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Field hydroponics assessment of salt tolerance in *Cenchrus ciliaris* (L.): growth, yield, and maternal effect

Mónica Ruiz[A,C] *and Edith Taleisnik*[B]

[A]Estación Experimental Agropecuaria INTA San Juan, Calle 11 y Vidart s/n, Pocito, CP 5427 San Juan, Argentina.
[B]CONICET, Instituto de Fisiología y Recursos Genéticos Vegetales Centro de Investigaciones Agropecuarias (IFRGV-CIAP, formerly IFFIVE) INTA, Camino a 60 Cuadras, Km 5.5, X5020ICA Córdoba, Argentina.
[C]Corresponding author. Email: moruiz@sanjuan.inta.gov.ar

Abstract. Soil salinity and sodicity have long been major constraints to increasing crop production in many parts of the world. The introduction of salt-tolerant perennial species is one of the most promising alternatives to overcome salinity problems. *Cenchrus ciliaris* (L.) is a highly drought-tolerant species but there are few available reports on its salt tolerance. The purpose of this work was to assess this trait in two widely used cultivars (Biloela and Texas) and to determine whether cultivation under salinity affected seed germination and plant fitness in the next generation. Trials were performed under field hydroponics conditions. Plants were grown for 5 months in 1000-L PVC boxes containing washed river sand, and were automatically irrigated with a commercial nutrient solution to which NaCl was gradually added to provide to provide average season electrical conductivity (EC) levels of 9, 15, and 19 dS/m. Controls had EC 4 dS/m. Vegetative growth in both cultivars was similarly affected by salinity, and grain yield diminished because of a decreased number of spikelets per plant. Significant growth and yield reductions were registered at EC ~10 dS/m, and growth continued to decrease with a very small slope as salinity increased, indicating that this species has moderate salt tolerance. Salinity decreased seed germination percentage; however, germination was higher in seeds obtained from plants that had been grown under saline conditions for one season. Growth was similar in plants obtained from seeds that originated from non-salinised and salinised plants. These results suggest that persistence of *C. ciliaris* in saline soils would not be limited by diminishing plant performance but, rather, by grain yield and seed germination.

Additional keywords: abiotic stress, arid soils, buffel grass, fodder, salinity, seed yield.

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Introduction

Soil salinity and sodicity have long been major constraints to increasing crop production in Australasia, Asia, and South America (Rengasamy 2006; Taleisnik *et al.* 2009), and anthropogenic salinity caused by deforestation and overgrazing contributes to the aggravation of the problem (Mahajan and Tuteja 2005; Manchanda and Garg 2008). The introduction of salt-tolerant perennial species is one of the most promising alternatives to overcome salinity problems (Asch *et al.* 2000; Rengasamy 2006; Suyama *et al.* 2007).

In the semi-arid Chaco region of Argentina, cattle are grown mainly on forage grasses, both native and introduced. However, due to the steady growth of agriculture, cattle production is being displaced to so-called marginal areas, defined by climate and soil constraints such as salinity. This condition affects over 30 million hectares in Argentina. The introduction of salt-tolerant forages to these areas would increase their productivity, and information on salt tolerance of potentially suitable species is essential for this purpose (De León 2004).

Cenchrus ciliaris L. (Paniceae, Poaceae), known as African foxtail grass, buffel grass, or anjangrass, is a perennial C_4 grass common in dry sandy areas (Ayerza 1981; Butt *et al.* 1992; Quero Carrillo *et al.* 2007). It is of tropical Eurasian origin and has been successfully introduced in many tropical and subtropical areas for grazing purposes (Quero Carrillo *et al.* 2007). This species is particularly suitable as a forage due to its low establishment cost, high yields and nutritional level, tolerance to drought conditions and crop pests, and its ability to withstand heavy grazing and trampling by livestock (Clayton *et al.* 2006; FAO 2009). Cultivar development in *C. ciliaris* has focussed on increasing growth rates and tolerance to stress conditions (Ayerza 1981). Most authors agree that *C. ciliaris* is highly drought-tolerant (Keya 1998; Ludlow *et al.* 1985; Wilson and Ludlow 1983); however, the few available reports indicate that it exhibits only moderate salt tolerance and is less salt-tolerant than *Chloris gayana*, *Cynodon dactylon*, and *Panicum antidotale* (Graham and Humphreys 1970; Ayerza 1981).

In general, correlation between glasshouse selection (survival at high salinity) and performance in the field is weak (Munns and James 2003). Short-term growth experiments in the greenhouse may not reveal differences among genotypes that differ in long-term biomass production or yield (Munns and Tester 2008).

