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Increasing salinity tolerance of grain crops: Is it worthwhile?

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Abstract

The productivity of wheat and barley was compared in soils of different salt concentrations with a limited water supply. Productivity was assessed as total dry weight or dry weight per unit of water used (water use efficiency, WUE). Barley achieved the highest productivity because it used more of the available water and it had a greater WUE for above-ground dry weight. However, when WUE for total organic weight of roots and shoots was determined, or WUE was corrected for grain production, wheat and barley had the same productivity. In two experiments in drying soils with different salt concentrations but the same amount of soil water, wheat and barley had a higher dry weight than salt-tolerant grasses and they were more productive than C_4 halophytes and non-halophytes when adjusted for water use. In one experiment, sown at a low plant density, barley and wheat used less water than some halophytes and they completed their life cycle leaving some water behind in the soil. Their higher WUE did not compensate for their lower water use. However, when all species were sown at a high density, wheat and barley were either as productive or more productive than the most salt-tolerant species, including a C_4 halophyte, as they used all the available water and had the highest WUE. A sunflower cultivar was similarly more productive than a salt-tolerant relative. The contribution that salt-tolerant relatives of wheat, barley and sunflower can make to genetically improving the productivity of these species in dry saline soils is questioned.

Introduction

Understanding salinity tolerance in plants so as to eventually use this knowledge to genetically increase the tolerance of crop or pasture species is an active research pursuit. As saline soils are extremely variable, salt tolerance is usually assessed by growing plants in salinized nutrient solutions so that their root zone is at a constant salt concentration. These conditions may be satisfactory for studies on marsh plants, or plants growing in tidal zones, or for experiments aimed at understanding the effects of salt on plant growth, but they are not representative of the conditions in which plants grow in their natural or agricultural habitats. Hence they may lead to misleading conclusions and the formulation of inappropriate selection criteria to genetically improve productivity in saline soils.

Economically important species growing in soil experience variable soil water contents depending on irrigation, rainfall, leaf area and evaporative demand. Salinity may reduce the availability of this water because of its effect on soil water potential and it may also reduce total water use because leaf area, transpiration and growth are all reduced by salinity. Productivity of agricultural species on salt-affected soils will depend firstly on whether they are able to use all of the available water, as the more water used the more productive they will be, and secondly on how efficiently the water is used i.e. how much growth per unit of evapotranspiration. Manipulating water use and water-use efficiency genetically or through management are likely to be more important than criteria presently suggested to genetically improve salt tolerance and productivity in saline soils. Criteria suggested to improve salinity tolerance arise from studies in salinised nutrient solution. For example, salt exclusion mechanisms, Na/K discrimination and compartmentation of solutes within cells (Yeo and Flowers, 1986). It is suggested that these are of limited importance when it comes to improving productivity in salt-affected soils.

This study contrasts the productivity of wheat and barley, two species where research efforts to improve their salinity tolerance have been greatest, with numerous halophytic species as well as herbaceous crop and pasture species, when grown in drying saline soils. Productivity was determined on a dry weight basis or the dry weight per unit of water used. The species chosen to contrast with the C_3 wheat and barley were several C_4 species, including two C_4 halophytes that exclude salt and were presumed to have a markedly higher water use efficiency (McCree and Richardson, 1987; Rawson et al., 1977) and grasses with an ability to tolerate extreme salt concentrations, as well as other crop pasture species.

