

Response of *Chloris gayana* cultivars to salinity.

1. Germination and early vegetative growth

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Abstract

The effects of salinity on germination, vegetative growth, regrowth after clipping, osmotic adjustment and ion accumulation were evaluated in 6 cultivars of *Chloris gayana* at the early stages of growth. Two tetraploid cultivars, Boma and Callide, and 4 diploid ones, Bell, Katambora, Pioneer and a local accession of Pioneer, were included in the study.

The rate of water uptake in seeds was not affected by salinity (0–400 mM NaCl); however, saline solutions delayed or altogether inhibited germination. Nevertheless, seeds of all the cultivars tested retained viability in 100 and 200 mM NaCl solutions, and germination percentages achieved after transfer to distilled water were not lower than 60%. Growth in all the cultivars was reduced at high salinities and cv. Boma was the most sensitive. This cultivar also had relatively lower Na and higher K accumulation in leaf tissues, and lower Na excretion via salt glands, than the other cultivars analysed.

Introduction

Salinisation is an important cause of agricultural restriction in soils. About one-tenth of the surface of the continents is covered by different kinds of salt-affected soils, the majority of which are saline (Szabolcs 1991). Approximately 129 Mha are considered saline in South America (Szabolcs 1991) and in the Argentinean Arid Chaco, several million hectares climatically

suitable for cattle raising are affected by salinity distributed in patches where pasture productivity is considerably reduced (Angueira 1986).

Chloris gayana is known for its salt tolerance and ability to withstand dry conditions, soil salinity and light frost (Bogdan 1969); nevertheless, it ranged intermediate in a salt-tolerance study involving 5 other forage crops: *Cynodon dactylon*, *Leptochloa fusca*, *Distichlis spicata*, *Paspalum vaginatum* and *Medicago sativa* (Pasternak *et al.* 1993). As *Chloris gayana* is especially suitable for cultivation under the environmental conditions prevailing in the Argentinean Dry Chaco, it is desirable to increase its salt tolerance to adapt it to the salt-affected soils of the area.

Tolerance of high soil salinity at germination and emergence, as well as in later growth stages, is among the traits that could confer performance advantages in saline environments (Rains 1991). Germination and seedling establishment are considered to be the most critical stages of the life cycle under saline conditions (Ungar 1978). The capability to germinate under saline conditions is essential for ensuring the natural resowing of the pasture. Vigorous growth at the seedling stage has been used as a criterion for selecting salt-tolerant individuals and increasing salt tolerance in many species (McKimmie and Dobrenz 1987). In *Chloris gayana*, the regeneration capability after multiple clippings significantly contributed to increased salt tolerance after selection pressure with high salinity was exerted (Malkin and Waisel 1986).

Though Na and Cl provide energetically economical osmotica for adjusting to low external water potential (Wyn Jones and Gorham 1983), excessive accumulation of these ions invariably results in reduced growth (Greenway and Munns 1980). The management of excess Na and Cl, and the balance between these ions and others such as K, which are essential for normal metabolic functions, is one of the key aspects of

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the adaptation of plants to saline soils. In the Triticeae, salt tolerance is associated with enhanced ability to discriminate between K and Na in the soil solution, and to accumulate K preferentially and exclude Na (Gorham *et al.* 1985; Schachtman *et al.* 1989).

The purpose of this study with *Chloris gayana* was to assess, at the early stages of growth, the existence of intraspecific variability for physiological traits associated with salt tolerance. The effects of salinity on germination, vegetative growth, regrowth after clipping, osmotic adjustment and ion accumulation were evaluated in several cultivars of this species.

Materials and methods

The following cultivars or ecotypes of *Chloris gayana* (Kunth) were included in this study: tetraploid cultivars Boma and Callide, and diploid cultivars Pioneer, Katambora, Bell, and a local accession of Pioneer, referred to as Pioneer Local.

Effect of salinity on imbibition and germination

Low water potential in the medium can affect the rate of imbibition (Ungar 1978). In order to begin germination tests with fully imbibed seeds, the effects of salinity on the rate of imbibition were assessed for seeds of cv. Katambora.

