Emirates Journal of Food and Agriculture. 2020. 32(8): 577-582
doi: 10.9755/ejfa.2020.v32.i8.2134
http://www.ejfa.me/

RESEARCH ARTICLE

Effect of salinity stress on quinoa germination. Influence of ionic and osmotic components

Sebastián Edgardo Buedo[a]*, Juan Antonio González[a]

[a]*Fundación Miguel Lillo, Instituto de Ecología, Miguel Lillo 251, CP 4000 Tucumán, Argentina*

ABSTRACT

Quinoa is a salinity tolerant species that can be used as a complementary crop in saline soils in many parts of the world. Previous studies, mostly referred to the influence of sodium chloride, have shown that according to the genetic material there are different salinity degrees of tolerance. In general, germination decreases with increasing salinity. However, there are few quinoa studies related to the components of saline stress (ionic and osmotic factors). In this study, the influence of both factors, in the presence of NaCl and KCl salts on CICA Var cultivated in the Argentina Northwest was evaluated. The seeds were germinated under different salt concentrations (0, 100, 200, 300, 400 mM NaCl and KCl) and in PEG_{8000} in solutions osmotically equivalent to the concentrations of sodium and potassium salts. The results showed that up to 200 mM of NaCl and KCl, germination reached values higher than 90% and after 300 mM of salts the rate and final germination decreased. The ionic factor of both salts has the greatest influence on germination. This result can be explained by the physiological adjustment that this variety, originally from the mountainous area of Peru, displayed against the edaphic and microclimatic conditions of the cultivation site in the Argentine Northwest (1,995 m asl).

Keywords: Lonic; Osmotic; Quinoa; Salinity; Tolerance

INTRODUCTION

Even though quinoa (*Chenopodium quinoa* Willd) is a halophyte species (Adolf et al., 2012; Ruiz et al., 2014) it shows different degrees of salinity tolerance and water stress depending on the ecotype studied (Ruiz et al., 2015; Causin et al., 2020). These different degrees of tolerance allow the species to be used under different edaphic conditions along an altitudinal or latitudinal gradient in many parts of the world. It is estimated that 800 million hectares of arable land around the world are currently affected by salinity (FAO, 2008) and that due to the effect of climate change plus inappropriate agricultural practices, this area could increase during the present century (Fedoroff et al., 2010). These new conditions put world food security at risk (Fedoroff et al., 2010). Thus, salt stress stands as one of the environmental factors with a strong influence on all crops, since it could limit both their development and productivity. Considering that the vast majority of traditional crops correspond to glycophyte species (Munns, 1993), the need arises to seek new perspectives and / or face new agricultural approaches in order to face this problem. Against this background, the quinoa crop represents an alternative for supporting different degrees of salinity in the soil and being able to grow under extreme conditions (Mujica et al., 2001). Since it has been observed that in field conditions the germination of quinoa is relatively low (around 20%), making it necessary to use many seeds to obtain an acceptable germination in terms of plants per hectare (Boero et al., 2000). This situation contrasts with the germination obtained in the laboratory, which is greater than 90%, depending on the variety used (Boero et al., 2000; González and Prado, 1992). The low percentages of germination obtained in the field have led to the formulation of several hypotheses referring to the effects of salinity, low nighttime and high daytime temperatures, drought, or the combination of these factors (González and Prado, 1992; Prado et al., 2000; Koiro and Eisa, 2008).

Munns et al. (1995) and Zhu (2003) postulated that decrease in germination caused by salinity is the result of the joint action of two stressors: the water, produced by the osmotic effect of soil salt (osmotic dehydration) and the toxic one derived from the excessive intakes of

***Corresponding author:**
Sebastián Edgardo Buedo, Fundación Miguel Lillo, Instituto de Ecología, Miguel Lillo 251, CP 4000 Tucumán, Argentina.
E-mail: sebuedo@lillo.org.ar