Materials and methods

Three experiments were conducted in a glasshouse maintained at about 25°C during the day and 14°C at night. In all experiments plants were grown in tubes 0.5 m long and 0.11 m diameter. Tubes were filled with about 6 kg of river loam and carefully packed so they had a similar bulk density. They contained a rubber bung in their base to prevent drainage that could be removed if required. Salinised nutrient solutions were prepared by adding a 5 : 1 (g/g) NaCl to $CaCl_2$ mixture to half-strength Hoaglands solution. About 500 mL of the required saline solutions were added to each tube containing the rubber bung depending on the treatment. After several hours bungs were removed and the tubes were allowed to drain. This flushing procedure was repeated several times until the conductivity of the drainage liquid matched that of the salinized nutrient solution added. Different treatments were imposed in each experiment (details below) and there were two replications of all treatments. After seedlings emerged no further water or saline-nutrient solution was added to tubes in any experiment. A 4 cm layer of perlite was placed on the soil surface to prevent evaporation of water. Tubes were weighed each week and plants were harvested when dead. At harvest above-ground plant parts were separated into stems, leaves and reproductive structures (if any), which were then oven dried and weighed. Soil was removed from each tube, weighed and then oven dried at 70°C for 7 days and then reweighed to calculate the percentage of total soil water used by the plant. Water use efficiency (WUE) was calculated as the ratio of total above ground dry weight to water used between emergence and plant death unless otherwise stated.

Experiment 1

Clipper barley and Condor hexaploid wheat (cultivars grown commercially in Australia) were sown in tubes in late November. There were seven salt concentrations with an electrical conductivity (EC) of the drainage water of 0 (no salt), 3, 6, 9, 12, 15, and 18 $dS\,m^{-1}$. Three seeds were sown 2 cm deep in each tube and the top 2 cm of soil of all tubes was kept moist with a little tap water so that germination and emergence was uniform. Barley emerged about 1 day earlier than wheat and the highest salt concentrations delayed emergence by about 4 days. Tubes were thinned to 1 healthy plant. Leaf length and width of all main stem leaves and tillers were measured weekly as well as the time when leaves died.

Experiment 2

Thirteen salt tolerant and sensitive species were grown including two genotypes each of barley and hexaploid wheat. These are listed in Table 1. Plants were sown over an extended period beginning in mid-May for the slowest growing species through to July for the fastest growing species to ensure that the period of fastest growth coincided in all species. The sowing order was *Puccinellia*, *Hordeum maritima*, *Atriplex* and *Amaranthus*, *Thinopyrum* and *Trifolium* and

Table 1. Species grown in Experiment 2 with reference to any known characteristics of salt tolerance

Species
- *Hordeum vulgare* cv CM67
  - Salt tolerant 6-row barley. (Richards et al., 1987; Rawson et al., 1988)
- *Hordeum vulgare* cv Clipper.
  - Possibly salt sensitive 2-row malting barley. (Rawson et al., 1988)
- *Hordeum maritima* (Sea-barley grass)
  - Selection from a salt scald in Western Australia. Seed supplied by C. Malcolm, WA Dept of Agriculture.
- *Triticum aestivum* cv Kharchia
  - Salt tolerant Indian wheat (Kingsbury and Epstein, 1984; Rawson et al., 1988)
- *Triticum aestivum* cv Yecora.
  - High yield spring wheat.
- *Thinopyrum elongatum* cv Tyrell (tall wheatgrass).
  - Salt tolerant grass (McGuire and Dvorak, 1981)
- *Puccinellia ciliata* (Saltmarsh grass).
  - Salt tolerant grass. Seed supplied by C. Malcolm
- *Trifolium subterranean* cv Woogenellup.
  - Presumed salt sensitive pasture legume.
- *Trifolium alexandrinum* (Berseem clover).
  - Salt tolerant pasture legume (Wingers and Läuchli, 1982)
- *Medicago sativum* cv Hunter River (lucerne).
  - Moderately salt tolerant, deep rooted pasture legume (R.W. Downes pers. com.)
- *Helianthus annuus* cv Hysun 31.
  - High yielding hybrid sunflower.
- *Helianthus argophyllum*
  - Salt-tolerant relative of sunflower (R.W. Downes pers comm.)
- *Atriplex nummularia* (Old man saltbush).
  - C4 halophyte with salt glands.
- *Atriplex lentiformis* (Quail bush)
  - C4 halophyte
- *Amaranthus edulis* (pigweed).
  - C4 weed

Medicago, *Helianthus argophyllum*, wheat, barley, and sunflower was sown last. Plants in the control treatment were sown up to 21 days later than the salt treated plants.