Seeds (0.1 g) were placed in pre-weighed, water-permeable bags made of synthetic fabric that did not absorb water. The bags containing the seeds were submerged in NaCl solutions of various concentrations: 0, 100, 200 and 400 mM, approximately equivalent to ECs of 0, 10, 20 and 40 dS/m, respectively (United States Salinity Laboratory Staff 1954), and were weighed daily. Before weighing, each bag was centrifuged for 2 minutes at low speed in a table centrifuge to remove excess water and seed weight was obtained by subtraction. There were 5 replications per salt concentration.

Germination tests were carried out on seeds of 5 cultivars: Bell, Callide, Katambora, Pioneer and Pioneer Local. Seeds (0.1 g) were surface disinfected with 1% NaClO₃, imbibed for 3 days in sterile saline solutions of various concentrations (0, 100, 200 and 400 mM NaCl), and transferred to plastic disposable trays with hermetic lids, containing filter paper moistened in the

same solutions. Paper and solutions were sterilised before use to prevent the development of pathogens. Germinated seeds were counted and discarded every 3 days during a 9-day experimental period. In order to determine whether ungerminated seeds retained viability after this period, they were transferred to trays containing filter paper moistened with distilled water. Germination was assessed after 3 additional days. There were 8 replications per cultivar and treatment, and the experiment was repeated twice.

Effect of salinity on seedling growth and regrowth after clipping

Seeds of cv. Pioneer, Pioneer Local, Katambora, Bell, Boma and Callide were sown in vermiculite in the greenhouse; experiments were carried out from July to October 1995. Seedlings, 5–7 cm high, were transferred to plastic net frames which held a 1 cm-thick vermiculite layer and were placed over 4.5 L plastic trays containing water. One week after transfer, when roots emerged through the net, the water in the trays was replaced with half-strength Hoagland solution (Hoagland and Arnon 1950), with or without 100 mM NaCl. Controls were not salinised but the greenhouse water supply contained 25 mM NaCl. In some of the trays, NaCl concentration was gradually increased (50 or 100 mM/d), until final concentrations of 25 (controls), 100, 200 and 400 mM were attained. There were 2 trays per treatment/cultivar. The nutrient medium, including NaCl, was replaced once a week.

Five plants from each cultivar were randomly selected and plant height was measured at weekly intervals from the initiation of the salt treatments. Relative elongation rates were calculated as $(\ln A_2 - \ln A_1) / (t_2 - t_1)$, where A is plant height and t is sampling time. The experiment lasted for 1 month.

Plant tops from 5 plants per cultivar/treatment combination were harvested at the end of the experiment, leaving 7-cm stubble. Stolons were weighed separately, and fresh weight, dry weight and leaf area were determined on the remaining fraction of the tops. Total top weight was calculated, as well as the ratios between fresh weight and dry weight, and dry weight to leaf area (succulence). Plants were allowed to regrow, and were clipped 4 times, at bi-weekly intervals first and then once a week. Results were subject to

ANOVA, and differences among means were estimated by Tukey's test (Statistica 1992)

Ion concentration in leaf blades

Na and K were determined by flame photometry in samples from the youngest expanding leaves. Leaf segments were cut, thoroughly rinsed in deionised double-distilled water, weighed and placed in 0.1 N HNO₃ for at least a week. Ion concentration was determined both in the rinsing water (as described by Liphshitz and Waisel 1974) and in the HNO₃ solution, in order to estimate the magnitude of excretion by salt glands and the ion concentration in the leaf tissues.