Received: 14 May 2020; **Accepted:** 28 July 2020

ions (cations and anions) such as Na^+ and Cl^- into cells. In halophyte plants the decrease in germination is mainly due to the low osmotic potential of the soil, since the absorption of ions by the cells is limited or efficiently regulated by the metabolism of the plant (Adolf et al., 2012). In quinoa, there is little background that addresses the relative contribution of each of the aforementioned factors (osmotic and toxic) to the overall effect produced by salt stress such as the studies by Delatorre-Herrera and Pinto (2009), who studied 4 Chilean genotypes exposed to increasing concentrations of NaCl and Panuccio et al. (2014) who in the Titicaca variety, in addition to exposed it to increasing concentrations of NaCl, also did it with KCl. The importance of this type of study lies in the fact that, as demonstrated by Koyro and Eisa (2008), the effect of the sodium ion affects not only germination but also seed yield and quality. This is why, in this context, the following study objectives are proposed: i) to evaluate the effect that different concentrations (0, 100, 200, 300 and 400 mM) of NaCl and KCl produce on the germination response, ii) Determine the proportion in that the ionic and osmotic component contribute to the total effect of sodium and potassium salts. What will allow to characterize quinoa var. CICA in terms of resistance to osmotic or ionic factor of saline stress.

MATERIAL AND METHODS

Ch. quinoa CICA Var. seeds were used for germination tests, which were cultivated during the last 20 years in the experimental field of the National Institute of Agricultural Technology (INTA), located in Encalilla (Amaicha del Valle, Tucumán, 26° 36' S, 65° 55' O, Argentina) at 1,965 m asl.

Germination tests were carried out with both NaCl and KCl at concentrations of 0, 100, 200, 300 and 400 mM in growing medium. For this, petri boxes of 5 cm diameter were cleaned and rinsed with distilled water. Seeds of uniform size were selected. We evaluated four replicates of 50 seeds for each treatment. Germination was also evaluated with polyethylene glycol of molecular mass 8000 (PEG_{8000}) in solutions osmotically equivalent to the concentrations of the sodium and potassium salts. The ionic and osmotic effect of the salts was calculated in those saline concentrations that caused a decrease in germination above 50%. The calculations were made according to Munns et al. (1995).

Before incubation, the seeds were sterilized with a 2% sodium hypochlorite solution for 2 minutes and immediately rinsed with distilled water three times and dried on filter paper. After this sterilization they were germinated using a 2 ml volume of the NaCl and KCl solutions to hydrate the seeds at the beginning of each treatment. There was no further addition of these solutions. The incubation temperature was 28 °C, in an electronically controlled chamber (±1 °C). Germinated seed counts were performed every 2 hours and those with a radicle of length equal to or greater than 2 mm were considered as such. The total incubation time was 20 hours for both treatments.

The osmotic potential of the saline solutions (NaCl and KCl) was calculated applying the Van't Hoff equation as proposed by Sánchez-Díaz and Aguirreolea (2013).

Determined the osmotic potential of the saline solutions, the corresponding calculations were made to determine the amounts of PEG_{8000} to be used in each treatment. For this, the procedure of Parmar and Moore (1968) was followed.

With germination data in the different treatments (NaCl, KCl and PEG_{8000}) germination curves were performed as a function of time. These were fitted to a non-linear model (sigmoid curve), thus obtaining its graph and its corresponding equation. From the equation of the curves generated by the model, the T_{50} was calculated, which is the time at which 50% of the germination occurs.

The treatments with NaCl and KCl were taken as factors and the concentrations of the salts (0, 100, 200, 300 and 400 mM) as factor levels. The final germination percentage data were applied to the analysis of variance (ANOVA). When the differences were significant, the Tukey test was applied with a significance level of 0.05%. OriginPro 9.0 (SR1) was used to adjust the germination data as a function of time. The R version 3.4.4 program (R Development Core Team, 2018) was also used for the analysis of data variance (ANOVA) and the agricolae package (De Mendiburu, 2009), for analysis of normality and heterogeneity of the data.

RESULTS

Efect of NaCl and KCl on germination

Fig. 1 A and B show the sigmoid curves adjusted to the germination percentages in NaCl and KCl solutions, respectively. In both cases, a triphasic pattern in germination was observed: Phase I from the start to 6 h of incubation, the control for both factors reached an approximate 10% germination, while the other levels of both factors ranged between 0 and 5% according to concentration. In phase II, between 6 and 14 h, exponential growth was recorded in the germination percentages. In both factors (Na and K), germination decreased as the concentration of the considered ion increased.

