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EFFECT OF MIXED-SALT SALINITY ON GROWTH AND ION RELATIONS OF A QUINOA AND A WHEAT VARIETY

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ABSTRACT

Salinity is among the most widespread and prevalent problems in irrigated agriculture. Many members of the family Chenopodiaceae are classified as salt tolerant. One member of this family, which is of increasing interest, is quinoa (*Chenopodium quinoa* Willd.) which is able to grow on poorer soils. Salinity sensitivity studies of quinoa were conducted in the greenhouse on the cultivar, “Andean Hybrid” to determine if quinoa had useful mechanisms for salt tolerant studies. For salt treatment we used a salinity composition that would occur in a typical soil in the San Joaquin Valley of California using drainage waters for irrigation. Salinity treatments (EC_e) ranging from 3, 7, 11, to 19 dS m^{-1} were achieved by adding MgSO_4 , Na_2SO_4 , NaCl , and CaCl_2 to the base

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nutrient solution. These salts were added incrementally over a four-day period to avoid osmotic shock to the seedlings. The base nutrient solution without added salt served as the non-saline control solution (3 dS m^{-1}). Solution pH was uncontrolled and ranged from 7.7 to 8.0. For comparative purposes, we also examined Yecora Rojo, a semi-dwarf wheat, *Triticum aestivum* L. With respect to salinity effects on growth in quinoa, we found no significant reduction in plant height or fresh weight until the electrical conductivity exceeded 11 dS m^{-1} . The growth was characteristic of a halophyte with a significant increase in leaf area at 11 dS m^{-1} as compared with 3 dS m^{-1} controls. As to wheat, plant fresh and dry weight, canopy height, and leaf area did not differ between controls (3 dS m^{-1}) and plants grown at 7 dS m^{-1} . Beyond this threshold, however, plant growth declined. While both quinoa and wheat exhibited increasing Na^+ accumulation with increasing salinity levels, the percentage increase was greater in wheat. Examination of ion ratios indicated that $\text{K}^+:\text{Na}^+$ ratio decreased with increasing salinity in both species. The decrease was more dramatic in wheat. A similar observation was also made with respect to the $\text{Ca}^{2+}:\text{Na}^+$ ratios. However, a difference between the two species was found with respect to changes in the level of K^+ in the plant. In quinoa, leaf K^+ levels measured at 19 dS m^{-1} had decreased by only 7% compared with controls. Stem K^+ levels were not significantly affected. In wheat, shoot K^+ levels had decreased by almost 40% at 19 dS m^{-1} . Correlated with these findings, we measured no change in the $\text{K}^+:\text{Na}^+$ selectivity with increasing salinity in quinoa leaves and only a small increase in stems. In wheat however, $\text{K}^+:\text{Na}^+$ selectivity at 3 dS m^{-1} was much higher than in quinoa and decreased significantly across the four salinity levels tested. A similar situation was also noted with $\text{Ca}^{2+}:\text{Na}^+$ selectivity. We concluded that the greater salt tolerance found in quinoa relative to wheat may be due to a variety of mechanisms.

Key Words: Quinoa; Wheat; cv. Yecora Rojo; Salinity; Salt stress; Ion accumulation

INTRODUCTION

Because of increases in global population, world agriculture must produce a greater yield per unit area than ever before and/or more land taken into



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cultivation. Irrigated agriculture takes on a special importance in this regard as it has a high yield per unit area and is less dependent than nonirrigated systems on the uncertainties of weather.^[1] Although accurate data are lacking, current estimates reveal that nearly one-half of all irrigated lands, about 2.5×10^8 ha, are seriously affected by salinity or water logging.^[2] All irrigation waters contain dissolved salts. These salts can concentrate in the root zone as much of the water, but little of the salt, is taken up by the plant. Rhoades and Loveday^[2] calculated that each application of a 100-mm depth of irrigation water containing 500 mg salt L⁻¹ can add 500 kg of salt to each hectare of land. Without proper leaching or drainage to remove this salt, it will increase in the root zone with each irrigation.