There were three treatments common to all species, a control flushed with half-strength Hoaglands solution and two salt treatments flushed with salt (NaCl and CaCl$_2$) in half-strength Hoaglands with an EC of either 10 or 20 dS m^{-1}. An extra salt treatment of EC 15 dS m^{-1} was included for the wheat and barley cultivars. In this experiment roots were washed from the soil of all tubes and any extraneous organic matter was removed from the roots. Root samples were dried at 70°C, weighed and then placed in a crucible and ashed at 600°C and then weighed to determine the organic weight of the root sample. Above-ground plant parts were also weighed and ashed to determine mineral content and organic weight.

Experiment 3

Tubes were prepared as before and flushed with one of four salt concentrations. These were half-strength Hoaglands with added NaCl and CaCl$_2$ to give conductivities of 0, 5, 10 and 15 dS m^{-1}. Species grown were *Atriplex nummularia*, *Amaranthus edulis*, *Helianthus argophyllus*, *Helianthus annuus* cv Hysun 31, *Thinopyrum elongatum* cv Tyrell, as in Experiment 2. Also, hexaploid wheat cv. Isis, a winter wheat not expected to reach floral initiation in the glasshouse, cv Songlen, a wheat chosen for its osmotic adjustment (Morgan, 1983) and two 6-row barleys, CM67 as in Experiment 2, and Betzes chosen for its later maturity time. Sowing time was again staggered so that the most rapid growth period of each species coincided. Sowing of *Atriplex* and *Amaranthus* in the 10 and 15 dS m^{-1} salt treatments commenced in August and was followed by *Thinopyrum* and *H. argophyllum* 4 days later, wheat 8 days later and barley 7 days later again. The 0 and 5 dS m^{-1} treatments were sown 7 days after the 10 and 15 dS m^{-1} treatments. About 5 plants were established in each tube.

Results and discussion

Experiment 1

Despite plants having access to the same amount of water, substantial differences in above-ground dry weight were found between treatments and between Clipper barley and Condor wheat (Fig. 1a). Surprisingly, dry weight in both species increased as salt concentration increased and was only less than the controls at the highest salt concentrations. Barley had a greater weight in all treatments. Variation in dry weight between different salt treatments and between barley and wheat came about primarily because of differences in WUE, viz. the ratio of above-ground