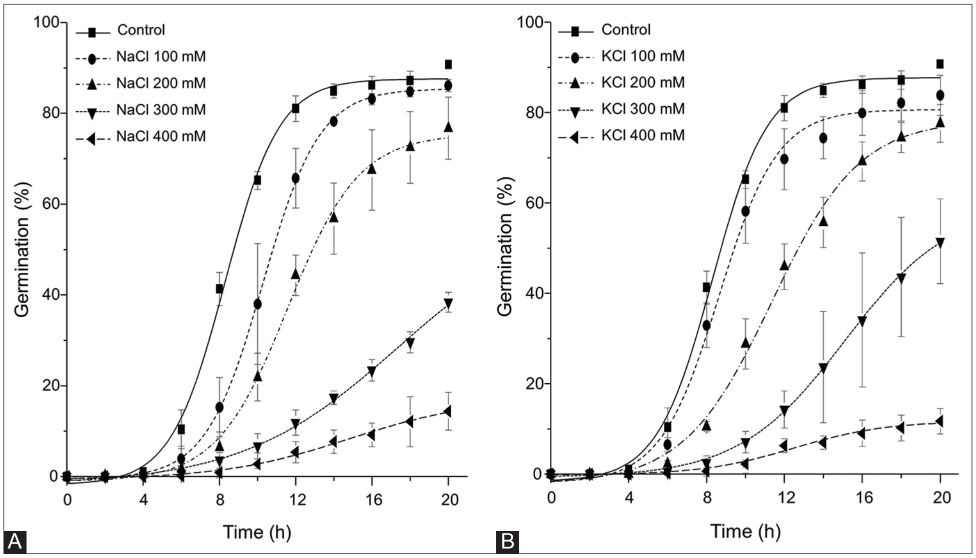

Fig 1. A & B. germination curves of *Ch. quinoa* var CICA as a funtion of time exposed to different level of salinity (NaCl y KCl).

Finally, phase III, between 14 and 20 h of incubation, comprised the asymptotic part of the curve and corresponded to the moment when the maximum germination percentage was reached.

The T_{50}, which corresponds to the time required to reach 50% of the maximum germination, is summarized in Table 1, its analysis shows that the time required to reach the T_{50} increased gradually depending on the level of the factor.

The analysis of variance showed a gradual decrease in the final percentages of germination in the levels of both factors with respect to the control (PG = 90.4%), at 100 mM a non-significant decrease of 4.3% and 6.6% in the factors with NaCl and KCl respectively. At the concentration of 200 mM of both salts, a significant reduction ($p \leq 0.05$) of 13.7% and 12.8% (according to Table 1) was registered respectively with respect to the control. Between salts there was only a significant difference at 300 mM, with 38.4% of the germination power for NaCl and 51.5% for KCl (Fig. 2). Finally, at 400 mM the germinative power fell to 14.4% for the NaCl factor and 11.7 for the KCl case.