With the exception of rice (*Oryza sativa* L.) and corn (*Zea mays* L.), tolerance to salinity in irrigation water is moderate to high among most of the major cereal grains, including sorghum (*Sorghum bicolor* L.), wheat (*Triticum aestivum* L.), triticale (*Triticale spp.*), rye (*Secale cereale* L.), oats (*Avena sativa* L.), and barley (*Hordeum vulgare* L.).^[3] A dicot of increasing interest, quinoa (*Chenopodium quinoa*, Willd), may have potential as a crop on salt-affected land.^[4-6] There are data indicating quinoa is tolerant to salinity.^[7]

Quinoa was first domesticated in the Andes and is now widely grown in the highlands of Chile, Bolivia, Ecuador, Perú, and Northwestern Argentina.^[8-10] While quinoa is less known outside these regions, it has many desirable agronomic traits.^[9]

While the actual and molecular biological mechanisms of plant salt tolerance are largely unknown, it is thought to be associated with lower Na⁺ levels in the tissue.^[11-18] In the case of wheat, Omielan et al.^[16] found salt tolerance is related to the selectivity for K⁺ over Na⁺. Suhayda et al.^[19] found a strong relationship between tissue K⁺:Na⁺ ratio and salt tolerance in barley (*Hordeum vulgare* L.) and suggested this trait could be used as a selection criterion in the breeding of salt-tolerant barley cultivars.

In addition to their function as important grain crops, several members of the family Chenopodiaceae and Gramineae are tolerant of salinity.^[20] Therefore, the present study examined the effects of a mixed-salt salinity on growth and tissue ion levels of quinoa in order to determine if quinoa may have a place in irrigated agriculture where highly saline agricultural drainage waters predominate. For comparative purposes, we examined a semi-dwarf wheat variety, Yecora Rojo, which is thought to be "moderately tolerant".

Thus, this study was undertaken to determine the salt tolerance profile of quinoa and examine its ion uptake relative to a moderately salt tolerant grain, wheat. Based on this comparison, insight into the mechanism(s) of salt tolerance may be possible. We used a mixed-salt salinity using formulations in which Na⁺, SO₄²⁺, Cl⁻, and Mg²⁺ are the predominant ions.



MATERIALS AND METHODS

Plant Material

Seed of a semi-dwarf wheat (*T. aestivum* L. cv. Yecora Rojo) was obtained from Foundation Seed and Plant Materials Service (Davis, CA). Quinoa (*C. quinoa* Willd. cv. "Andean Hybrid") was obtained from Thompson and Morgan (Jackson, NJ). Seeds of both wheat and quinoa were sown in the same tanks on 31 October, 1997 at a depth of 5 to 10 mm into 24 sand tanks in a temperature-controlled greenhouse set at 28°C day/18°C night temperature regime. The greenhouses were located at Riverside, California (33°58'24"N latitude, 117°19'12"W longitude). Light averaged 501 $\mu\text{mol m}^{-2} \text{s}^{-1}$ with a minimum of 100 and a maximum of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the day. Each tank measured $1.2 \times 0.6 \times 0.5$ m deep and contained washed sand having an average bulk density of 1.4 Mg m^{-3} , and an average volumetric water content of $0.34 \text{ m}^3 \text{ m}^{-3}$ at saturation. Seed of each species was sown in two rows spaced 10 cm apart, and the plants were subsequently thinned to a spacing of 3.8 cm within each row, to give 15 plants per row. Plants were irrigated twice daily with a nutrient solution containing the following (in mM): 2.5 Ca^{2+} , 1.25 Mg^{2+} , 15 Na^+ , 3 K^+ , 6.0 SO_4^{2-} , 7.0 Cl^- , 5.0 NO_3^- , 0.17 KH_2PO_4 , 0.050 Fe as sodium ferric diethylenetriamine pentaacetate (NaFeDTPA), 0.023 H_3BO_3 , 0.005 MnSO_4 , 0.0004 ZnSO_4 , 0.0002 CuSO_4 , and 0.0001 H_2MoO_4 made up with City of Riverside, CA, municipal water. This base nutrient solution ($EC_i = 3.0 \text{ dS m}^{-1}$) served as the control treatment. Treatment-replication combinations were irrigated from a 765 L reservoir. Irrigations were of 10 min duration, which allowed the sand to become completely saturated, after which the solution drained into the reservoirs for reuse in the next irrigation. Water lost by evapotranspiration was replenished automatically each day to maintain constant electrical conductivities in the solutions.