Long-term experiments under field conditions, with controlled substrate composition and electrical conductivity (EC), may render more reliable information on relative salt tolerance. In this work, we have used a field hydroponics setup to assess salt tolerance in *C. ciliaris* cultivars.

In wheat and other cereals, genotypic differences in germination show little or no correlation with later growth in saline solution (Zeng and Shannon 2000; Zeng *et al.* 2002; Munns *et al.* 2006). Nevertheless, assessing salt tolerance at the germination stage is essential for estimating pasture persistence in saline soils. In several species, environmental factors affecting mother plant development, such as temperature, light quality, daylength, and water and nutrient availability, influence seed germination (Fenner 1991; Wuff *et al.* 1994; Fenner and Thompson 2005; Galloway 2005). This influence may increase survival chances under unfavourable conditions in the subsequent generation (Fenner 1991). In *C. ciliaris*, increased germination has been observed in seeds obtained from plants exposed to high temperatures, high nutrient concentration, and short days, whereas the opposite has been found in seeds coming from water-stressed plants (Sharif-Zadeh and Murdoch 2000). It has also been reported that seeds from plants grown under salt stress germinated in higher proportions and earlier than those from non-salinised controls (Amzallag 1994; Zandt and van Mopper 2004). Nevertheless, the effect of plant salinity exposure on the seed salt tolerance (maternal effect) has not been extensively studied (Fenner and Thompson 2005).

The purpose of this work was to assess salt tolerance in the most widely used *C. ciliaris* cultivars and to determine whether cultivation under salinity affected seed germination and resulting plant fitness in the next generation. This information will contribute to understanding the potential persistence penalties associated with the establishment of *C. ciliaris* in salt-affected marginal areas and the possibility of using such areas for seed production.

Materials and methods

In this research, a hydroponics system installed in the field was used, which combined the advantages of a controlled system (Suyama *et al.* 2007) with exposure of the plants to actual environmental conditions prevailing in the target zone. Two *C. ciliaris* cultivars were studied; cv. Biloela is rhizomatous and can grow up to 1.5 m high, while cv. Texas 4464 is the most widely used cultivar in Latin America and is non-rhizomatous and can grow up to an average of 50 cm. Three consecutive trials were conducted under field hydroponics conditions at Estación Experimental Agropecuaria INTA San Juan, Pocito, Argentina (31°37′S, 68°32′W).

Scarified seeds of each cultivar were sown on 21 December 2006, 21 February 2008, and 12 December 2008 in 1000-L PVC containers (1 m by 1 m by 1 m; Fig. 1*a*) filled with washed river sand. Emerged seedlings were thinned to either 27 (trial 1) or 18 (trials 2 and 3) plants per container). Harvests were in May for trials 1 and 3, and in June for trial 2.

Plants were irrigated with a commercial nutrient solution (ammonium nitrate : potassium nitrate : phosphoric acid at 10 : 4 : 2 mg/L, EC 3 dS/m) applied through a drip system supplying 12 L nutrient solution at a rate of 1044 mL/m^2, four times a day (at 08 : 00, 11 : 00, 14 : 00, and 16 : 00). The nutrient solution drained into tanks from which it was pumped again to irrigate the trials (See Fig. 1*b*, *c*). Levels of EC of drainage solutions (EC_{ds}) were monitored daily, and water lost by evapotranspiration was replenished to ensure constant salinity levels. Solutions were renewed every 5 days.

Salinisation was imposed 52, 33, and 65 days after sowing in trials 1, 2 and 3, respectively. Irrigation solution salinity was increased gradually (over 9 days) by adding NaCl to the nutrient solution until the final conductivities (EC_{is}) of 8, 13, and 18 dS/m were attained. Non-salinised controls were irrigated with 3 dS/m solutions (trials 1 and 2). Four replicates of each salinity level were used, giving a total of 16 containers per trial. In trial 3 plants were irrigated only with 18 dS/m.

By an accepted definition, when the EC in the saturated extract (EC_e) is <4 dS/m, the salinity level is generally considered to be low (Munns *et al.* 2012). Moderate salinity occurs at EC_e 4–8 dS/m and high salinity at EC_e >8 dS/m (Munns *et al.* 2012). Assuming saturated paste represents at least a 2-fold dilution of soil solution at field capacity (United States Salinity Laboratory Staff 1954), then EC_e 4 dS/m would equate to EC 8 dS/m in soil solution at field capacity. Graham and Humphreys (1970) showed that *C. ciliaris* cv. Biloela maintained relatively high yields when cultivated in a nutrient solution with 80 mM NaCl (equivalent to ~8 dS/m), so it was decided to use this level as the lowest salinity treatment (above controls), and to establish two further salinity levels (intermediate and high). Since sand is free-draining, the EC in the drainage solution (EC_{ds}) reflected the root-zone salinity, and therefore, EC_{ds} levels of 13 and 18 dS/m would be considered high. Between trials, the sand was extensively washed with water (EC 0.7 dS/m) until this conductivity was registered in the drainage solution.

