always not sufficient. Therefore, one possibility is to look for new varieties that will be able to grow under reduced or minimal amounts of water and a second one is to adapt existing ones to the extreme growth conditions. In this study, we concentrated on the latter one. The outstanding root traits of genotype 233 permit quick root growth and elongation under non-irrigating conditions and an efficient use of available water at deep layers in the soil.

Besides important information collected from plants grown in pots or nutrient solution on physiological characteristics of both genotypes, the real benefit to agriculture could be derived from the different field experiments. The potential of one of them to survive drought, to exploit deep water and to give early yields from late sowings, is very promising. Sorghum cultivation in a double-cropping system may provide a new alternative for efficient use of

residual water in the soil, especially on periods of non agricultural exploitation.