

Research Article

Effect of environmental factors on the germination of *Megathyrus maximus*: an invasive weed in sugarcane in Argentina

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The authors declare to not have conflict of interest.

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HIGHLIGHTS

- The seed dormancy was strongly associated with the presence of glumes.
- Germination does not depend on light; It occurs under a 12-h-light-dark photoperiod and in complete darkness.
- Germination occurs over a wide range of temperatures. However, it is not tolerant to hydric and saline stress.

ABSTRACT

Background: *Megathyrus maximus* (Jacq.) is a perennial weed that affects many crops. In Argentina, sugarcane is the most affected.

Objective: Study effective techniques to break dormancy and the effect of environmental factors on the germination of this weed.

Methods: Experiments were carried out in cabinet incubators twice, with five replicates per treatment. The experimental unit was made up for 50 seeds.

Results: Seed dormancy was strongly associated with the presence of glumes. Manual extractions of glumes and immersion in sulphuric acid were the most effective techniques for breaking dormancy. *Megathyrus maximus* did not depend on light to germinate, and it did so both under a 12 h-light-dark photoperiod and in complete darkness, with maximum mean germination percentages of 73 and 76%, respectively. Mean germination percentage (G) and coefficient of germination (CG: number of germinated seeds per day) showed that this weed responded to a wide range of temperatures, the optimal varied between 25 and 35 °C. Both mean germination percentages and CG decreased as osmotic potential became increasingly negative (0 MPa to -0.6 MPa), and as sodium chloride solution concentrations increased (10 to 130 mmol L⁻¹). No germination was observed at -0.8 MPa and with a 150 mmol L⁻¹ sodium chloride solution.

Conclusions: The optimal germination conditions for *M. maximus* can be found in central sugarcane areas in Argentina, since soils are in ideal conditions and are kept under irrigation. In marginal areas, *M. maximus* germination would depend on rainfall and certain sodium chloride concentrations in the soil.

1 INTRODUCTION

Megathyrus maximus (Jacq.) B.K. Simon & S.W.L. Jacobs var. *maximus*, formerly known as

Panicum maximum, is native to Africa and belongs to the Poaceae family. It is a perennial and robust weed that may be up to 4 m tall and spreads by seeds. This species is shade-tolerant and frost-susceptible

(Holm et al., 1977; Chaila and Sobrero, 2009). It was introduced in almost every tropical country around the world as forage, then it spread to forest edges, savannahs and crops, thus becoming a pest. The crops most affected by *M. maximus* worldwide are sugarcane (*Saccharum officinarum* L.) and cotton (*Gossypium hirsutum* L.) (Williams and Baruch, 2000).

In Argentina, sugarcane is grown across several agroecological regions with different physiographic, climatic and edaphic characteristics. It is cultivated in areas with 600 mm annual rainfall and salt contents of up to 50 mmol L⁻¹ (Zuccardi and Fadda, 1985). *Megathyrsus maximus* is regarded as one of the five most important perennial species that affect sugarcane. This is due to the morphological similarities between them, which allow the weed to remain unnoticed, at least in the initial stages (Holm et al., 1977). For several years, the infested areas were restricted to the central sugarcane region. Nowadays, there is a higher number of invaded sugarcane fields as a consequence of important changes in crop management, in particular the switch from intensive soil tillage to reduced tillage. In this scenario, yield losses can be as high as 60% (Chaila et al., 2010).

In general, in perennial grasses multiplication occurs mainly through vegetative reproduction, whereas sexual reproduction is in the background (Benson and Hartnett, 2006). Thanks to their long rhizomes, *Panicum repens* and *Sorghum halepense* populations grow and spread rapidly (Hossain et al., 1996; Prostko et al., 1997). By contrast, *M. maximus* has short rhizomes (Holm et al., 1977), which do not promote significant population growth and dispersion (Cabrera, 2016). Multiplication by basal division is possible (Salariato et al., 2006), but the cuttings exhibit low survival rates when separated from their mother plants (Cabrera, 2016).