Growth and grain yield

Plants were cut at ground level at the end of growth period (May) in trials 1 and 2, and then dried at 70°C for 48 h. Shoot and leaf dry weight, and the number of tillers and spikes per plant and spikelets per spike were registered at harvest.

Ears were covered with a net bag and mature grains were collected once a month in trial 2 (5 March, 11 April, 30 May 2008), and yield per plant was calculated. Average weights of 100 grains were determined. Grains were scarified by rubbing them between two rough rubber surfaces, a procedure that safely removed the glumes without affecting the seed coats. Seeds were stored at 20°C and 20% relative humidity.

Leaf ion content

A subsample of leaves (1 g) was harvested at the end of the growth season (May 2008), washed, and dried at 70°C. Dry material was then ashed at 500°C for 6 h and the ashes were dissolved in 20% H_2SO_4 and filtered through a 205-μm-thick, 12.5-cm-diameter paper disc (Qualy brand, J Prolab, Brazil), with 14-μm pores. Concentrations of Na^+ and K^+ in the extracts were determined with a flame photometer (Analyst 200; PerkinElmer, Waltham, MA, USA). Selectivity of K^+/Na^+ ($S_{K+/Na+}$) was defined as the ratio of K^+/Na^+ concentrations in leaf tissues and in the irrigation solution.

Fig. 1. Field hydroponics system: (*a*) view of the 1000-L PVC containers with *C. ciliaris* plants; (*b*) details of the drainage collector system at the bottom of each PVC container; (*c*) tank for drainage collection in trial 1.

Maternal effects

To evaluate salinity maternal effects, seeds collected from the various treatments in trial 2 were sown in the field hydroponics containers on 12 December 2008. These plants grew for 50 days longer than those in trial 2, during the most active summer days. All plants were harvested in May 2009, at the end of the growth period. Plants were cut at ground level and dried at 70°C for 48 h. Shoot and leaf dry weight were measured, as were the numbers of tillers and spikes per plant. Mature seeds were collected once a month (5 March, 11 April, 30 May) and stored at 20°C and 20% relative humidity.

Plants in all containers were irrigated with non-salinised (EC_{is} 3 dS/m) nutrient solution for 45 days and salinity was then gradually increased by 5 dS/m every 7 days until it reached 18 dS/m.

Germination under salt stress

Seeds collected from plants from trial 1 (3, 8, 13, and 18 dS/m) and trial 3 (18 dS/m) were scarified and treated with a fungicide solution. Twenty-five seeds were sown in 9-cm Petri dishes containing various NaCl solutions (–0.5, –1.0, –1.5, –2.0, –2.5,–3.0 MPa). Distilled water was used as a control. Dishes were incubated in the dark at 25°C and germinated seeds (root emergence) were counted daily for 15 days.

Data analyses

The experimental design for trials 1 and 2 was a split-plot with block arrangements (Cochran and Cox 1957; Kuehl 2001). The main plot was the salinity level (3, 8, 13, 18 dS/m), the secondary plot was the two *C. ciliaris* cultivars (Biloela, Texas), and there were four replicates. The data were analysed using the InfoStat statistical package (Di Rienzo *et al*. 2008). Data were subject to a two-way analysis of variance and Tukey multiple comparison post-tests.

Percentage-of-control values for vegetative growth parameters in trials 1 and 2 were subject to a multivariate analysis of variance. All statistical tests were conducted at $P = 0.05$. To characterise the response to salinity and compare both cultivars, we estimated the slopes of the relationships among the various vegetative parameters, and the seed yield, to the average salinity in the drainage solution, and then estimated at which salinity 10, 25, and 50% decreases were observed.

For the maternal effect experiment, the main plot was the salinity treatment to the mother plants (3, 8, 13, 18 dS/m). The statistical model was:

$$y_{ijk} = \mu + \rho_i + \alpha_j + \gamma_{ij} + \beta_k + (\alpha\beta)_{jk} + \varepsilon_{ijk}$$

where y_{ijk} is the response on *i*th block of the level of *j*th treatment factor and the effect of level *k* of cultivar factor; ρ_i is block effect; α_j is salinity treatment effect or salinity treatment to mother plants; γ_{ij} is experimental error attributed to block and salinity treatment; β_k is cultivar effect; $(\alpha\beta)_{jk}$ is salinity treatment and cultivar interaction; and ε_{ijk} is experimental error attributed to block, salinity treatment, and cultivar.