Salinization commenced on 4 November 1997 when plants reached the two-leaf stage. Equivalent amounts of salts were added over a four-day period to avoid osmotic shock to the seedlings. These irrigation waters were prepared to simulate the mixed-salt saline drainage waters frequently encountered in the San Joaquin Valley of California. Final ion compositions are shown in Table 1. The final electrical conductivities of the irrigation waters (EC_i) were: 3 (control), 7, 11, and 19 dS m^{-1} . The pH of the solutions was not controlled and ranged from 7.7 to 8.0 across treatments.

Quinoa was harvested near the end of the vegetative stage on 2 January 1998, 56 days following complete salinization. Wheat was harvested 22 December 1997 following 45 days of complete salinization, when most plants were at the jointing or booting stage of development (mean Zadoks scale was 4.7, data not presented). The height to the tallest leaf of each 10 central plants in each row was determined. The



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Table 1. Composition of Mixed-Salt Solutions Used to Irrigate Quinoa and Wheat^a

Salinity Level EC_i (dS m ⁻¹)	Ca	Mg	Na	K	SO ₄	Cl
	Milliequivalents per Liter					
3 (Control)	7.0	4.9	21.5	2.4	21.8	10.6
7	14.6	11.5	50.9	3.4	51.7	24.7
11	20.3	19.6	87.0	3.9	84.0	42.2
19	26.9	37.9	167.8	5.6	150.4	81.3

^aPlants were irrigated twice daily.

plants were then cut at the soil surface and above-ground fresh weights were determined. Leaf area of five plants was determined using a LICOR LI-3000 leaf area meter (Lincoln, NE). Plant tissues were dried at 60°C to a constant weight and weighed.

Plant Ion Analysis

The irrigation waters were analyzed at weekly intervals by inductively coupled plasma optical emission spectrometry (ICPOES) to confirm that target ion concentrations were maintained. Oven-dried shoots were ground and stored in acid-washed vials. Total S, total P, Ca²⁺, Mg²⁺, Na⁺, and K⁺ were measured on nitric-perchloric acid digests of shoot tissue by ICPOES. Chloride was determined by coulometric-amperometric titration.

The K⁺:Na⁺ selectivity was calculated according to Pitman^[21] where

$$S_{K,Na} = \left(\frac{\text{K content}}{[\text{K}] \text{ medium}} \right) : \left(\frac{\text{Na content}}{[\text{Na}] \text{ medium}} \right)$$

The Gapon selectivity constant relates the equivalent fractions of the exchange ions to the activities of the same ions in solution and is usually expressed for Ca–Na exchange. The Gapon was calculated using:

$$K_g = \frac{E_{Ca} a_{Na}}{[E_{Na} (a_{Ca^{2+}})^{0.5}]}$$

As expressed above, E is the equivalent fraction of a given cation and a is the activity of the ion in solution.



Statistical Analysis

Experimental design was a randomized block with six tanks. Main effects of salinity (3, 7, 11, and 19 dS m⁻¹) were evaluated by analysis of variance and General Linear Models procedures using SAS.^[22]

RESULTS

Growth Responses

We found no significant reductions in plant height, leaf area, or fresh weight of quinoa until the electrical conductivity of the irrigation water exceeded 11 dS m⁻¹ (Table 2). The salinity response of quinoa was characteristic of a halophyte with an increase in growth seen at moderate salinity levels.^[23] We observed an increase in both the leaf area and dry weight of plants grown at 11 dS m⁻¹, as compared to controls grown at 3 dS m⁻¹, however, the increase was not significant. In regards to wheat, plant fresh and dry weight, canopy height, and leaf area did not differ between controls (3 dS m⁻¹) and plants grown at 7 dS m⁻¹ (Table 2). Beyond this threshold, however, growth declined significantly at 11 dS m⁻¹, and was least in plants grown at 19 dS m⁻¹. Tiller number, which

Table 2. Effects of Mixed-Salt Salinity on Selected Growth Characteristics in Quinoa and Wheat

Salinity (dS m ⁻¹)	Fresh Wt. (g)	Dry Wt. (g)	Leaf Area (cm ²)	Canopy Height (cm)	Tillers (Numbers)
Quinoa					
3 (Control)	13.6 a	0.9 ab	182.9 b	30.4 a	N.A.
7	13.3 a	1.0 ab	187.6 b	31.2 a	N.A.
11	15.9 a	1.2 a	252.3 a	32.0 a	N.A.
19	9.4 b	0.8 b	166.1 b	23.0 b	N.A.
Wheat					
3 (Control)	8.9 a	1.3 a	174.2 a	53.4 a	4.6 a
7	7.6 a	1.2 a	138.8 a	52.6 a	4.3 a
11	4.3 b	0.8 b	85.5 b	44.4 b	3.6 b
19	2.4 c	0.5 c	41.1 c	36.6 c	2.4 c

Values are means of 10 plants taken from six replicate tanks. Means followed by a different letter are significantly different by Fisher's protected LSD test at the 5% level of probability. N.A.—Not applicable.