Most invasive plants, such as *M. maximus* (Williams and Baruch, 2000), primarily rely on seed dispersal and seedling recruitment for population establishment and persistence (Ebrahimi and Eslami, 2012). Weed emergence is possible when seeds are non-dormant, and/or when environmental conditions (humidity, temperature and gas exchange) are adequate. Dormancy is the temporary failure of viable seed to germinate under external environmental conditions that later trigger germination, when the restrictive state has ended (Radosevich et al., 2007). In grasses, germination may be inhibited by physical dormancy, that is to say physical factors, as for example seed covering. This rules out the effect of environmental

factors on seed germination (Radosevich et al., 2007). Flower structures (lemma and palea) and seed covering were identified as major factors contributing to physical dormancy (Adkins et al., 2002; Richard et al., 2016). *Megathyrsus maximus* possesses dormant seeds (Smith, 1970; Martins and Silva, 1998). Different techniques were tested to break dormancy, leading to differing results (Smith, 1970; Martins and Silva, 1998). This suggests that differential responses are obtained depending on biotype origin. Whereas in the USA Smith (1970) found that immersion of *M. maximus* seeds in sulphuric acid was the best treatment, in Brazil (Martins and Silva, 1998) found better responses when seeds were exposed to thermal treatments.

Among the environmental conditions that affect seed germination, temperature is the most important one in the case of non-dormant seeds. Specifically, soil temperature is essential for germination timing and rate (Guillemin et al., 2013). Light can influence the germination of many warm season grasses through the phytochrome system. This environmental factor can explain the stimulating effect of tillage on weed seedling emergence. Many weed seeds that require light for germination normally emerge when they are close to the soil surface (Adkins et al., 2002). Under conventional tillage, a great proportion of seeds remain buried more deeply into the ploughed soil (Ghersa and Martinez-Ghersa, 2000), which keeps them unexposed to light.

Osmotic and salt stress also play an important role, as germination is typically delayed or completely inhibited depending on stress intensity and duration, with seed genetic background also playing a role (Ebrahimi and Eslami, 2012). Ability to germinate under moisture or saline stress conditions is an asset for the species, since these conditions often prevent other species from growing (Javaid and Tanveer, 2014). In Argentina, studying the ability of the seeds of this grass to germinate under water and/or salt stress is important, considering the agroecological distribution of sugarcane in the country (Zuccardi and Fadda, 1985).

There are *M. maximus* biotypes that have become adapted to different soil and environmental conditions worldwide (Holm et al., 1977). In Argentina, no research has been conducted on the effect of environmental factors on *M. maximus* germination. Therefore, this study aims to evaluate the effect of different scarification methods on dormant *M. maximus* seeds, and to determine the influence of environmental factors on the germination of non-dormant seeds:

constant and alternating temperatures, light alternation and continued darkness, and water and salt stress. This information will contribute to the development of new sugarcane management strategies and the improvement of already existing ones.

2 MATERIALS AND METHODS

2.1 Seed source and preparation

Megathyrus maximus seeds - Mature caryopses that were surrounded by two glumes were collected in March 2014, by shaking panicle-type inflorescences gently. The collection of caryopses, hereafter called seeds, came from plants that had grown in sugarcane fields in Tucumán, Argentina (26°43'55" and 27°46'38"S longitude, and 65°15'33" and 65°34'13"W latitude). They were air-dried, and then stored in paper bags at 18 ± 2 °C and low relative humidity (15%) until trials began in June 2014. Before starting the study, visibly damaged seeds were excluded and visibly viable seeds were surface sterilized in a 0.5% sodium hypochlorite solution for 10 min, and then rinsed with tap water for 5 min (Ramirez et al., 2014).