Results

Growth system stability

Drainage solutions had, on average, a higher EC level than the irrigation solutions (Fig. 2), and the levels were approximately constant throughout the growth season. In both trials, EC_{ds} peaks were registered on extremely dry days, and values were below the average on the occasional rainy days. These results indicate that the experimental setup provided reliably constant salinity treatments while the plants were exposed to field environmental conditions.

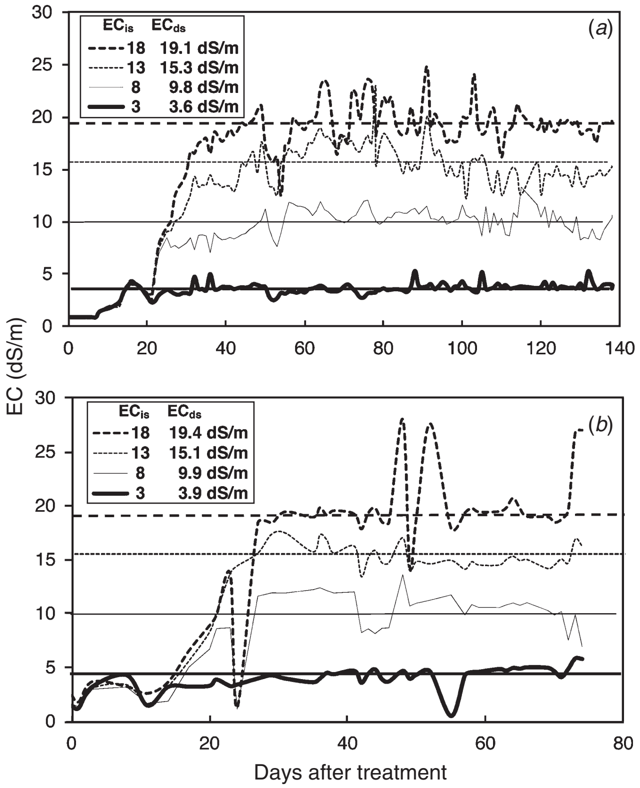

Fig. 2. Irrigation solution (EC_{is}) and drainage solution (EC_{ds}) electrical conductivities in the various salinity treatments in (*a*) trial 1 and (*b*) trial 2. Horizontal lines are the EC_{is} values in both graphs; curves are EC_{ds}. In the key, average season EC_{ds} is indicated next to the EC_{is} used.

Vegetative growth and yield

Table 1 compares the results of trials 1 and 2 on height, tillers per plant, and shoot dry weight. Plant density was higher in trial 1, and this affected both height and tillers per plant. Nevertheless, the responses of both cultivars to salinity were statistically similar in both trials, as can be deduced from the non-significant *P*-level in the salinity × cv. and trial × salinity × cv. interactions. Further growth results are shown only for trial 2.

A progressive decrease in shoot dry weight and tiller number as a function of the EC in the nutrient solution was observed; however, significant differences from controls were registered only in the two higher salinity treatments (Fig. 3). Slopes of linear fits for tillers per plant *v.* EC_{ds} were –2.2 and –1.2, and for dry weight per plant *v.* EC_{ds} were –8.1 and –4.0, in each case for Biloela and Texas, respectively. Mean 10, 25, and 50% vegetative growth reductions were registered at ~9, 11, and 15 dS/m, in both cultivars.

The number of spikelets per plant in both cultivars was significantly reduced by the 8 dS/m salinity treatment (EC_{ds} 9.9 dS/m), and remained low, although not significantly different, at the higher salinity treatments (Table 2). Salinity did not affect average grain number per spikelet and grain weight.

Leaf-blade ion accumulation

Changes in leaf-blade ion accumulation in response to salinity were similar in both cultivars. Increasing concentrations of Na^+ in leaves as a function of the salt treatment (Table 3) were observed, whereas K^+ concentrations decreased. Nevertheless, K^+/Na^+ ratios remained high, >1 in all cases, and $S_{K+/Na+}$ was also high, especially in cv. Texas.

Table 1. ANOVA results (*P*-values) of the effects of salinity on vegetative growth of two cultivars of *C. ciliaris* (cvv. Biloela and Texas) grown using irrigation solution salinities (EC_{is}) of 3, 8, 13, and18 dS/m in two consecutive trials, and average values of vegetative parameters per trial and cultivar

Within a column, means followed by the same letter are not significantly different (at $P = 0.5$)