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contributes greatly to grain yield of Yecora Rojo, responded similarly to salinity as the other growth traits.

Ion Accumulation

Kuiper^[24] suggested that high-salt concentration in the root zone could influence the uptake and transport of major ions such as K^+ and Ca^{2+} . We analyzed ion content of shoot tissues to determine the effect of our mixed-salt solutions on ion uptake. Results indicated that in quinoa Na^+ levels increased. The increase was only 4-fold and 3-fold in leaf and stem tissue, respectively (Table 3). With respect to Na^+ and K^+ accumulation, quinoa seems to behave more like barley or kochia than wheat.^[25] In wheat, mean Na^+ levels in the shoot increased over 6-fold with increasing salinity. Apparently, a difference exists in the regulation of net Na^+ uptake between quinoa and wheat.

Although increased ion accumulation is a common response to salinity, ion ratios may be more important in determining ion toxicity. For instance, Cramer et al.^[26] suggested ion ratios may provide insight into ion antagonisms. In both the stems and leaves of quinoa, increasing salinity reduced the $K^+ : Na^+$ ratio (Table 4). A similar situation was observed in wheat. However, the decrease in the $K^+ : Na^+$ ratio was much more dramatic with wheat. In plants grown at 11 dS m^{-1} , the $K^+ : Na^+$ ratio had decreased to 20% of the 3 dS m^{-1} control in wheat vs. 40% in quinoa. At the highest salinity level of 19 dS m^{-1} , the $K^+ : Na^+$ ratio was only 10% of the control value in wheat and 22% of the control in quinoa.

Several recent studies reported on the influence of ionic composition of the external medium on Ca-nutritional status of the plant, which is important in maintaining the selectivity and integrity of cellular membranes.^[19,27–30] In the present study, the $Ca^{2+} : Na^+$ ratio in quinoa leaves and stems decreased as salinity increased (Table 4). The $Ca^{2+} : Mg^{2+}$ ratio also decreased with increasing salinity; however, the absolute ratio was about four times lower in leaves than stems, which may reflect a greater level of Mg^{2+} in leaves due, in part, to the presence of more chlorophyll in these tissues. Increasing salinity also decreased the $Ca^{2+} : Na^+$ ratio in wheat.

A plant's ability to selectively absorb K^+ in environments which have a large excess of Na^+ may be an important determinant of salt tolerance.^[16] In order to investigate $K^+ : Na^+$ selectivity in quinoa, we calculated $K^+ : Na^+$ selectivity. Quinoa leaves displayed a high $K^+ : Na^+$ selectivity value at 3 dS m^{-1} . We found no significant change in $K^+ : Na^+$ selectivity to the highest salinity level tested (19 dS m^{-1}). But the situation was somewhat different in stems, which displayed a small increase in $K^+ : Na^+$ selectivity with increasing salinity (Table 5). In wheat shoots, $K^+ : Na^+$ selectivity was initially much

**Table 3.** Tissue Ion Concentrations in Quinoa and Wheat Grown at Four Levels of Mixed-Salt Salinity in the Irrigation Waters