2.2 Initial seed dormancy test

A test was first carried out to corroborate that freshly harvested *M. maximus* seeds were dormant (data not shown). Subsequently, the efficiency of chemical, thermal and mechanical treatments in breaking dormancy was tested as follows:

Seeds were immersed in concentrated (95%) sulphuric acid for:

- 1) 3 min;
- 2) 5 min;
- 3) 10 min.

In all the cases, the treatment was followed by immersion in tap water for 9, 15 and 30 min, respectively.

- 4) Seeds were watered with a 0.2% potassium nitrate solution.
- 5) Glumes were removed by rubbing the seeds with sandpaper blocks (sandpapering).
- 6) Glumes were extracted by hand.
- 7) Seeds were first immersed in hot water (70 °C) for 5 min, and then in tap water for 2 min (thermal shock).
- 8) Seeds were kept at 40 °C for 5 h.

9) Some seeds did not undergo scarification and were used as a control (Martins and Velini, 1997; Martins and Silva, 1998; Ramirez et al., 2014).

2.3 General protocol for germination tests

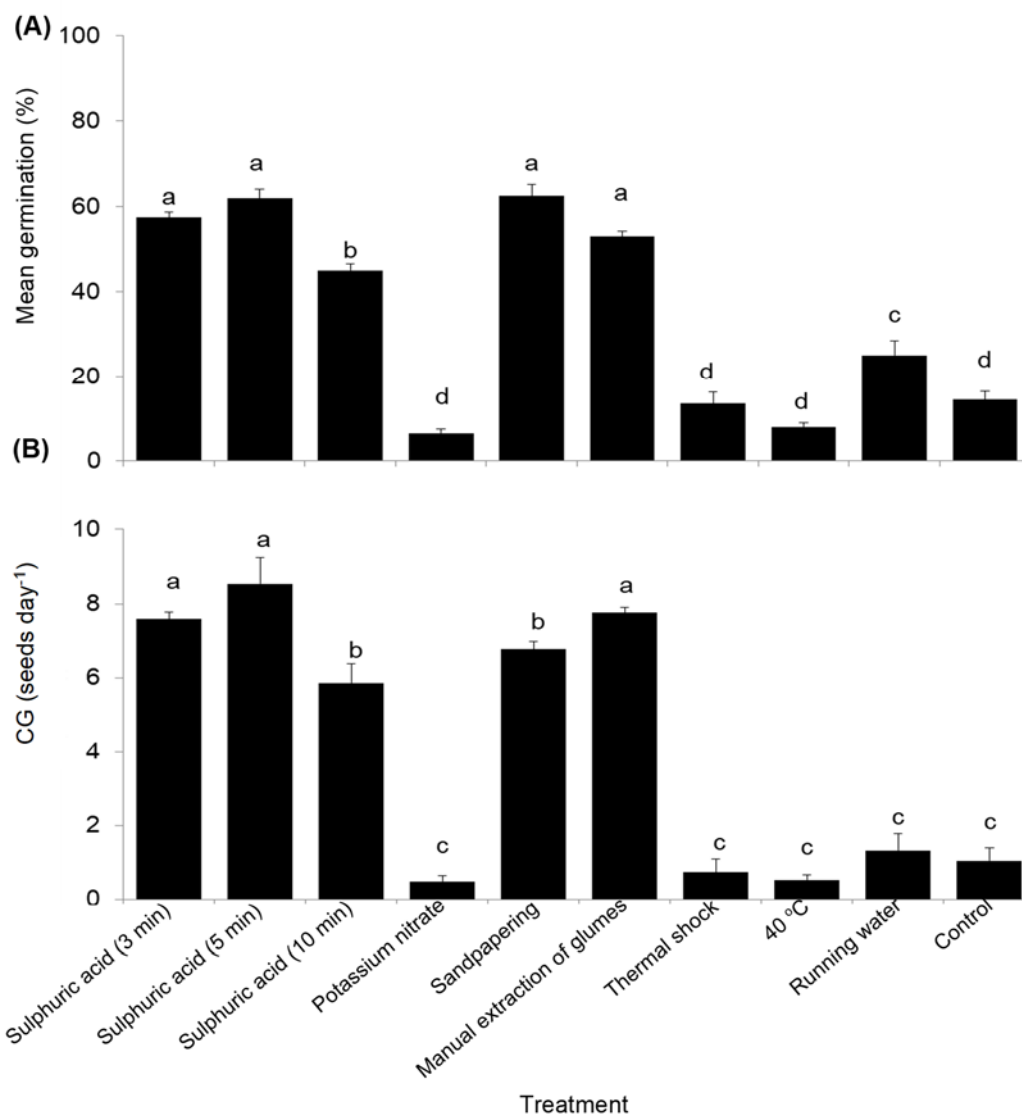
According to the results of the initial seed dormancy test, the main barriers to germination seemed to be the glumes. Therefore, for all germination tests, glumes were removed through immersion in concentrated (95%) sulphuric acid for 5 min, followed by washing with deionized water for 15 min (Figure 1). Then, 50 seeds were placed on 9 cm diameter Petri dishes containing two pieces of Whatman No.1 filter paper, moistened with 2 mL of distilled water, or with solutions having different salt concentrations or osmotic potentials. The Petri dishes were sealed with parafilm (to avoid moisture loss) and kept in cabinet incubators at fluctuating day/night temperatures of 35/15 °C, with a 12 h light photoperiod, except in the study of the effect of light and temperature. Light in the cabinet incubators was provided by cool white fluorescent tubes, with a $35 \mu\text{mol m}^{-2} \text{s}^{-1}$ irradiance. Humidity was kept constant by adding distilled water. Germination was recorded every day for a 15 day period, with seeds being considered germinated when their emerged radicle was at least 2 mm long. Germinated seeds were removed after each count, and the remaining seeds, which had not germinated, were tested for viability at the end of each trial, using tetrazolium tests.