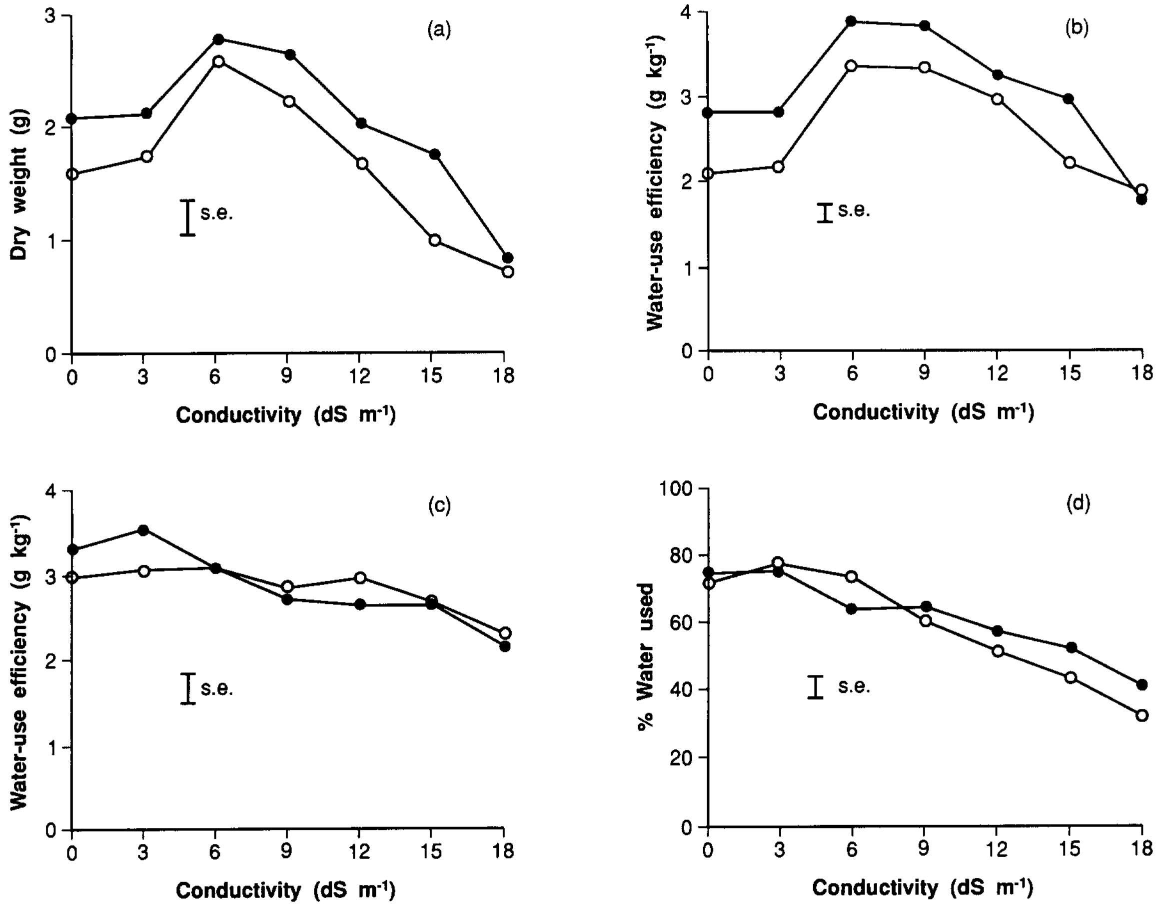

Fig. 1. Comparison of barley (●) and wheat (○) grown in different salt treatments for **a**) above-ground plant weight, **b**) water use efficiency, **c**) water use efficiency after covariate adjustment for grain weight, and **d**) percentage of total soil water used at plant death. The standard error for a difference between wheat and barley at any salt content is shown in each figure. Conductivities are of the drainage water at the time of sowing.

dry weight to total water used, rather than to differences in total water use (Fig. 1b).

Variation in WUE was very similar to variation in dry weight and WUE was highest at the intermediate salt concentrations and only fell below the control at the highest salt level. This increase casts doubt on an increased respiration rate as being important in saline soils except perhaps at the highest salt concentration (Yeo, 1983). Factors that may increase WUE as a result of salinity are firstly, that stomatal conductance may decline without a corresponding fall in assimilation capacity, and secondly, that salt may be sequestered in old leaves, resulting in an apparent increase in WUE. A third factor may be that root growth is less in the salt treatments than in the control and above-ground growth may be correspondingly higher. The latter two factors are examined further in the next experiment.

The increase in WUE attributed to an altered gas exchange could be large. Discrimination against the stable isotope ^{13}C, a measure of WUE (Farquhar and Richards, 1984), can decline by as much as 5×10^{-3}‰ when C_3 species are grown in salinised solution or soils (Brugnoli and Lauteri, 1991; Guy et al., 1988). As a reduction of 1×10^{-3}‰ corresponds to an increase in WUE of about 15% (Farquhar and Richards, 1984), then an altered gas exchange could account for a large part of the increase in WUE, which was about 50% in the intermediate salinity treatments in both wheat and barley (Fig. 1b). Nevertheless, this contrasts with measurements of the gas exchange of wheat and barley grown with and without salinity where no differences in instantaneous WUE were found (Rawson, 1986).

Grain was produced by plans in most salt treatments and hence in the treatments where WUE was high. Grain was presumably produced because plants in the higher salt concentrations had a reduced leaf area and thus lower rate of water use. This in turn extended the duration of growth in the salt treatments and allowed the plants to complete their lifecycle and produce grain. No grain was produced in the control or low salt treatment as plants exhausted the soil water supply before anthesis and died. A reanalysis of WUE using grain weight as a covariate was highly significant (Table 2) and when WUE values are adjusted for the covariate then WUE in fact declined slightly with increasing salt concentration (Fig. 1c). This indicates that the apparent increase in WUE of plants in saline soils arose from a redistribution of carbon from the roots and/or from an increased sink strength that affects gas exchange (Blum et al., 1988). If the latter is important presumably stomatal conductance is reduced more than assimilation capacity in plants setting grain or both. In the covariance analysis differences between wheat and barley were not significant and neither was the interaction between species and treatment.