Osmotic potential and osmotic adjustment

Samples for measurement of osmotic potential and calculation of osmotic adjustment were taken from either the youngest leaf or from recent regrowth after clipping. Samples were thoroughly washed in distilled water and carefully blotted before being inserted into the barrel of a 1 ml syringe and immediately frozen with liquid air. To measure osmotic potential, samples were thawed just prior to the measurement, a drop of sap was extracted on to a disk of filter paper by pressing the plunger of the syringe and immediately introduced into the chamber of a Wescor HR 33T psychrometer (Turner 1981). Readings were taken at the dew point setting after a 3-min equilibration period. Osmotic adjustment was calculated from osmotic potentials corrected by the water fraction of the tissue. Osmotic adjustment for each salt treatment was the percent of osmotic potential increase of the corrected data with respect to controls.

Results

Effect of salinity on seed imbibition and germination

Maximum imbibition was attained after 3 days and was not influenced by salinity (Figure 1). This assay was run using only 1 cultivar. It was assumed that the response would be similar for the other cultivars, as has been reported for barley (Bliss *et al.* 1986). In the following germination tests, seeds were imbibed for 3 days in the various saline solutions prior to beginning the test itself.

Germination rate was initially fast and declined afterwards, indicating that most of the seeds germinated in the first 3 days. A significant decline in germination rate was observed at 100 mM NaCl in all cultivars except Callide, which may be explained by its slow germination rate under control conditions (Figure 2). No seeds germinated at 400 mM NaCl. When ungerminated seeds were transferred from the saline solutions to water, germination percentages after 3 further days approached control levels at 100 mM NaCl and were higher than 60% at 200 mM NaCl (Figure 3), indicating that a large percentage of seeds retained viability. All cultivars responded similarly to this procedure. Except for cv. Callide, some seeds of the other cultivars retained viability even at 400 mM NaCl.

Seedling growth

Leaf relative elongation rates (LRER) decreased as a function of the salt concentration in the root medium (Figure 4). Elongation rates were reduced to 50% by 100 mM NaCl in cv. Boma and by concentrations ranging between 200 and 300 mM NaCl in the rest of the cultivars. Early vigorous growth distinguishes the tetraploid cultivars used in this study; however, at this stage, LRER had slowed down in both cultivars, as can be seen from the LRER values at the beginning of the experiment.

In shoots, salinity also reduced fresh weight accumulation, the ratio between fresh and dry weight and the concentration of dry weight per unit leaf area in these plants (Table 1). It did not, however, affect the number of stolons per plant at this stage. Furthermore, no significant interactions of cultivar × salinity were detected for any of these parameters.

Table 1. Results (F values) from ANOVAs assessing the effects of salinity on the accumulation of fresh weight per plant (FW), the ratios of fresh to dry weight (FW/DW), dry weight to leaf area (DW/LA), and the number of stolons per plant (S/p), on 6 cultivars of *Chloris gayana*. Asterisks denote highly significant values at P<0.01.

Effect	Degrees of freedom	FW	FW/DW	DW/LA	S/p
Cultivar	5	2.71**	1.36	10.84**	2.69**
Salinity	3	31.92**	15.73**	3.35**	0.58
Interaction	15	0.83	3.36	0.31	0.72
Error	92				