Salinity (dS m ⁻¹)	Ca	Mg	Na	K	P	S	Cl
(μmoles/g dw)							
Quinoa							
Leaves							
3	399 a	784 ab	251 c	3,061 a	295 a	191 c	452 c
7	361 b	781 ab	446 b	2,903 ab	237 b	254 b	562 bc
11	291 c	723 b	601 b	2,919 ab	181 c	262 b	787 b
19	239 d	811 a	1,080 a	2,848 b	152 d	441 a	1,125 a
Stems							
3	379 a	167 b	326 c	2,928 a	53 a	99 c	805 d
7	380 a	185 ab	630 b	3,052 a	52 a	158 b	1,038 c
11	305 ab	160 b	668 b	3,174 a	57 a	196 b	1,280 b
19	256 b	204 a	1,099 a	3,008 a	55 a	380 a	1,662 a
Wheat							
Shoot							
3	84 a	102 c	34 c	1,165 a	193 a	137 c	378 b
7	86 a	123 b	78 c	1,147 a	216 a	144 ab	401 a
11	80 a	146 a	140 b	939 b	215 a	177 a	348 b
19	63 b	157 a	220 a	708 c	177 a	177 a	368 b

Values are means of 10 plants taken from six replicates.



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Table 4. Effects of Mixed-Salt Salinity on Ion Ratios (Dry Weight Basis) in Quinoa and Wheat

Salinity (dS m^{-1})	$\text{K}^+ : \text{Na}^+$	$\text{Ca}^{2+} : \text{Na}^+$	$\text{Ca}^{2+} : \text{Mg}^{2+}$
Quinoa			
Leaf			
3	12.6 a	1.6 a	0.5 a
7	7.0 b	0.8 b	0.5 b
11	5.1 bc	0.5 c	0.4 c
19	2.8 c	0.2 d	0.3 d
Stem			
3	9.0 a	1.2 a	2.3 a
7	5.1 b	0.6 b	2.1 ab
11	4.8 b	0.5 c	1.9 b
19	2.7 c	0.2 d	1.3 c
Wheat			
Shoot			
3	33.3 a	2.4 a	0.8 a
7	14.8 b	1.1 b	0.7 b
11	7.4 c	0.6 c	0.6 c
19	3.2 d	0.3 d	0.4 d

Values are means of six replicate tanks.

higher than in quinoa leaves (318 vs. 113 at 3 dS m^{-1}), and unlike quinoa $\text{K}^+ : \text{Na}^+$ selectivity decreased significantly across the four salinity levels tested.

In order to evaluate the effects of increasing salinity on quinoa's ability to accumulate Ca^{2+} , we followed procedures of Suarez and Grieve,^[31] whose proposed ion-exchange theory could be used in examining Ca^{2+} and Na^+ uptake. The Gapon selectivity constant, K_g , which relates the equivalent fractions of the exchange ions to the activities of the same ions in solution was determined.

Data presented in Table 5 show $\text{Ca}^{2+} : \text{Na}^+$ selectivity in quinoa leaf and stem tissue did not vary significantly across salinity levels. This suggested an adaptation to salt stress in quinoa involves the ability to accumulate Ca^{2+} in the presence of increased levels of external Na^+ . Interestingly, a similar response was observed with respect to $\text{Ca}^{2+} : \text{Mg}^{2+}$ selectivity. While increased Mg^{2+} levels in the irrigation water may influence Ca^{2+} uptake in plants, the level of Mg^{2+} did not significantly change in the leaves up to 19 dS m^{-1} and only slightly increased past 11 dS m^{-1} in the stems (Table 3). Coinciding with this finding

**Table 5.** Effect of Mixed-Salt Salinity on the Selectivity Coefficients ($S_{K,Na}$) and Gapon Constant (K_g) in Quinoa and Wheat

Salinity (dS m ⁻¹)	$S_{K,Na}$	K_g	
	K ⁺ : Na ⁺	Ca ²⁺ : Na ⁺	Ca ²⁺ : Mg ²⁺
Quinoa			
Leaf			
3	113.0 a	0.66 a	0.28 ab
7	104.7 a	0.55 a	0.32 ab
11	113.3 a	0.57 a	0.35 a
19	98.7 a	0.47 a	0.37 a
Stem			
3	80.7 bc	0.46 a	1.23 b
7	76.5 c	0.46 a	1.37 ab
11	107.4 a	0.52 a	1.56 a
19	100.3 ab	0.49 a	1.67 a
Wheat			
Shoot			
3	318 a	0.95 a	0.44 a
7	233 b	0.82 b	0.48 a
11	182 c	0.75 b	0.48 a
19	96 d	0.62 c	0.51 a

is the observation that Ca²⁺:Mg²⁺ selectivity tended to increase with increasing salinity in both the leaves and the stem (Table 5). The Ca²⁺:Na⁺ selectivity response was much different in wheat than quinoa (Table 5). Absolute values were somewhat higher, and Ca²⁺:Na⁺ selectivity in wheat decreased as salinity increased, although the decrease was not significant between 7 and 11 dS m⁻¹. The Ca²⁺:Mg²⁺ selectivity ratio in wheat was unaffected by changes in salinity.