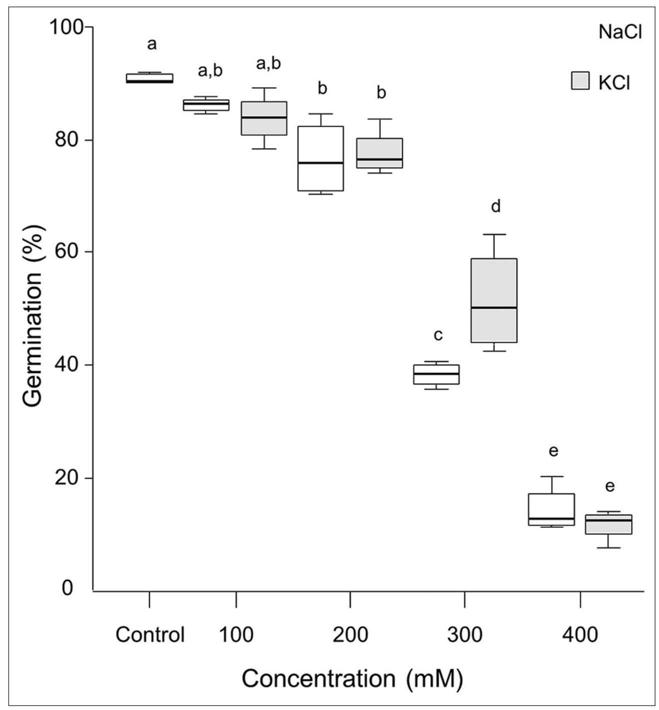

Fig 2. Box-plot of the germination percentages of *Ch. Quinoa* var. CICA for each treatment. *Different letters indicate significant differences* (*Tukey*, $p \leq 0.05$).

Efect of PEG_{8000} on germination

Fig. 3 shows the germination curves obtained with PEG_{8000} at equimolar concentrations at the levels of the Na and K factors. The curves obtained are similar to those obtained with NaCl and KCl, but in some cases a certain reduction in the duration of the stages is observed. At the equiosmlarities of 100 and 200 mM of NaCl or KCl, higher germination percentages were obtained than those of the control in distilled water. In the presence of PEG_{8000}, there was no drop in germination power above 50% in any of the levels, which did occur after 300 mM in treatments with Na and K salts (Fig. 4).

Ionic and osmotic effect calculation

The ionic and osmotic effect produced by the corresponding salt was calculated in the PEG_{8000} levels that caused a decrease in the final germination percentage. Table 2 shows the incidence of ionic and osmotic effects on the final percentage of germination. In this case CICA is affected by both types of stress but with a higher incidence of the

Table 1: Final germination porcentaje and T_{50} of *Ch. quinoa* var. CICA for each treatment. *Different letters indicate significant differences* (*Tukey, P*≤0.05) *between the levels of each factor*

Treatment		Control	100 mM	200 mM	300 mM	400 mM
NaCl	Germination (%)	90.4 (1.0)[a]	86.1 (1.3)[a]	76.7 (6.8)[b]	38.4 (2.2)[c]	14.4 (4.2)[d]
	T_{50}	8 (0.3)[a]	10 (0.8)[b]	11 (0.5)[b,c]	15 (0.8)[c,d]	14 (0.5)[d]
KCl	Germination (%)	90.4 (1.0)[a]	83.8 (4.4)[a,b]	77.6 (4.2)[b]	51.5 (9.2)[c]	11.7 (2.8)[d]
	T_{50}	8 (0.3)[a]	9 (0.5)[a]	11 (0.4)[b]	15 (1.2)[b]	12 (0.2)[c]

Table 2: Contribution to decreased germination of *Ch. quinoa* var CICA from the ionic and osmotic effects

Treatment	Concentration (Mm)	Ionic Effect (%)	Osmotic Effect (%)	Total Effect (Ionic+osmotic) (%)	Ratio (Ionic effect/osmotic effect)	Proportion (Ionic effect/total effect)
NaCl	300	42.6	15.1	57.7	2.8	73.8
	400	52.2	31.9	84.1	1.6	62.0
KCl	300	28.1	15.1	43.2	1.9	65.0
	400	55.2	31.9	87.1	1.7	63.3