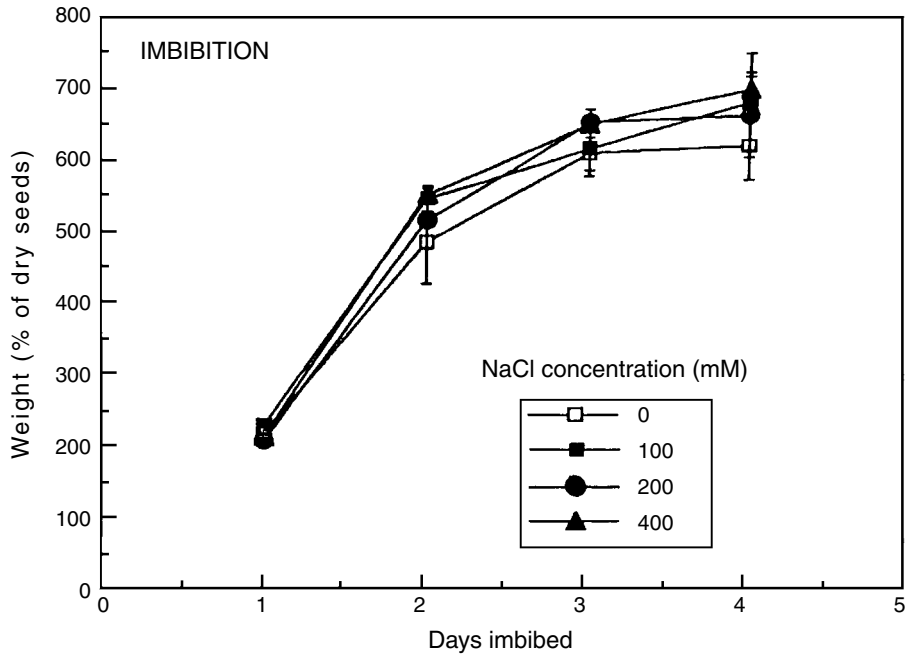


Figure 1. Effect of salinity on the rate of imbibition of *Chloris gayana* seeds. Results are means \pm standard error of 5 replicates.

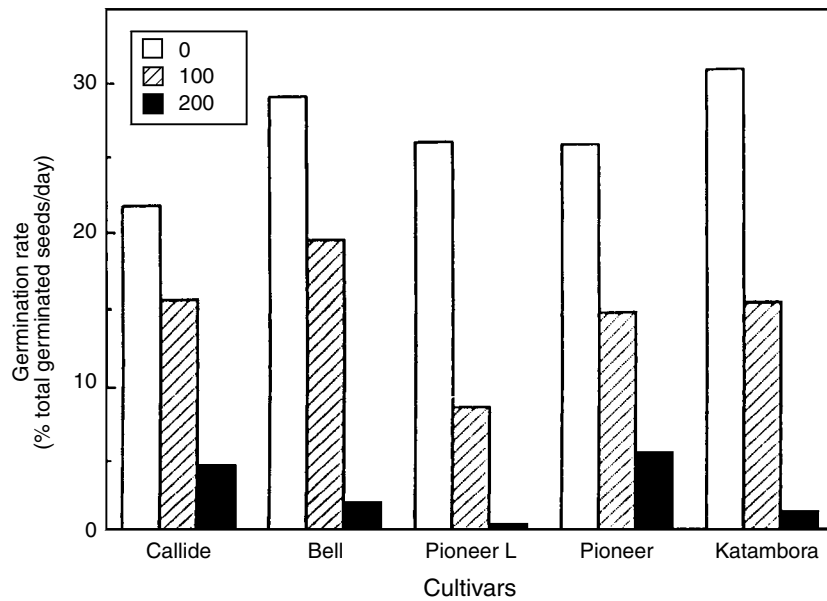


Figure 2. Effect of salinity on the initial germination rate of *Chloris gayana* seeds. Germination rate is the slope of the percentage of germination as a function of time. All rates measured at 100 and 200 mM NaCl were significantly different from controls ($P < 0.01$), except in Callide where these differences were registered only at 200 mM NaCl.