DISCUSSION

Salt tolerance and ion accumulation were investigated in *C. quinoa* grown using irrigation waters of a mixed-salt salinity typical of drainage waters found in the San Joaquin Valley of California. These are salt solutions with characteristically high pH values of around 8.0. Results could have important implications for irrigated agriculture, because quinoa is (a) a broad-leaf grain crop that



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reportedly thrives on poorer soils,^[32] and (b) a member of the Chenopodiaceae family that is known to comprise many salt-tolerant plant species. We found growth responses of quinoa to increasing salinity levels were typical of halophytic species. Leaf area increased by almost 40% in plants irrigated with 11 dS m⁻¹ compared with 3 dS m⁻¹ controls. Growth then decreased when irrigation waters exceeded 11 dS m⁻¹. Using the Maas^[33] classification that is usually cited, quinoa would be considered “tolerant”, regardless of what measure of growth (fresh weigh, dry weight, leaf area, or plant height) is used to evaluate this trait.

We should point out that the Maas^[33] classification system is based on electrical conductivity of a saturated-soil extract (EC_e) while our treatments were reported as conductivity of irrigation water (EC_i). However, assuming a leaching fraction of 15–20%, the EC_i value is multiplied by 1.5 to obtain an equivalent EC_e value.

In our experiments, quinoa maintained relatively low levels of Na⁺ in both stems and leaves unlike its halophytic relatives in the Chenopodiaceae which often accumulate large amounts of Na⁺ and Cl⁻ even at low salinity levels.^[20] At the lower salinity levels tested, growth of quinoa was not influenced by the Na⁺ levels in either the leaves or the stems. This insensitivity to internal Na⁺ levels extended up to 7 dS m⁻¹, a range across which Na⁺ levels in leaves increased by almost 80%; that is, from 251 mmol kg dry wt⁻¹ at 3 dS m⁻¹ to 446 mmol kg dry wt⁻¹ at 7 dS m⁻¹. There was no change in growth of fresh weight, dry weight, leaf area, or plant height between 3 and 7 dS m⁻¹ (Table 2).

The situation at 11 dS m⁻¹ is less certain. The level of Na⁺ in leaf tissue was about 446 mmol kg dry wt⁻¹ at 7 dS m⁻¹ to 601 mmol kg dry wt⁻¹ at 11 dS m⁻¹, an increase of almost 35%. Although mean values for fresh weight, dry weight, and plant height also increased, the increase at 11 dS m⁻¹ was not significant. However, a significant increase in total leaf area was detected across this salinity range. It should be noted that although the increase in Na⁺ level in leaves between 7 to 11 dS m⁻¹ was not significant at the 5% level, it was significant at the 8% level. If the increase is not real, then Na⁺ accumulation cannot explain the observed increase in growth.

Vegetative growth in semi-dwarf wheat, Yecora Rojo, appeared to be affected negatively by increased tissue-levels of Na⁺ with growth decreasing past 7 dS m⁻¹. Maas^[33] reported growth in semi-dwarf wheat (cv. “Probred”) began to decline at a salinity level of about 8.5 dS m⁻¹. Values for electrical conductivity in the present study are reported as conductivity of the irrigation water (EC_i); whereas, the classification of Maas^[33] is based on the conductivity of the saturated-soil extract (EC_e). Using a leaching fraction of 15–20%, typical for most tile-drained soils, 7 dS m⁻¹ EC_i value would equate to about 10.5 EC_e .