	Height (cm)	No. of tillers per plant	Shoot dry weight (g/plant)
		P-values	
Trial	0.0001	<0.0001	0.5611
Block	0.1514	0.4994	0.2168
Salinity (S)	<0.0001	0.0093	0.0035
Cultivar (cv.)	<0.0001	0.0005	<0.0001
Trial × S	0.0100	0.0029	0.5806
Trial × cv.	0.3635	0.0114	0.0285
Salinity × cv.	0.3508	0.3736	0.1284
Trial × S × cv.	0.5527	0.4700	0.8013
		Average values per trial and cultivar	
Trial 1, Biloela	96.81a	12.16b	108.81a
Trial 2, Biloela	64.69c	48.00a	138.71a
Trial 1, Texas	79.19b	9.69c	61.38b
Trial 2, Texas	51.09d	34.47b	44.35b

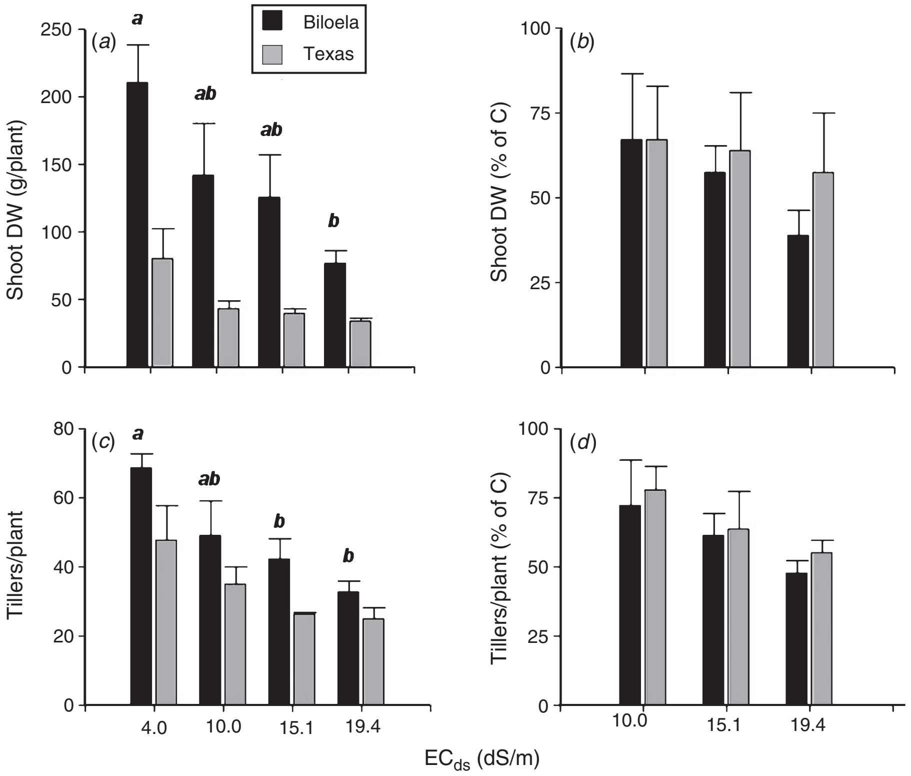

Fig. 3. Effect of drainage solution salinity (EC_{ds}) on shoot dry weight and tiller number of *C. ciliaris* plants cvv. Biloela and Texas in trial 2: (*a*) shoot dry weight (g/plant), (*b*) shoot dry weight as percentage of control, (*c*) tiller number per plant, (*d*) tiller number as percentage of control. Capped lines are standard errors; bars with the same letter are not significantly different at $P = 0.05$. Tukey test results were identical for both cultivars, so letters are shown for Biloela.

Table 2. Effect of salinity on yield components in *C. ciliaris* plants grown under a range of salinities in trial 2

Within a cultivar and parameter, means followed by the same letter are not significantly different (at $P = 0.5$)

Cultivar	EC_{ds} (dS/m)	No. of spikelets per plant	Grains per spikelet	100-grain weight (g)
Biloela	3.9	134.00a	77.67a	0.201a
	9.9	96.00b	77.68a	0.191a
	15.1	82.50b	82.17a	0.198a
	19.4	74.75b	86.92a	0.193a
Texas	3.9	107.75a	74.84a	0.218a
	9.9	85.63b	63.33a	0.213ab
	15.1	70.13b	62.34a	0.214ab
	19.4	53.25b	59.50a	0.212b

Table 3. Leaf K^+ and Na^+ concentrations, and K^+/Na^+ selectivity ($S_{K+/Na+}$) in *C. ciliaris* plants grown under a range of salinities

Within a cultivar and parameter, means followed by the same letter are not significantly different (at $P = 0.5$). Results are from trial 1