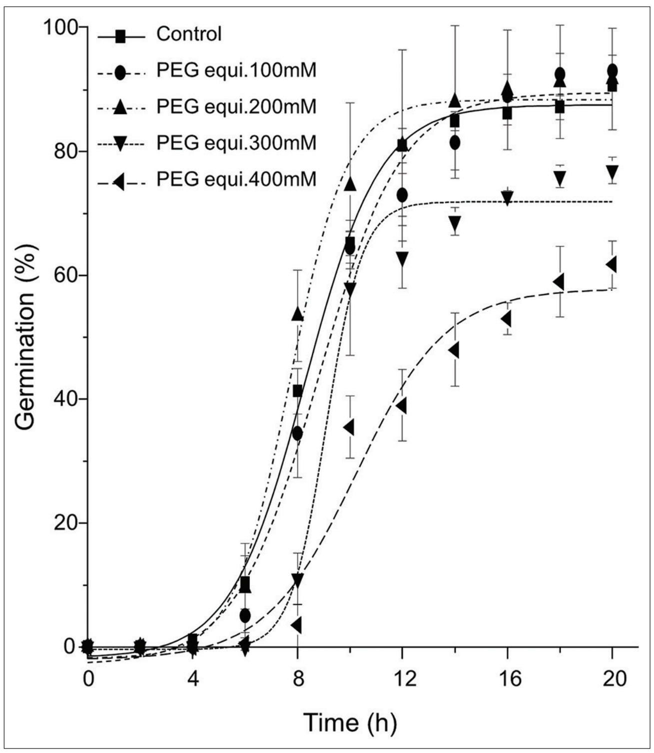

Fig 3. Germination curves of *Ch. quinoa* var. CICA exposed to PEG_{8000} at osmotically equivalent to the concentrations of the sodium and potassium salts.

ionic effect in both concentrations and with both salts. This is clearly reflected in the ionic / osmotic ratio (Table 2).

DISCUSSION

Ungar (1996) postulated that the tolerance of the seeds to salinity should be considered at two levels: 1) the germination power under saline stress conditions and 2) the capacity of the seed to resume the germination process once the salinity was canceled. In relation to the former, our results demonstrate that quinoa can germinate under saline stress conditions and that the percentage and speed of germination are dependent on the level of salinity.

Being quinoa a halophyte species, the first effects due to salinity are revealed from 300 mM (NaCl or KCl) causing a decrease of 52% and 39% respectively. These results are consistent with previous studies carried out on the Sajama variety, which tolerated up to 250 mM of NaCl without affecting the final germination percentage, although the time necessary to reach similar germination percentages was affected (González and Prado 1992; Ruffino et al., 2010). Jacobsen et al. (2003) working with the Kancolla variety obtained up to 75% germination at 57 mS/cm^{-1} (~ 570 mM) after 7 days of incubation. For his part, Ruiz-Carrazco evaluated 4 Chilean genotypes subjected to increasing salinity between 150 and 300 mM NaCl, only one resulted with germination completely inhibited at the highest salt concentration; the rest showed reductions between 15% and 30% of the final germination percentage (Ruiz Carrazco et al., 2011). On the other hand, Gonzalez and Prado (1992) demonstrated the ability of quinoa to resume the germination process once the salinity stress has been eliminated. Thus, under the Ungar (1996) hypothesis, quinoa is a salinity-tolerant species.

Furthermore, it is known that K^+ is an essential macronutrient for plants (Bonilla, 2013), representing the most abundant cation in the vacuole and the main osmolyte in the cell. The background in the literature regarding the effect of this cation on the germination of quinoa seeds is scarce. Panuccio and collaborator (2014) in the Titicaca variety carried out tests with KCl using concentrations between 2.54 and 10.16 mM, they reported reductions in germination power ranging from 4% to 14%; being significant those that occur at concentrations of 7.62 and 10.16 mM. In turn, they did not observe changes in the T_{50} value for all the concentrations tested. However, in the present study, the CICA variety was tolerant to