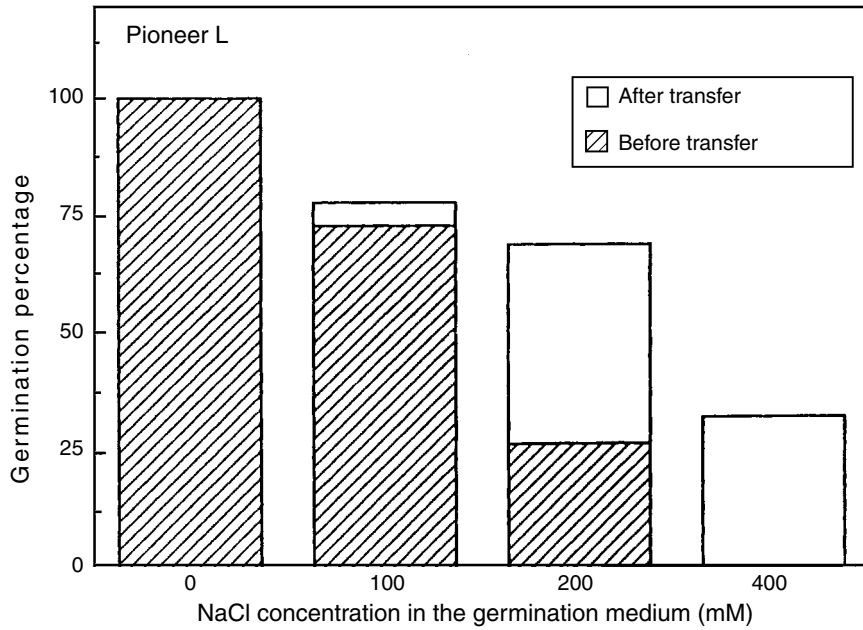


Figure 3. Germination percentage of *Chloris gayana* cv. Pioneer L seeds, after 9 days in NaCl solutions of various concentrations (hatched columns). Ungerminated seeds were transferred to distilled water on day 9 and the germination percentage was determined after 3 additional days (clear columns.)

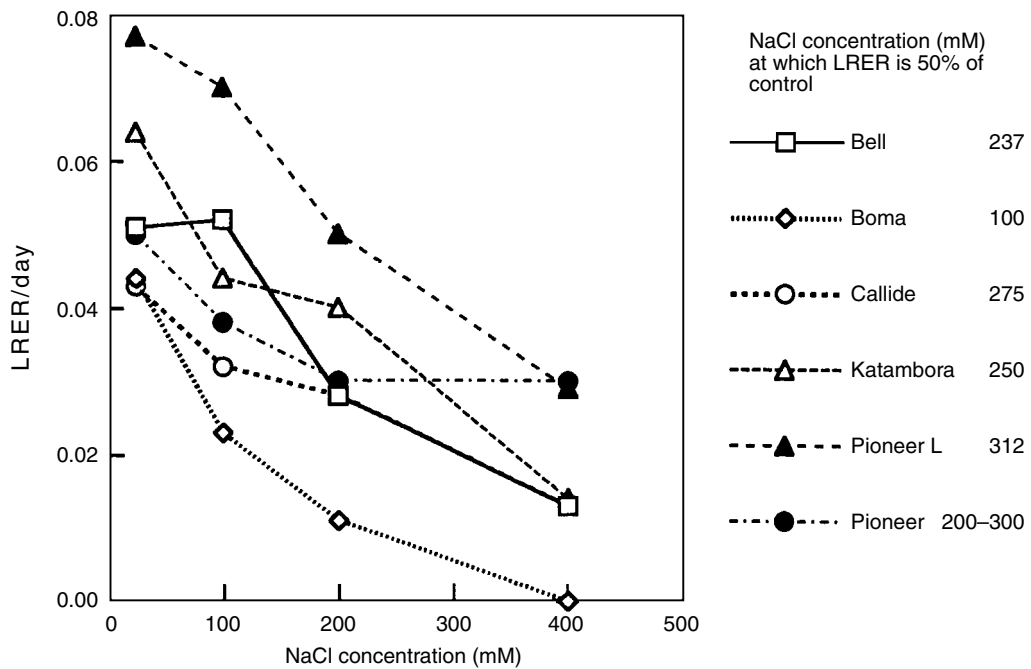


Figure 4. Effect of salinity on leaf relative elongation rates (LRER) in 6 cultivars of *Chloris gayana*. Each point is the mean of 5 plants. Standard errors did not exceed 10% of the means and were omitted for the sake of clarity.

Regrowth after clipping was also affected by salinity, but all cultivars responded similarly to this treatment (results not shown). Cumulative regrowth was reduced to 50% of controls by NaCl concentrations close to 300 mM, the same level which affected leaf extension.