Cultivar	EC_{ds} (dS/m)	K^+ (μmol/g DW)	Na^+	K^+/Na^+ ratio	$S_{K+/Na+}$
Biloela	3.6	1127.9a	68.7c	17.63a	–
	9.8	855.5b	147.0bc	6.01b	95ab
	15.3	803.1b	277.2ab	3.33b	109b
	19.1	689.3c	423.7a	1.70b	81a
Texas	3.6	1017.3a	58.9b	17.67a	–
	9.8	802.4b	119.2ab	6.87b	108ab
	15.3	710.4bc	193.7ab	4.18bc	137b
	19.1	615.8c	341.3a	2.30c	110a

Maternal effects (germination, vegetative growth)

In both cultivars, the effects of salinity on vegetative growth were generally similar for plants obtained from seeds that originated in non-salinised and salinised plants (Fig. 4). Salinity in the media decreased seed germination (Fig. 5). Seeds obtained from salt-treated plants had higher germination percentages in both control and saline solutions than those obtained from non-salinised plants (Fig. 5*a*, *b*). This stimulation effect was observed if mother plants had been salt-treated for only one season, as seeds derived from plants subject to salinity for two consecutive seasons did not show this promotive effect (Fig. 5*c*, *d*).

Discussion

Yield assessment conducted in field trials provides the most reliable information on salt tolerance; however, spatial and temporal variability in soil salinity (Richards 1983) makes it

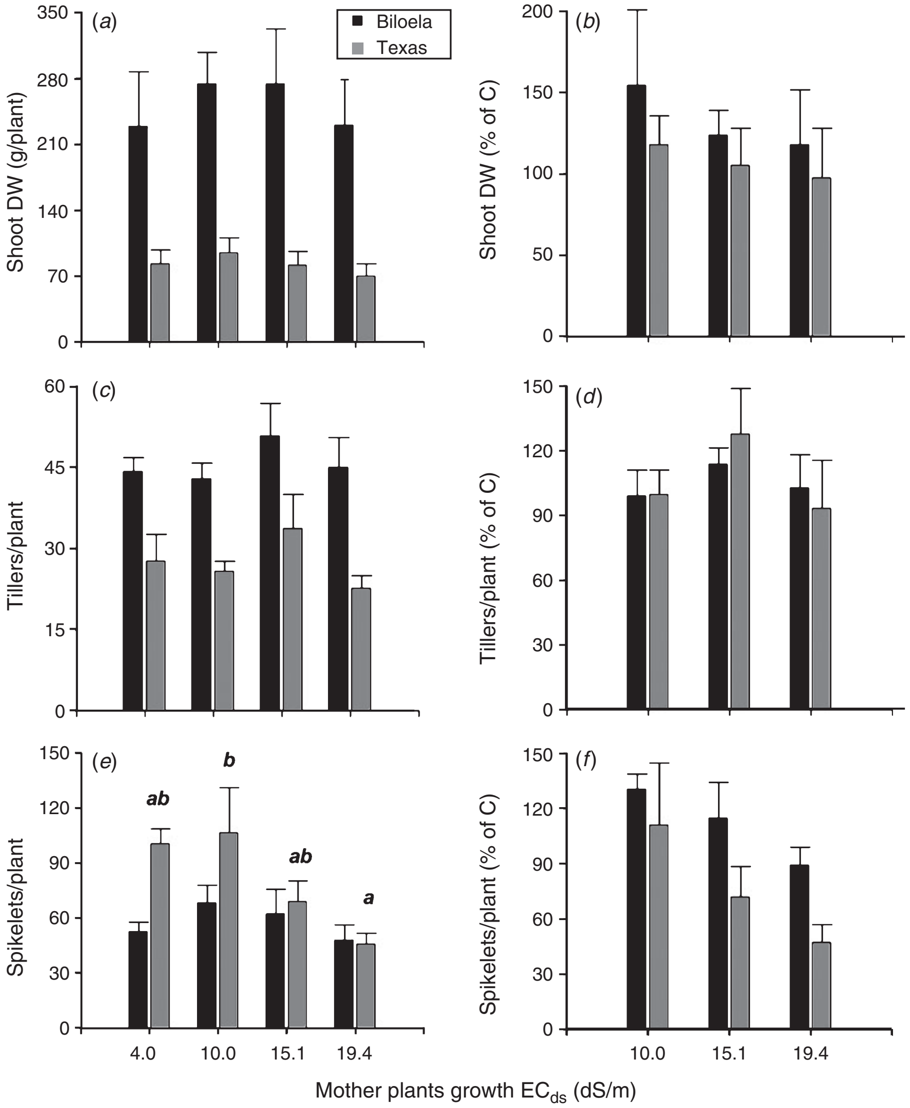

Fig. 4. Effect of salinity treatments to *C. ciliaris* mother plants (EC_{ds}) on vegetative and reproductive components in their offspring, irrigated with 18 dS/m in trial 3: (*a*) shoot dry weight (g/plant), (*b*) shoot dry weight as percentage of control, (*c*) tiller number per plant, (*d*) tiller number as percentage of control, (*e*) spikelet number per plant, and (*f*) spikelet number as percentage of control. Capped lines are standard errors; bars with the same letter are not significantly different at $P = 0.05$. Tukey test results were identical for both cultivars, so letters are shown for Texas.