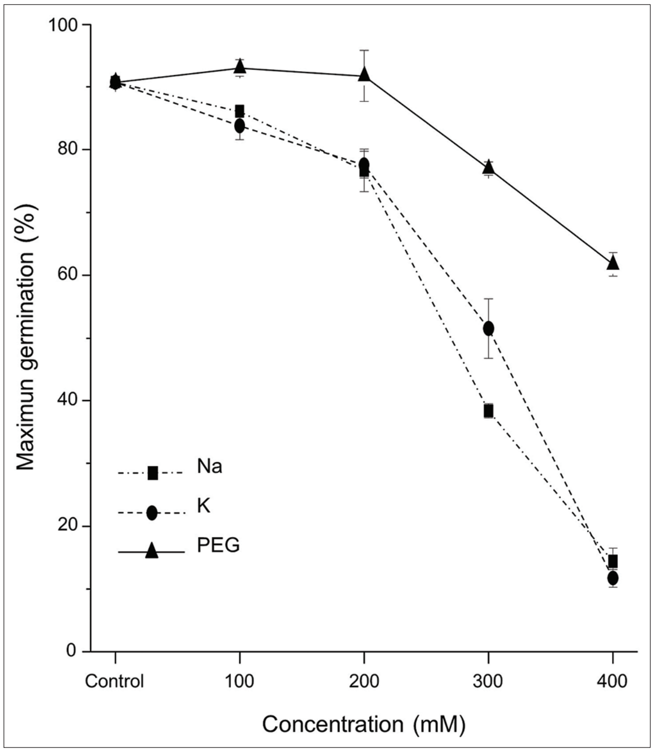

Fig 4. Maximun germination of *Ch. quinoa* var. CICA exposed to increasing levels of sallinity (NaCl and KCl) and equivalent of PEG_{8000}.

concentrations higher than those used by Panuccio (Panuccio et al., 2014). Thus, in the presence of 100 and 200 mM KCl, the germinative power of var. CICA showed little significant reductions, 7% and 13% respectively. While, at 200 mM an increase of 2 h was obtained in the T_{50} with respect to the control; even so, the times recorded for this variety are much lower than those reported for the Titicaca variety. At higher concentrations (300 and 400 mM) KCl reduces the final germination percentage and lengthens the duration of the process, similar to what happens in the presence of NaCl at the same concentrations.

Although some authors support that Na salts are more harmful than K salts (Panuccio et al., 2014). The results of this study revealed that the presence of moderate concentrations (100 and 200 mM) of NaCl or KCl, equally affect the germination rate of quinoa seeds and that only from the 300 mM concentration there is a deleterious effect more pronounced than at the first concentrations. According to Demidchik et al. (2002) the presence of high concentrations of NaCl in the medium induce alterations in the absorption of K^+, causing a reduction in the cellular levels of this ion; which is detrimental to the plant by causing stem weakness, growth retardation due to loss of turgidity and greater sensitivity to attack by pathogens. Therefore, maintaining an optimal K^+/Na^+ ratio is essential to achieve better tolerance or adaptation to salt stress (Munns and Tester, 2008).

The excess of salts in the soil induces alterations in cellular metabolism not only due to the toxicity of the absorbed ions, but also due to the water restriction (saline drought) that the plant undergoes (Tuteja, 2007). In this context, this paper also analyzed the relative contributions of the osmotic and ionic effects of salt treatments on germination. The results obtained showed that at high concentrations (300 and 400 mM) of NaCl or KCl, the osmotic effect was the one with the lowest incidence on the germination process of the CICA variety, with values of the ionic effect/osmotic effect ratio between 1.6 and 2.8 (Table 2). In accordance with this result, Delatorre-Herrera and Pinto working with 4 Chilean varieties of quinoa (Amarilla, Roja, Hueque and Pucura), reported for 3 of them values of 1.1 to 1.8 for this relationship in the presence of 400 mM de NaCl (Delatorre Herrera and Pinto 2009). Contributions of the osmotic effect of 75% in the presence of NaCl and 66% when KCl is present, were reported for the Titicaca variety (Panuccio et al., 2014).

CICA, is a Peruvian variety obtained from Amarilla de Marangani at 3,600 m asl. Taking into account its origin, a greater contribution of the osmotic effect on the ionic one would be expected as reported by other authors (Delatorre Herrera and Pinto, 2009). However, it should be mentioned that the CICA seeds used in this study come from crops grown in a mountain valley in the province of Tucumán (Argentina) at 1,995 m asl for 20 years. Therefore, our results would be a demonstration of the plasticity of this variety to the new edaphic and microclimatic conditions. The soil of the cultivation site was informed to have pH= 8.4 and EC= 2.0 dS m^{-1} (Erazzu et al., 2016).

The results of this study, together with those obtained by other researchers, reveal the existence of complex interactions between the ionic and osmotic effects of salt during the germination of quinoa seeds. Undoubtedly, these effects would be related to the origin of the varieties used, as Delatorre-Herrera and Pinto (2009) demonstrated.