The other determinant of productivity in drying saline soils is the total amount of water used by plants. In this experiment more water was left behind in the soil as salinity increased (Fig. 1d). This could be due to a reduced leaf area and a reduced leaf area duration as a result of salinity and hence incomplete water use before maturity, or to plants being unable to lower their water potential sufficiently to match the lower potential of the drying saline soil thereby leaving water behind. The former suggestion is favoured for several reasons. In the control and EC3 treatment both wheat and barley averaged 5 tillers (including the main stem) per plant whereas in the EC15 and EC18 treatment wheat and barley plants had a single main stem only and no tillers. Maximum kernel weight achieved was 48 mg for barley and 30 mg for wheat and there was no evidence for a decline in kernel weight at the highest salt levels which was expected if plants died prematurely. Furthermore, although there were no differences between barley and wheat at the low salinity levels, at higher levels there was a consistent trend for barley to use more water than wheat and this was associated with a larger leaf area in barley (data not presented but see Rawson et al., 1988).

Table 2. Analysis of variance for water use efficiency in Experiment 1 with covariance adjustment for grain weight

Source	df	MS	VR
Barley vs wheat	1	0.0027	0.09
Salt treatments	6	0.494	16.9***
Species × Salt	6	0.077	2.6^{NS}
Covariate	1	1.332	45.7***
Residual	13	0.029	

^{NS} Not significant, *** $p < 0.001$.

Experiment 2

This experiment was designed to firstly, contrast wheat and barley with a wider range of species, and secondly, to investigate whether a reduced root mass and a higher salt content in plant tissues may contribute to an apparently higher WUE in wheat and barley in drying saline soils. Because plants used different amounts of water and accumulated different amounts of salt in their tissues, comparisons between species are mainly based on WUE values for the total organic weight of plants rather than total dry weight.

The duration of growth increased in all species as salinity increased (Table 3). Lucerne was the most extreme as it used all the available water in the control treatment and died after 62 days whereas in the highest salt treatment it survived for 261 days despite having no additional water after planting. The longer duration of growth in wheat and barley in the salt treatments enabled plants of both species to produce grain in the EC10 and 15 treatments but in the EC20 treatment only wheat produced grain.

WUE of genotypes in each treatment, determined on the organic weight of roots and shoots rather than total dry weight, are given in Table 4. Wheat again had a greater WUE in the

Table 3. Duration of growth (days) in control and salt treated plants in Experiment 2. Species with a similar growth duration in the three treatments have been grouped together and the number of species in each group are given in parenthesis after each generic name. Standard error for difference between any two values = 8 days

Species	Conductivity (dS m^{-1})		
	0	10	20
Lucerne (1)	62	105	261
Puccinellia (1)	137	158	140
Atriplex (2)	99	99	134
Thinopyrum, *Hordeum* (4)	55	106	135
Trifolium (2)	62	100	96
Triticum (2)	58	70	102
Helianthus, *Amaranthus* (3)	50	70, 110[a]	77, 113[a]

[a] *H. argophyllum, Amaranthus.*

Table 4. Water use efficiency (g kg^{-1}) of genotypes grown in saline soils. Values are for whole plants including roots and were calculated from ashed plant parts. Standard error for difference between any two values = 0.3 g kg^{-1}