Na and K accumulation

Na and K concentration were determined in the youngest expanding leaf of plants grown at 200 mM NaCl. Na accumulation was obviously higher in salinised plants than in controls, but it was significantly ($P < 0.01$) lower in cv. Boma than in the rest (Table 2). Under control conditions, no differences in K or Na accumulation were observed among cultivars. K concentration in leaves of salt-treated plants was lower than in controls in all cultivars except Boma. Under saline conditions, Boma accumulated significantly higher K concentrations in leaves than the other cultivars. Consequently, the K/Na ratio was significantly higher in cv. Boma than in the rest, both under control and salinised conditions.

Salt glands, found in this species on both leaf surfaces (Lipschitz *et al.* 1974), had the same density on both surfaces. There were, however, fewer glands in cv. Boma than in the diploid cultivar, Katambora; on the abaxial surface, the number of glands per mm² was 7.86 ± 1.58 and 15.43 ± 2.56 , in each cultivar, respectively. The ratio between excreted and internal Na varies with the level and duration of the salt treatment (Lipschitz and Waisel 1974). Nevertheless, it

was always lower in cv. Boma than in the other cultivars (Table 2 and other data not shown), and the differences among cultivars exceeded the differences in gland density.

Relative water concentration, osmotic potential and osmotic adjustment in developing leaves

Relative water concentration decreased 10% on average between controls and the highest salinity treatment in all the cultivars. As well, osmotic potentials tended to decrease (become more negative) as the NaCl concentration of the medium increased (Figure 5). The percentage of osmotic adjustment was higher in the tetraploid cultivars than in the diploids at the higher salinity levels (Figure 6).

Discussion

Effect of salinity on seed water uptake and germination

Water uptake by dry seeds is a triphasic process under optimal conditions (Bewley and Black 1994); the first 2 phases correspond to imbibitory water uptake, prior to radicle emergence, while the third takes place only in germinating seeds and is concurrent with radicle elongation. The kinetics of water uptake in Phases I and II is influenced by the properties of the seed as well as by the environment, where low water potential may delay imbibition (Ungar 1978; Bliss *et al.* 1986). However, in our experiments, imbibition

Table 2. Na and K concentration, K/Na quotient and ratio between excreted and internal Na contents in young leaves of 6 cultivars of *Chloris gayana* grown under control or salinised (200 mM NaCl) conditions. Figures are the mean of 5 measurements per cultivar/treatment combination. In salinised plants and within parameters, values followed by different lower case letters are significantly different ($P < 0.01$). In K/Na ratios, values followed by different upper case letters are significantly different at ($P < 0.01$).

Cultivar	Treatment	Na Conc.	K Conc.	K / Na	Na Excr./Na Int.
		($\mu\text{mol/ g FW}$)	($\mu\text{mol/ g FW}$)		(%)
Boma	Control	36.41	59.76	1.66 C	3.8
	Salinised	77.66 a	65.19 a	0.85 b	2.3
Bell	Control	44.93	56.72	1.27 AB	9.0
	Salinised	110.79 bc	48.10 b	0.44 a	19.5
Katambora	Control	45.84	50.53	1.11 A	0.3
	Salinised	104.38 bc	39.53 b	0.38 a	10.2
Callide	Control	35.20	51.59	1.47 BC	1.5
	Salinised	97.26 b	43.56 b	0.45 a	11.5
Pioneer L	Control	50.21	55.13	1.10 A	2.0
	Salinised	117.70 c	46.12 b	0.39 a	9.4
Pioneer	Control	45.95	49.13	1.07 A	0.7
	Salinised	116.94 c	34.66 b	0.30 a	17.2