2.4 Effect of temperature and light

Optimal temperature and light conditions for germination were evaluated in cabinet incubators, with both a 12 h light/12 h dark, and a 24 h dark photoperiod. With both, temperatures were kept constant at 10, 15, 20, 25, 30, 35, 40, and 42°C, but they were also alternated between the following values: 20/10 °C, 25/15 °C, 30/20 °C, 35/15 °C and 35/25 °C. For germination in complete darkness, dishes were wrapped in an aluminium foil layer and placed in black plastic bags. Germinated seeds were counted at the end of the trial.

2.5 Effect of water stress

The effect of water stress on germination was evaluated by incubating *M. maximus* seeds in solutions with different osmotic potentials: 0, -0.2, -0.4, -0.6, -0.8, and -1.0 MPa. These were prepared by dissolving polyethylene glycol 6000 in distilled water. The solutions and filter papers were renewed every 2 days.



Vertical bars represent the standard error of the mean. Different lowercase letters above columns indicate significant differences among treatments, including the control (at $P=0.05$).

Figure 1 - Effects of different scarifying treatments on mean germination percentage (A) and CG (coefficient of germination) (B) of *Megathyrsus maximus* seeds.

2.6 Effects of salt stress

The effect of salt stress on germination was evaluated by incubating *M. maximus* seeds in 0, 10, 30, 50, 70, 90, 110, 130, 150 and 200 mmol L⁻¹ sodium chloride solutions (NaCl). The solutions and filter papers were replaced every 2 days.

2.7 Data analysis

For all experiments, mean germination percentage and coefficient of germination (CG) were calculated. CG represents the number of germinated seeds per day and calculates seed germination speed. High CG values mean that a seedling sample is more vigorous than another. CG was calculated with the following mathematical expression (Maguire, 1962):

$$CG = (G_1/N_1) + (G_2/N_2) + \dots + (G_n/N_n)$$

where: CG = coefficient of germination; G = number of germinated seeds in each count; N = number of days elapsing between imbibition and each count.