CONCLUSION

The results obtained suggest that quinoa in the CICA variety is sensitive to the presence of Na^+ and K^+ ions in the growing medium, both affecting germination in the same way, which would prevent achieving acceptable levels of emergency when cultivated in saline fields despite that adult plants can survive and tolerate salinity very well as other authors report. However, this variety behaves as drought tolerant, since it was the osmotic effect that contributed the least to the total effect of the salts, so this variety could be recommended for planting in soils of the NOA region (Argentine Northwest) affected by the lack of water and slightly saline.

Funding

This work was funded by Miguel Lillo Foundation (Miguel Lillo 251, Tucumán, Argentina) Project B-0004-1.

ACKNOWLEDGMENTS

The authors thank Dr Fernando Prado for his valuable contributions to this research.

Author Contributions

Buedo S.E. performed the germination assays, statistical analyses, helped to interpret the results and prepareed the manuscript. González J.A. conceptualized the idea, designed and coordinated the experiments, helped to interpret the results and revised and improved the manuscript. Funding acquisition and Project administration was carried out by González J.A.

REFERENCES

Adolf, V. I., S. E. Jacobsen and S. Shabala. 2012. Salt tolerance mechanisms in quinoa (*Chenopodium quinoa* Willd.). Environ. Exp. Bot. 92: 43-54.

Boero, C., J. A. González and F. E. Prado. 2000. Efecto de la temperatura sobre la germinación de diferentes variedades de quinoa (*Chenopodium quinoa* Willd.). Lilloa. 40: 103-108.

Bonilla, I. 2013. Introducción a la nutrición mineral de las plantas. Los elementos minerales. In: J. Azcón-Bieto and M. Talón, (Eds.), Fundamentos de Fisiología Vegetal. 2th ed. McGraw-Hill, Inc., New York, pp. 103-121.

Causin, H. F., D. A. E. Bordon and H. Burrieza. 2020. Salinity tolerance mechanisms during germination and early seedling growth in *Chenopodium quinoa* Willd. Genotypes with different sensitivity to saline stress. Environ. Exp. Bot. 172: 103995.

Delatorre-Herrera, J. and M. Pinto. 2009. Importance of ionic and osmotic components of salt stress on the germination of four quinua (*Chenopodium quinoa* Willd.) selections. Chilean J. Agric. Res. 69: 477-485.

De Mendiburu, F. 2009. Una Herramienta de Análisis Estadistico Para la Investigación Agrícola. Thesis, Universidad Nacional de Ingeniería, Peru.

Demidchik, V., R. J. Davenport and M. Tester. 2002. Non selective cation channels in plants. Annu. Rev. Plant Biol. 53: 67-107.

Erazzú, L. E., J. A. González, S. E. Buedo and F. E. Prado. 2016. Efectos de la densidad de siembra sobre *Chenopodium quinoa* Willd (quinoa). Incidencia sobre variables morfológicas y rendimiento de grano en la variedad CICA cultivada en Amaicha del Valle (Tucumán Argentina). Lilloa. 53: 12-22.

FAO. 2008. Land and Plant Nutrition Management Service, Food and Agriculture Organization. Available from: http://www.fao.org/ag/agl/agll/spush. [Last accessed on 2019 Mar 17].

Fedoroff, N. V., D. S. Battisti, R. N. Beachy, P. J. M. Cooper, D. A. Fischhoff, C. N. Hodges, V. C. Knauf, D. Lobell, B. J. Mazur, D. Molden, M. P. Reynolds, P. C. Ronald, M. W. Rosegrant, P. A. Sanchez, A. Vonshak and J. K. Zhu. 2010. Radically rethinking agriculture for the 21st century. Science. 327: 833-834.

González, J. A. and F. E. Prado. 1992. Germination in relation to temperature and different salt concentration in *Chenopodium quinoa*. Agrochimica. 36: 101-107.

Jacobsen, S. E., A. Mujica and C. R. Jensen. 2003. The resistance of quinoa (*Chenopodium quinoa* Willd.) to adverse abiotic factors. Food Rev. Int. 19: 99-109.