difficult to obtain reproducible information. The advantages of using a hydroponic system are that the saline conditions can be controlled and constantly monitored. A disadvantage of using this system is that plants may not express the same differences in growth and ion composition that they may if grown in soil (Tavakkoli *et al.* 2010). In our experiments, washed river sand substrate was used and was irrigated with a well-defined nutrient solution under field conditions. The technique was based on that of Wang (2002), who used well-graded river sand, and was able to reproduce results for volumetric heat capacity and thermal conductivity of soil, as well as water retention capacity. The use of 1-m^3 containers to grow the plants allowed more realistic root and shoot development than may have been obtained using smaller pots, and enabled the growth medium to be effectively monitored by continually analysing both the irrigation and drainage solutions. Rainfall in the San Juan region is scarce during the summer (mean annual precipitation 10 mm and radiation 2000 µmol/(m^2.s)), making it an ideal site for this type of experiment.

Previous research has suggested that both cultivars of *C. ciliaris* have moderate levels of salt tolerance (Graham and Humphreys 1970; Ayerza 1981). Decreases of 50 and 70% in height and shoot fresh weight have also been reported at EC 30 dS/m in cvv. Texas and Biloela by Lanza Castelli *et al.* (2010), who tested seedling growth in short-term liquid culture experiments. In our trials, similar growth reductions occurred at

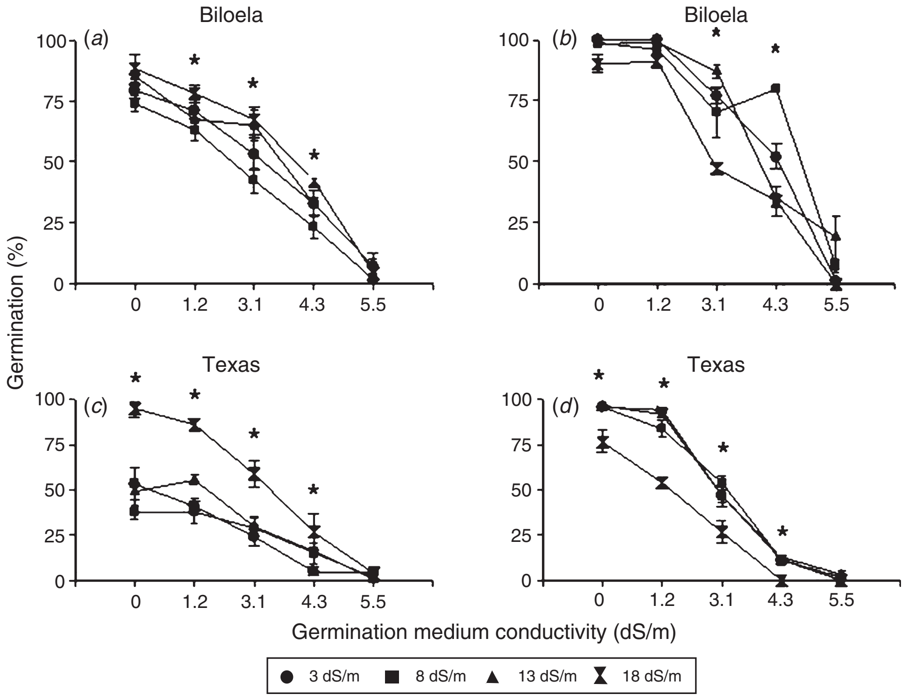

Fig. 5. Effect of salinity on the germination of *C. ciliaris* cvv. Biloela and Texas. (*a*, *b*) Seeds obtained from plants grown in trial 1, using irrigation solution salinities (EC_{is}) 3, 8, 13, and 18 dS/m. (*c*, *d*) Plants obtained from seeds from trial 1, grown under EC_{is} 18 dS/m in trial 3; germination was tested in seeds from those plants. Symbols under the graphs in (*c*) and (*d*) indicate the salinity levels in trial 1. *Significance differences ($P < 0.05$).

lower salinity, average 50% vegetative growth reductions were registered at ~15dS/m, and in contrast to that work, growth in both cultivars was similarly affected. In general, early vegetative growth is reported to be more salt-sensitive than later vegetative stages (Läuchli and Grattan 2007), so the higher susceptibility shown in our research was probably due to the plants being exposed to multiple environmental stresses (high temperature and irradiance), in addition to salinity, during an entire growth season. The similarity between cultivars in their levels of salt tolerance contrasts with other research obtained from salinised liquid cultures under controlled conditions, which indicated cultivar differences in salt tolerance (Griffa *et al.* 2010; Lanza Castelli *et al.* 2010). The discrepancies between these results may be due to the different environment in which trials were performed (multiple stresses in the field *v.* controlled in a greenhouse), as well as the type of growth medium (liquid or sand) used in both cases (Tavakkoli *et al.* 2010).