All experiments were carried out twice, with five replicates per treatment. A completely randomized split-plot design was used in the temperature and light test. The main plots were allotted to constant and alternating temperature tests, and the sub-plots were used for studying the effect of light. The rest of the trials presented a completely randomized design. Mean germination percentage and CG obtained in the dormancy and in the temperature and light tests were analysed using generalized linear models. A binomial distribution was considered for mean germination percentage through the logit linking function, and a normal distribution was considered for CG with an identity linking function. The 0.05% DGC test was

used to evaluate differences among treatment averages (Di Rienzo et al., 2013) with $P < 0.05$. This test uses the multivariate technique of cluster analysis. To determine water and salt stress effects on mean germination percentage, non-linear regression models were used. For CG response, linear and quadratic regressions were considered. The best model was chosen on the basis of the lowest AIC (Akaike Information Criterion) value and an appropriate distribution of residues. The data from all the experiments were analysed using Infostat and R software (Di Rienzo et al., 2013; R Core Team, 2015).

3 RESULTS AND DISCUSSION

3.1 Initial seed dormancy test

With regard to effective techniques for breaking dormancy, the best ones were physical and chemical scarification. The highest mean germination percentages were obtained with immersion in sulphuric acid for 3 and 5 min (57% and 62%, respectively), manual extraction of the glumes (53%), and sandpapering (47%). The 10 min immersion in sulphuric acid treatment showed lower intermediate values (45%) (Figure 1A). CG showed similar results with both 3 and 5 min immersion in sulphuric acid (7.6 and 8.5 seeds day⁻¹, respectively) and manual extraction of glumes (7.8 seeds day⁻¹). These treatments showed the highest values with no significant differences among them. The 10 min immersion in sulphuric acid and sandpapering treatments presented significantly lower values than the other treatments (5.9 and 6.8 seeds day⁻¹, respectively), and significantly higher values than the control (1.0 seeds day⁻¹) (Figure 1B).

The way in which the seeds responded to the different treatments reveals the importance of seed covering for *M. maximus* germination. This is in agreement with previous studies that showed that in tropical grasses, like *Panicum virgatum* or *Sporobolus phleoides*, seed covering was responsible for germination inhibition (Duclos et al., 2014; Richard et al., 2016). The seed tissue enclosing the embryo plays a primary role in regulating germination and dormancy (Richard et al., 2016). It prevents both gaseous exchange and radicle sprout (Adkins et al., 2002). When sulphuric acid or sandpapering partially removes the seed covering, the seed is then ready for the soaking process that enables germination. This behaviour has also been observed in grasses like *Sorghum halepense* and *P. virgatum* (Duclos et al., 2014). In our study, manual extraction of glumes showed similar results to those obtained with

the sulphuric acid and sandpapering treatments, suggesting that in *M. maximus*, dormancy is strongly associated with the presence of glumes.

Regarding the other treatments, seeds of the Argentine biotype watered with a 0.2% potassium nitrate solution, kept at 40 °C for 5 h, or given a thermal shock (5 min in water at 70 °C), presented the lowest mean germination percentages (between 13% and 6%), like the control (Figure 1A). CG values for these treatments were also similar to those of the control (Figure 1B). Nitrogenized substances and thermal treatments stimulated mean germination percentages in other populations of this weed (Martins and Silva, 1998). In Brazil, for example, mean germination percentage increased by 7% and 13.5% with nitrogenized substances and thermal treatments, respectively (Martins and Silva, 1998).

All in all, considering that manual extraction of glumes and chemical treatments with sulphuric acid broke dormancy to similar extents, it is very likely that the main barriers to *M. maximus* seed germination are the glumes.