Species	Conductivity (dS m^{-1})		
	0	10	20
Puccinellia	2.2	1.8	0.7
H. maritima	2.5	2.5	1.8
Thinopyrum	2.4	2.4	1.8
Medicago	2.2	1.9	0.3
T. subterranean	2.4	–	0.2
T. alexandrinum	1.8	1.6	0.7
A. lentiformis	2.7	3.4	3.0
A. nummularia	2.7	3.7	3.0
A. edulis	4.1	3.3	–
H. argophyllum	2.4	1.3	1.4
H. annuus	2.5	2.4	1.1
Kharchia	2.5	3.2	1.5
Yecora	2.6	3.3	1.9
CM67	2.7	2.3	2.4
Clipper	2.7	2.6	1.9

intermediate salt concentrations (data for EC15 not shown) than in the controls but WUE was lower in the highest salt concentration. Values for the barley cultivars were not significantly different to the control values at all salt concentrations. In the control treatment the C$_4$ species, *Amaranthus edulis* had the highest WUE; wheat, barley and two *Atriplex* species were next highest whereas the legumes and the marsh grass, *Puccinellia*, had the lowest WUE. At the intermediate salt level, WUE of *Atriplex* increased to the same extent as wheat, whereas in the other species WUE either decreased or remained the same. At the highest salt level WUE fell dramatically in all three legumes and in *Puccinellia*, less in both *Helianthus* species, and less again in wheat, barley, *Thinopyrum*, *Hordeum maritima* and the *Atriplex* species. At the highest salt concentration, WUE in both *Atriplex* species was between the control and the intermediate salt concentration whereas in all other species it was less than the control values. The WUE of wheat and barley at EC15 was the same as at EC10 and significantly higher than at EC20.

Table 5 shows how much of the total soil water was used by plants from sowing until their death. Wheat and barley left water behind in the soil at the higher salinity levels as they did in Experiment 1. So did all other short-season determinate species. The only species that used all the available water were lucerne, both *Atriplex* species, *Helianthus argophyllum*, *Thinopyrum* and *Hordeum maritima*; all are long-season indeterminate species. This is consistent with Experiment 1 and supports the suggestion that the leaf area developed in the short-season determinate species in the salt treatments was insufficient to use all the available water. It is also worth noting that the root to shoot ratio (R/S on an organic carbon basis) was highest in the long season species. The R/S for lucerne in the highest salt level was a remarkably high 1.72 com-

Table 5. Percentage of total soil water used by plants grown at different salinities. Standard error for difference between any two values = 4%

Species	Salt concentration (dS m^{-1})		
	0	10	20
Puccinellia	79	72	55
H. maritima	76	71	67
Thinopyrum	74	72	72
Medicago	78	78	77
T. subterranean	77	73	34
T. alexandrinum	77	73	55
A. lentiformis	82	80	78
A. nummularia	82	80	80
A. edulis	74	73	66
H. argophyllum	76	74	71
H. annuus	77	73	36
Kharchia	75	51	35
Yecora	78	44	43
CM67	75	54	55
Clipper	75	57	51

Table 6. Root to shoot ratio at different salinities calculated on a total organic weight basis from ashed plant parts. Standard error for difference between any two values = 0.04

Species	Conductivity (dS m^{-1})		
	0	10	20
Puccinellia	0.04	0.05	0.06
H. maritima	0.34	0.06	0.10
Thinopyrum	0.27	0.26	0.13
Medicago	0.48	0.78	1.72
T. subterranean	0.17	0.20	–
T. alexandrinum	0.21	0.09	0.04
A. lentiformis	0.23	0.27	0.25
A. nummularia	0.24	0.21	0.19
A. edulis	0.30	0.14	0.20
H. argophyllum	0.32	0.22	0.10
H. annuus	0.19	0.11	0.06
Kharchia	0.25	0.07	0.08
Yecora	0.19	0.07	0.05
CM67	0.22	0.13	0.06
Clipper	0.22	0.08	0.08

pared to 0.22 for the *Atriplex* species and 0.06 for wheat and barley (Table 6). With the exception of lucerne and perhaps *Puccinellia* and *A. lentiformis*, the R/S ratio declined with salinity. The higher R/S values in the control could therefore account for part, but not all, of the lower WUE in the control treatment in Experiment 1.

The mineral or ash content of different species provides data on the most effective salt excluders (Table 7). The dicotyledons were far less effective than the grasses. As expected, mineral content of the *Atriplex* species was highest, followed by both *Helianthus* species and the legumes; it was apparent that both *Trifolium* species were unable to exclude salt at the highest salt level as the mineral content of leaves and stems increased. Mineral content in wheat, barley and *Puccinellia* leaves increased in the highest salt concentration whereas in *Thinopyrum* and *H. maritima* mineral content in leaves declined in both salt treatments relative to the control.