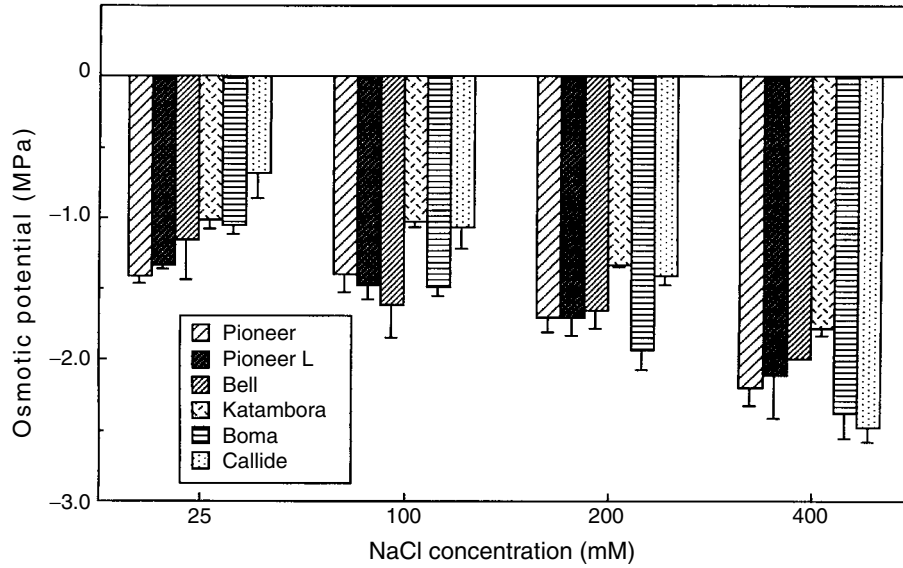


Figure 5. Osmotic potential in young leaves of 6 cultivars of *Chloris gayana* grown in Hoagland solution supplemented with various NaCl concentrations. Each bar is the mean \pm standard error of 5 measurements.

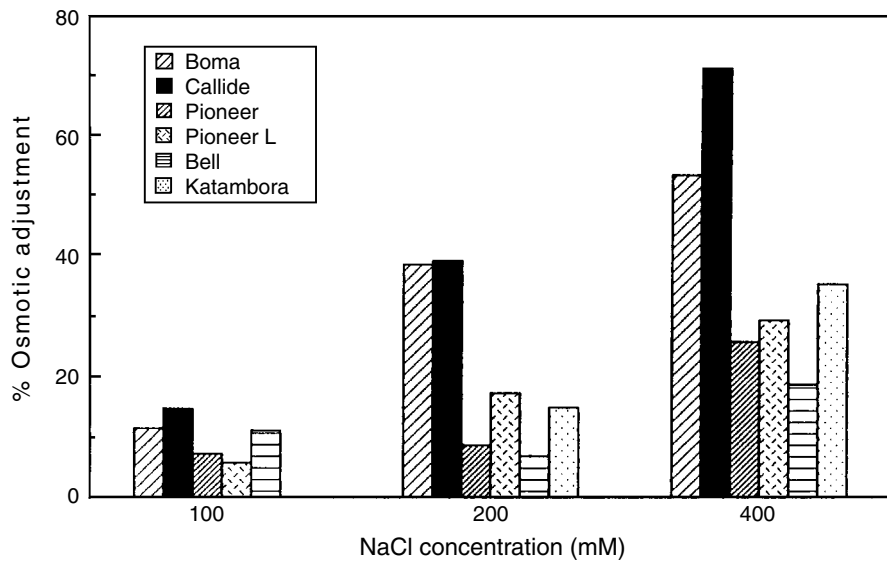


Figure 6. Osmotic adjustment in young leaves of 6 cultivars of *Chloris gayana* grown in Hoagland solution supplemented with various NaCl concentrations.

was not influenced by the range of salt concentrations we tested. Though the rate of imbibition was not affected, saline solutions delayed or altogether inhibited germination (Figure 2), and decreased the germination percentage. A differential sensitivity of these 2 parameters was reported for *Stylosanthes humilis*, where the germination rate was a more sensitive indicator of NaCl stress than percentage germination (Lovato *et al.* 1994), but such a difference was not evident in our case.