3.2 Effect of temperature and light

Megathyrsus maximus showed a great ability to germinate under a wide range of conditions. Mean germination percentage differed according to the interaction between temperature and light, which was significant ($P < 0.001$) (Table 1). In the 12 h light photoperiod tests, the treatments with the highest mean germination percentages (between 73% and 61%) were the ones at 35/25 °C, 25 °C, 30/20 °C, 25/15 °C, 20/10 °C, 30 °C, and 35/15 °C. Total darkness did not inhibit *M. maximus* germination, and the highest percentages were 76%, 65% and 63%, recorded at 35/25 °C, 20/10 °C, and 30/20 °C, respectively. As for CG, the best treatments were the ones at 35 °C, 30 °C, 35/25 °C, 30/20 °C, 25/15 °C and 35/15 °C, giving CG values which ranged between 14.35 and 8.27 seeds day⁻¹. These results were also found for *P. virgatum* (Duclos et al., 2014). In contrast, *Panicum dichotomiflorum* and *Panicum capillare* did not germinate in total darkness (Taylorson, 1980). Clearly, there are different responses even in the case of closely related species.

M. maximus germination under a 12 h light photoperiod and in total darkness was low at 15 °C (27% and 39%, respectively), and did not even occur at 10 °C and 42 °C. For these treatments, CG values were 1.54, 2.40 and 3.17 seeds day⁻¹, respectively (Table 1). A similar pattern was recorded for other

Table 1 - Mean germination percentage (means ± s.e.m.) and coefficient of germination (means ± s.e.m. in days) of *Megathyrus maximus* under different temperatures and light regimes

Temperature (°C)	Germination (%)		CG (days)
	Light (12 hours)	Darkness (24 hours)	Light (12 hours)
10	-	-	-
15	27 ± 2.4 d	39 ± 1.3 c	1.54 ± 0.1 c
20	49 ± 2.9 b	52 ± 0.9 b	2.40 ± 0.1 c
25	71 ± 1.0 a	40 ± 1.7 c	8.24 ± 0.8 b
30	62 ± 2.1 a	51 ± 1.6 b	13.15 ± 0.5 a
35	56 ± 1.5 b	47 ± 3.9 b	14.35 ± 1.4 a
40	7 ± 4.0 e	5 ± 1.3 e	0.80 ± 0.5 c
42	-	-	-
20/10	65 ± 2.6 a	65 ± 5.8 a	3.17 ± 0.3 c
25/15	67 ± 7.5 a	51 ± 1.3 b	8.48 ± 0.5 a
30/20	70 ± 3.7 a	63 ± 3.3 a	10.41 ± 0.5 a
35/15	61 ± 0.9 a	48 ± 1.4 b	8.27 ± 0.5 a
35/25	73 ± 2.5 a	76 ± 2.22 a	11.52 ± 0.9 a

Means in a column followed by the same letter are not significantly different according to the DGC test, at a 0.05 level. CG was not measured in complete darkness.

perennial tropical grasses, such as *Sporobolus indicus* and *Melinis repens* (Stokes et al., 2011; Rana et al., 2012).

Our results suggest that *M. maximus* could germinate under temperature and light conditions generated by sugarcane canopy or by crop residues in spring and summer. However, in autumn and winter, low temperatures might affect the germination process negatively.