In terms of the number of spikelets per plant, both cultivars were affected similarly by salinity; however, the number of grains per spikelet was not affected. These results suggest that seed production would be affected by salinity mainly through a reduction in the number of spikelets per plant.

Overall, our results indicate that growth and yield reductions begin to occur at EC_{ds} ~10 dS/m, and proceed with a very mild slope as salinity increases. Consequently, the *Cenchrus* cultivars included in these trials can be considered moderately salt-tolerant and similar to *Cynodon dactylon* (Suyama *et al.* 2007), *Cenchrus pennisetiformis*, and *Panicum turgidum* (Ashraf 2006). It would be feasible to plant these cultivars in salt-affected soils with EC levels of ~5 dS/m in the saturated paste extract (which corresponds, approximately, to EC_{ds} ~10 dS/m in our trials) and expect only minor decreases in biomass production and seed yield. Such soils are prevalent in the Bajos Submeridionales region of Santa Fé, in the weakly salinised soils in the Province of Córdoba, and in some areas in the Depresión del Salado in the Province of Buenos Aires (Taleisnik *et al.* 2008).

Concentrations of Na^+ in leaf tissues increased as a function of the Na^+ concentration in the irrigation solutions. However, tissue Na^+ concentrations were still below the concentration of K^+, suggesting that this species has efficient uptake mechanisms, at least to the leaves, that discriminate between both ions. The relatively low leaf Na^+ concentration attained may suggest that the negative effects of salinity were exerted mainly through osmotic effects (Munns and Tester 2008).

Reproduction in buffel grass is mainly by pseudogamic apospory apomixis, in that the embryo sac is generated from nucellar cells by mitosis (Spillane *et al.* 2001), but fertilisation of a polar nucleus is required for endosperm development and seed viability. Thus, reproduction in this species is considered to be pseudogamic apomictic (Dwivedi *et al.* 2007). Apomictically produced offspring are genetically identical to the parent plant, and therefore, plants with this type of reproduction are useful for evaluating the occurrence of maternal effects.

It has been reported for several species, including *C. ciliaris* (Sharif-Zadeh and Murdoch 2000), that exposure of mother plants to environmental factors such as temperature, light quality, daylength, and water and nutrient availability can influence seed germination in the following generation (Fenner 1991; Wuff *et al.* 1994; Wuff 1995; Fenner and Thompson 2005; Galloway 2005). In our research, we found that seeds derived from plants that had been salt-stressed for one generation germinated in higher proportions and earlier than those from non-salinised controls, as was previously reported in *Sorghum bicolor* and *Iris hexagona* (Amzallag 1994; Zandt and van Mopper 2004). However, the stimulating maternal effect was observed only during germination and early vegetative growth (Amzallag 1994). In *Plantago lanceolata*, in one of the few studies that followed progeny for more than one season, parental effects disappeared in the second year (Lacey and Herr 2000). Similarly, Laossi *et al.* (2010) reported that the increase in germination rates of seeds produced in the presence of earthworms during the first generation was not necessarily observed during the second generation. Maternal effects might change over time due to the nature and interaction of the two general mechanisms of maternal effects: seed quality and epigenetics. The former acts by determining the quality of seed storage reserves, hormones, and other materials (Fenner 1991). By contrast, epigenetic factors may be responsible for progeny performance for a longer time, even over several generations. Thus, each mechanism might alter progeny differently throughout the lifespan.

Conclusions

The results of this study show that salt tolerance, in terms of vegetative growth, was similar in *C. ciliaris* cv. Texas and Biloela and that yield reductions associated with salinity were due mainly to effects on the number of spikelets. Based on their response to salinity, it would be feasible to plant these cultivars in salt-affected soils with EC 5 dS/m in the saturated paste extract (which corresponds, approximately, to EC_{ds} 10 dS/m in our trials) with only minor decreases in biomass production and yield.

Transient maternal effects were detected as a stimulating effect of salinity in germination of seeds obtained from plants that had been grown under saline conditions for one season. Salinity in the media decreased seed germination; however, salinity did not impose seed-associated inherent growth penalties in the following generation. These results suggest that stand persistence in saline soils would not be limited by diminishing plant performance but, rather, by seed yield and germination.

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