Koyro, H. W. and S. S. Eisa. 2008. Effect of salinity on composition, viability and germination of seeds of *Chenopodium quinoa* Willd. Plant Soil. 302: 79-90.

Mujica, A., S. E. Jacobsen and J. Izquierdo. 2001. Resistencia a factores adversos de la quinua. In: A. Mujica, S. E. Jacobsen, J. Izquierdo and J. Marathee, (Eds.), Quinua (*Chenopodium quinoa* Willd.) Ancestral Cultivo Andino, Alimento del Presente y Futuro. Food and Agriculture Organization, UNA-Puno, CIP, Santiago, Chile, pp. 162-183.

Munns, R. 1993. Physiological processes limiting plant growth in saline soil: Some dogmas and hypotheses. Plant Cell Environ. 16: 15-24.

Munns, R., D. Schachtman and A. Condon. 1995. The significance of a two-phase growth response to salinity in wheat and barley. Aust. J. Plant Physiol. 22: 561-569.

Munns, R. and M. Tester. 2008. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol. 59: 651-681.

Panuccio, M. R., S. E. Jacobsen, S. S. Akhtar and A. Muscolo. 2014. Effect of saline water on seed germination and early seedling growth of the halophyte quinoa. AoB Plants. 6: plu047.

Parmar, M. T. and R. P. Moore. 1968. Carbowax 6000, mannitol, and sodium chloride for simulating drought conditions in germination studies of corn (*Zea mays* L.) of strong and weak vigor. Agron. J. 60: 192-195.

Prado, F. E., C. Boero, M. Gallardo and J. A. González. 2000. Effect of NaCl on growth germination and soluble sugars content in *Chenopodium quinoa* Willd. seeds. Bot. Bull. Acad. Sin. 41: 19-26.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org.

Ruffino, A. M. C., M. Rosa, M. Hilal, J. A. González and F. E. Prado. 2010. The role of cotyledon metabolism in the establishment of quinoa (*Chenopodium quinoa*) seedlings growing under salinity. Plant Soil. 326: 213-224.

Ruiz-Carrasco, K., F. Antognoni, A. K. Coulibaly, S. Lizardi, A. Covarrubias, E. A. Martínez, M. A. Molina-Montenegro, S. Biondi and A. Zurita-Silva. 2011. Variation in salinity tolerance of four lowland genotypes of quinoa (*Chenopodium quinoa* Willd.) as assessed by growth, physiological traits, and sodium transporter gene expression. Plant Physiol. Biochem. 49: 1333-1341.

Ruiz K. B., S. Biondi, R. Oses, I. S. Acuña-Rodríguez, F. Antognoni, E. A. Martinez-Mosqueira, A. Coulibaly, A. Canahua-Murillo, M. Pinto, A. Zurita-Silva, D. Bazile, S. E. Jacobsen and M. A. Molina-Montenegro. 2014. Quinoa biodiversity and sustainability for food security under climate change. A review. Agron. Sustain. Dev. 34: 349-359.

Ruiz, K. B., S. Biondi, E. A. Martínez, F. Orsini, F. Antognoni and S. E. Jacbsen. 2015. Quinoa a model crop for understanding salt tolerance mechanisms in halophytes. Plant Biosyst. Int. J. Dealing Aspects Plant Biol. 150: 357-371.

Sánchez-Díaz, M. and J. Aguirreolea. 2013. El agua en la planta. In: J. Azcón-Bieto and M. Talón, (Eds.), Fundamentos de Fisiología Vegetal. 2th ed. McGraw Hill-Inc., New York, pp. 17-30.

Tuteja, N. 2007. Mechanisms of high salinity tolerance in plants. Meth. Enzymol. Osmosens. Osmosignal. 428: 419-438.

Ungar, I. A. 1996. Effect of salinity on seed germination, growth, and ion accumulation of *Atriplex patula* (Chenopodiaceae). Am. J. Bot. 83: 604-607.

Zhu, J. K. 2003. Regulation of ion homeostasis under salt stress. Curr. Opin. Plant Biol. 6: 441-445.