3.3 Effect of osmotic stress

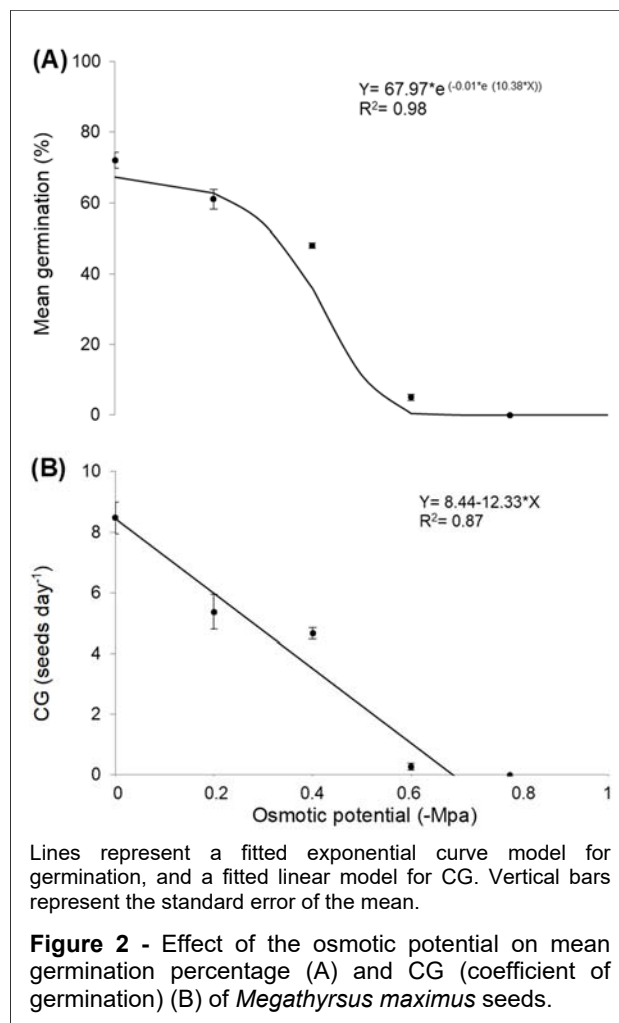
Megathyrus maximus seed germination followed an exponential model. Mean germination percentage decreased from 67% to 4% as water stress intensified between the potentials 0 and -0.6 MPa. Germination was completely inhibited at -0.8 MPa. The osmotic potential required for inhibiting 50% of germination was -0.54 MPa (Figure 2A). A linear regression equation was fitted to the CG data, since values decreased as osmotic potential diminished. The highest value (8.44 seeds day⁻¹) was obtained when there was no water stress, and the lowest value (1.04) was reached at -0.6 Mpa (Figure 2B). It has been reported that once *M. maximus* germinates and plants are well established, they are tolerant to brief drought spells. Moreover, they are well adapted to soils that are well-drained, fertile and which preferably have a sandy loam texture (Holm et al., 1977).

This behaviour was also recorded in other weed species adapted to sandy soils, such as *S. indicus* and *M. repens* (Stokes et al., 2011; Rana et al., 2012). Drought plays an important role not only in

determining germination rates, but also in influencing seedling development. If the seeds of these species germinate under a low water potential, seedling establishment might fail if drought continues (Van den Berg and Zeng, 2006). Instead, if the seeds do not germinate until the levels of humidity are appropriate, there is a strong likelihood that the seedlings will survive (Evans and Etherington, 1990). There are associations between rain or water availability and germination (Javaid and Tanveer, 2014). In Argentina, *M. maximus* germination is successful in irrigated sugarcane fields, whereas in non-irrigated plots it depends on rainfall, which is usually abundant in summer, with average values reaching up to 900 mm per year (Zuccardi and Fadda, 1985).