Seeds of all cultivars retained viability in 100 and 200 mM NaCl solutions, and germination percentages achieved after transfer to distilled water were not lower than 60%. Similar trends were observed in tomato by Kurth *et al.* (1986), who showed germination was not impaired by a 10-day exposure to 460 mM NaCl solution. Barley seeds retained viability after 4-day imbibition in a 1 M NaCl solution (Bliss *et al.* 1986). These results suggest that the germination stage would not limit the establishment of pastures of these cultivars in saline soils, since surface salinity in the field would have to exceed 20 dS/m (equivalent to a 200 mM NaCl solution) to significantly inhibit germination. A value this high would be considered unusual for arable lands (United States Salinity Laboratory Staff 1954). Rain during the germination period would decrease surface salinity and germination percentages could easily approach levels observed in the absence of stress. Such conditions prevail in the area for which these pastures are intended, where highest rainfall is registered in the period, December–March (unpublished data from La Maria Agrometeorological Station for the Province of Santiago del Estero in the Argentinean Dry Chaco).

Effect of salinity on growth

In general, the growth in all *Chloris gayana* cultivars tested was reduced at high salinities (Table 1; also Guggenheim and Waisel 1977). This indicates that this species can be grouped with other halotolerant monocotyledons in Group II of the classic diagram of Greenway and Munns (1980), along with species which grow very slowly above a certain NaCl concentration, and do not develop succulence (DW/FW ratio in Table 2). Shoot expansion and fresh and dry weight accumulation decreased as a function of salinity in all cultivars; however, cv. Boma was the most sensitive to

salinity (Figure 4). Boma is a tetraploid cultivar, and in previous comparisons between diploid and tetraploid cultivars, cv. Samford (tetraploid) was found to be more salt-sensitive than the diploid cultivars with which it was compared (Taleisnik and Grunberg 1993).

Leaf Na concentration and K/Na ratios

Leaf Na accumulation was lower in cv. Boma than in the rest (Table 2). The physiological basis for this difference was not explored in the present study and will be the subject of a following study. Salt glands are present in the foliar epidermis of this species (Lipshitz and Waisel 1974) and secretion of Na, K and Cl has been documented (Lipshitz *et al.* 1974). The contribution of secretion via salt glands to the Na balance of leaves was also lower in cv. Boma when compared with the others, partly due to the lower gland density per unit surface area. For a given salinity level, absolute Na excretion, the ratio of excreted to retained Na and the Na/K selectivity in excretion, were all lower in this cultivar than in the rest (Table 2). On the other hand, the percentage of osmotic adjustment (Figure 6) was higher in this cultivar, and in tetraploid cv. Callide, than in the diploid genotypes. The contribution of these 2 features (relatively lower Na accumulation combined with higher osmotic adjustment) to the salt susceptibility of cv. Boma requires an analysis of the contribution of organic and inorganic solutes to osmotic adjustment and of the energy cost of osmoregulation.

The K/Na ratios found in *Chloris gayana* are within the range of those reported for halophytic monocotyledoneae (Rozema 1991). The K/Na ratio in leaves has been associated with the relative salt tolerance of species within the Triticeae (Dvorak *et al.* 1994), where tolerant germplasm had higher K/Na ratios, on account of both high K and low Na accumulation (Shah *et al.* 1987). The same features have been associated with the salt tolerance of rice (Gregorio and Senadhira 1993). The opposite trend, however, was found in *Chloris gayana*, where Boma, the least tolerant cultivar, exhibited the highest K/Na ratio and K concentration. Similar results were reported previously for the tetraploid cultivar, Samford (Taleisnik and Grunberg 1993). On the other hand, in the tetraploid cv. Callide, ion accumulation was similar to that in the diploid

cultivars. Thus, the clue to these differences may reside in the origin of the polyploidy.

In summary, information from these studies indicates that *Chloris gayana* cv. Boma is relatively less salt-tolerant than the diploid cultivars surveyed. No differences in salt sensitivity were found among diploid cultivars in germination, early vegetative growth, ion accumulation or osmotic adjustment. Besides growth, the most conspicuous physiological differences between cv. Boma and the rest, in the response to salinity, were the relatively lower Na and higher K accumulation in leaf tissues, and the lower Na excretion via salt glands in Boma. The association between these features and salt sensitivity in this species, as well as the variability and heritability of these traits within ploidy level will be explored in further studies.

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