Experiment 3

In the previous experiments there was evidence that insufficient leaf area limited the water use of the short season species such as wheat, barley and sunflower. In this experiment plants were grown at a higher density so as to overcome the reduced leaf area. There were also fewer species and more salt treatments than in the previous experiment. The higher plant density had a substantial effect on growth duration and water use in all genotypes. Compared to plants in experiment 2, average growth duration was 9 and 34 days shorter in the control and EC10 treatment. However, salinity still extended growth duration compared to the control. The mean difference in

Table 7. Mineral content (as a % of oven dry weight) of leaves and stems grown at different salinities. Standard error for difference between any two values for both leaves and stems = 5%

Species	Conductivity (dS m^{-1})					
	0		10		20	
	Leaves	Stems	Leaves	Stems	Leaves	Stems
Puccinellia	7	5	11	8	13	12
H. maritima	14	9	10	7	11	9
Thinopyrum	14	10	11	10	11	5
Medicago	14	9	12	7	17	5
T. subterranean	12	14	–	–	28	33
T. alexandrinum	14	15	14	16	31	24
A. lentiformis	23	12	36	16	35	15
A. nummularia	23	15	30	18	31	17
A. edulis	19	19	20	27	–	–
H. argophyllum	21	16	24	19	29	22
H. annuus	18	19	23	25	32	37
Kharchia	13	9	15	14	19	14
Yecora	12	9	16	16	19	15
CM67	14	11	13	13	15	12
Clipper	14	12	15	15	17	16

duration between the control and EC15 treatment was 14 days.

Higher plant density increased the total water use by all plants in the higher salt concentrations compared to the earlier experiments. In contrast to the other experiments there were few differences in water use between treatments; as a percentage of soil water content the mean water use in the control was 72% and 69% in the highest salt treatment. The only genotypes in the high salt treatment unable to use all the available water were Songlen wheat and *A. edulis* that only used 50% of the total soil water. This data therefore confirms the suspicion that in the short-season species, soil water extraction was previously limited by leaf area rather than the low soil water potential. It indicates that the combined osmotic effect of both salinity and soil dryness should not prevent non-halophytes such as wheat, barley and *Helianthus annuus* from using all the available soil water. With the exception of Songlen wheat, they dried the soil to the same extent as the salt tolerant species of *Atriplex* and *Thinopyrum*. The difference arose before because the former group were determinate annuals and salinity decreased leaf growth and hence water use. The increased plant density in the annual species compensated for the reduced leaf growth per plant and enabled plants to use all the available water.

The WUE and above-ground dry weight (AGDW) increased as salinity increased (Table 8) and there was little evidence of a reduction in WUE at the highest salt concentration. As total water use was similar among the species, differences in WUE reflected differences in total above-ground dry weight (Table 8). Surprisingly, differences in WUE or AGDW between C_3 and C_4 species were not substantial. *Thinopyrum* and *H. argophyllum* had the lowest WUE and AGDW at most salinity levels whereas wheat and barley had the highest, being on average as high or higher than *Atriplex*. Root weights were not determined in this experiment; if they were of the same order as in Experiment 2 then the WUE of *Atriplex* would have been higher than in wheat and barley but this would have been offset by the higher mineral content of *Atriplex*.

General discussion

Wheat, barley and sunflower were more productive per unit of water used or on a dry weight basis than C_3 halophytes at all salt concentrations and were as productive as C_4 halophytes at all except the highest salt concentrations. Furthermore, plants grown in saline soils were often heavier than control plants grown in non-saline soils and they generally had a lower R/S ratio than the controls. These results are at variance with the usual findings for plants grown in salinised nutrient solutions and they lead one to question the value of results from nutrient solutions when determining salinity tolerance of different genotypes and when identifying the factors responsible for increasing salinity tolerance of crop species.