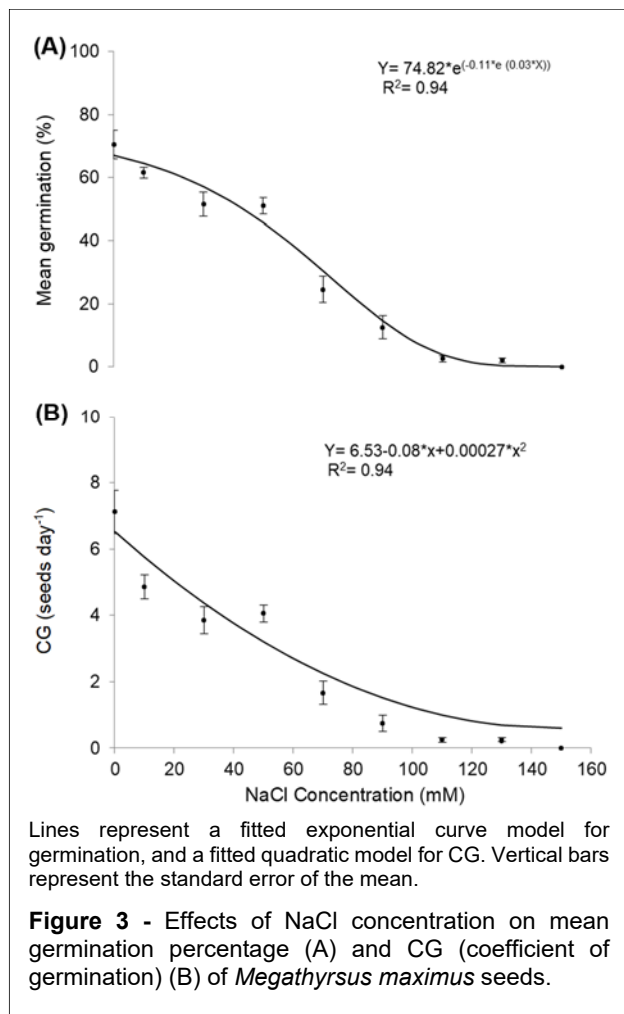
3.4 Effects of salt stress

A decreasing mean germination percentage was observed as NaCl concentration increased from 0 to 200 mmol L⁻¹. Mean germination percentage in the control treatment was 70%. Germination was higher than 50% at NaCl concentrations between 0 and 45 mmol L⁻¹, but it diminished by up to 2% at 130 mmol L⁻¹, and was completely inhibited at 150 mmol L⁻¹ (Figure 3A).



Lines represent a fitted exponential curve model for germination, and a fitted linear model for CG. Vertical bars represent the standard error of the mean.

Figure 2 - Effect of the osmotic potential on mean germination percentage (A) and CG (coefficient of germination) (B) of *Megathyrus maximus* seeds.



The relationship between *M. maximus* CG and salt concentration was described with a quadratic regression model. A decreasing CG was observed as NaCl concentrations increased. Control treatment CG was 7.12 seeds day⁻¹. At concentrations ranging between 10 and 70 mmol L⁻¹, CG decreased from 4.86 to 1.67 seeds day⁻¹, and amounted to less than 1 seed day⁻¹ with 90 to 130 mmol L⁻¹ NaCl (Figure 3B). Evidence found so far points to *M. maximus* not being a salt stress tolerant species. In general, maximum salt stress tolerance in grasses occurs with concentrations between 250 and 350 mmol L⁻¹ (Morgan and Myers, 1989). This effect seems to be more noticeable in CG than in mean germination percentage. In marginal sugarcane areas in Argentina, soil salt concentration fluctuates between 5 and 50 mmol L⁻¹ (Zuccardi and Fadda, 1985), hence *M. maximus* germination would be possible.

It should be taken into account that the effect of salts on germination is conditioned by other factors, such as humidity and soil texture, with the latter having a great influence on ion toxicity through soil cationic exchange capacity (Muscolo et al., 2013). Thus, it is necessary to consider salt stress in combination with these other factors when evaluating if a given area is suitable for *M. maximus* establishment and growth.

This work provides information about the conditions necessary for *M. maximus* seed to germinate successfully and exhibit good CG values, while also showing how the dynamics of this process is affected by extreme conditions. The available evidence suggests that glumes are most responsible for seed dormancy. In addition, it can be pointed out that the interaction between light and temperature under crop canopy or underneath its residues in certain sugarcane areas in Argentina would promote *M. maximus* germination. Lastly, as far as hydric and salinity stress are concerned, although *M. maximus* has proven not to be tolerant to these types of stress, its ability to germinate under conditions of up to a 130 mmol L⁻¹ concentration and a -0.6 MPa osmotic potential ensures its germination in sugarcane fields.

5 CONTRIBUTIONS

DCC: data collection and drafting of the article; MP: data analysis and interpretation; MTS: design of the work and critical revision of the article; SC: critical revision of the article and final approval of the version to be published.

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