In drying saline soils the determinants of dry matter production are firstly, how much soil

Table 8. Above-ground dry weight (AGDW, g) and water-use efficiency (WUE, g kg^{-1}) of genotypes at different salinities in Experiment 3. Standard error for difference between any two values for AGDW = 0.4 g and for WUE = 0.4 g kg^{-1}

	Conductivity (dS m^{-1})							
	0		5		10		15	
	AGDW	WUE	AGDW	WUE	AGDW	WUE	AGDW	WUE
Amaranthus	3.0	4.4	3.3	4.3	4.2	4.6	3.3	4.8
Thinopyrum	2.9	3.7	3.1	4.0	3.4	4.3	3.8	5.0
Atriplex	2.6	3.5	3.9	4.8	5.3	6.2	4.5	5.5
H. argophyllum	2.3	3.0	2.9	3.9	3.9	3.8	3.6	4.9
H. annuus	3.3	4.1	3.6	4.0	4.2	5.0	4.4	6.0
Songlen	2.8	3.8	4.3	4.9	5.3	5.6	4.9	6.4
Isis	3.1	4.1	3.0	3.5	3.7	4.3	3.9	4.7
Betzes	2.9	3.8	4.2	4.8	4.8	5.5	5.4	5.9
CM67	3.4	4.1	4.7	5.0	5.4	7.1	5.5	6.7

water is used, and secondly, how efficiently is it used i.e. the WUE. In experiments reported here both were found to be important. When plants were grown at low density in the intermediate and high salt treatments, short-season determinate species such as wheat, barley and sunflower, completed their lifecycle before using all the available soil water. This was because salinity reduced leaf area, leaf area duration and hence water use. In contrast, the long-season, indeterminate species, whose leaf area was also reduced, continued producing new leaves and ultimately used all of the available water. Thus the long season species ultimately produced more dry matter despite the finding in most species that their WUE was lower than in the determinate species. However, when plants were grown at a high density such that leaf area and transpiration in all species was higher, there was little variation among genotypes in total water use and even in the highest salt treatment of 15 dS m^{-1} the short-season non-halophytes used the same amount of water as the halophytes and other long-season species. The WUE then became the most important factor contributing to variation in dry matter production. Surprisingly, wheat and barley had about the same or a higher WUE and hence were more productive than all other species including the salt tolerant grasses and even C_4 species such as *Atriplex nummalaria*, although it is possible that the WUE of C_4 species was lower than expected due to light and temperature being suboptimal for them during these experiments (Pearcy and Ehleringer, 1984). Sunflower also was more productive than its salt-tolerant relative.

The high productivity achieved by wheat, barley and sunflower in drying saline soils compared to their more salt-tolerant relatives and in relation to the C_4 halophyte *Atriplex*, raises the question of whether attempts to genetically increase their salinity tolerance further, with the use of salt tolerant relatives, are likely to be successful. This has been raised before from a different perspective where it was argued that in saline fields further selection for salinity tolerance may not result in higher yields (Richards, 1983). It was argued that since salt-affected soils are highly variable in their salinity and that most of the yield comes from the least salt-affected areas, then increasing yield potential in favourable areas should result in higher field yields than increasing yield in the salt-affected areas. A different question is raised here. That is, whether the salt-tolerant relatives of wheat, barley and sunflower are likely to contribute to crop improvement in saline soils? The relatives have often been suggested as a source of increased salt tolerance for wheat and barley and there has been extensive research conducted on them (Forster et al., 1990; Gorham, 1990; McGuire and Dvorak, 1981). This study raises the possibility that, for productivity in saline soils that are not frequently irrigated, commercial varieties of wheat, barley and sunflower already exist that have superior productivity than their supposedly salt-tolerant relatives. Although the latter survive for longer in saline soils, they are less productive and it is unlikely that they will contribute to enhanced growth and yield of commercial varieties in saline soils.

It is likely that the main limitation to the yield of wheat, barley and sunflower in drying saline soils is an inadequate leaf area that prevents them from using all of the available water. By increasing the rate of leaf canopy development or duration either genetically (by increasing vigour or extending the duration of leaf development) or by management (by increasing sowing density) should overcome some of this limitation and result in higher yields in salt-affected regions.

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