It may be possible that growth in quinoa, unlike wheat, is stimulated by Na⁺, assuming the slight ($P < 0.10$) increase in Na⁺ uptake between 7 and 11 dS m⁻¹ is sufficient to influence cell expansion and growth. Growth response



to Na^+ may differ not only among species, but also among genotype.^[34] Na^+ -induced growth stimulation is caused mainly by its effect on cell expansion.^[35] In some cases, Na^+ can replace K^+ as an osmotic agent in the vacuole thus, generating the turgor needed for cell expansion. It has been suggested that Na^+ levels in the cell may exceed K^+ levels as it accumulates preferentially in the vacuoles.^[36] Indeed the level of $\text{Na}^+ + \text{K}^+$ in plants at 11 dS m^{-1} exceeded the level observed at 7 dS m^{-1} . At some point though, the increased Na^+ levels under salinity cannot be accommodated by the plant and growth decreases. Because growth decreased significantly at 19 dS m^{-1} , quinoa apparently tolerates intermediate increases in Na^+ levels, but growth is inhibited when higher levels of Na^+ are reached in the cells. $\text{Na}^+:\text{K}^+$ substitution experiments are planned which could help clarify the role of Na^+ in the growth response.

Results suggest the dicot crop, quinoa, like most of the major monocot cereal crops such as sorghum, wheat, triticale, rye, oats, and barley, exhibits high tolerance to salinity.^[37] In the case of wheat, Omielan et al.^[16] found salt tolerance is related to the selectivity for K^+ over Na^+ . Our data support this view. In quinoa, leaf K^+ levels measured at 19 dS m^{-1} had decreased by only 7% relative to controls (Table 3). Stem K^+ levels were not significantly affected. However with wheat, the shoot K^+ levels decreased by almost 40% at 19 dS m^{-1} .

Interestingly, a comparison of the $\text{K}^+:\text{Na}^+$ selectivity in the leaves of quinoa throughout the range of salinity tested indicates a remarkable level of consistency. This situation was not observed for wheat (Table 5). Grieve and Maas^[38] reported an inverse relationship in sorghum between the $\text{Na}^+:\text{Ca}^{2+}$ ratio in the irrigation waters and the $\text{K}^+:\text{Na}^+$ selectivity ($S_{\text{K,Na}}$). In our experiments with quinoa, we found no significant difference in $S_{\text{K,Na}}$ from 3 to 19 dS m^{-1} . Over this range the $\text{Na}^+:\text{Ca}^{2+}$ ratio in the irrigation waters increased from about 3.1 to 6.2. One possible explanation is that although Ca^{2+} levels in the shoot decreased with increasing salinity, $\text{Ca}^{2+}:\text{Na}^+$ selectivity (K_g) did not change significantly. This view is consistent with the findings of Reid and Smith^[39] who concluded that high salinity did not inhibit Ca^{2+} uptake to the shoot. Whatever the case, it is noteworthy that $\text{K}^+:\text{Na}^+$ selectivity ($S_{\text{K,Na}}$) appears to be regulated differently in quinoa than in wheat when grown under mixed-salt salinity. Perhaps quinoa represents an interesting model system of how a plant can regulate specific ion transport processes.

Mixed-salt salinity significantly decreased total P in quinoa leaves (Table 3). This is interesting because high Cl^- levels in irrigation water can lead to toxic level of P in the plant.^[40,41] Roberts et al.^[42] used ^{31}P -NMR techniques in corn and found toxic levels of P under saline conditions were due to a Cl^- -induced enhancement of P uptake and translocation. In the present study, the concentration of Cl^- in the external media increased almost 10-fold, which in quinoa led to a 3-fold increase in leaf Cl^- and a 2-fold in stem Cl^- . In contrast,

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salinity had no effect on P levels in wheat shoots. Higher Cl^- levels were found in wheat grown at 7 dS m^{-1} compared to other salinity levels.

Our current understanding of Cl^- transport suggests a weak antagonistic relationship between sulfate and chloride ions.^[43–45] Such a relationship may be operating in quinoa, as evidenced by increases in tissue S concentration as salinity increased (Table 3). Increased S in salt-stressed quinoa may be noteworthy, because grain with a high content of lysine and sulfur-containing amino acids, such as methionine and cysteine, is beneficial to human nutrition not only on earth but especially in long-term space exploration.^[46] Quinoa grown in solution culture produced seed with increased concentrations of all amino acids except cysteine and methionine.^[46] Thus, an interesting result from these sand tank experiments is the increase in shoot S levels when quinoa was irrigated with high sulfur-containing irrigation waters. Future work will determine if increased shoot S leads to increased cysteine and methionine concentrations in the seed.

In summary, it appears that the greater salt tolerance found in quinoa relative to wheat may be due to several mechanisms. One mechanism may be related its ability to tolerate high levels of Na^+ . Since leaf area in quinoa was greatest at 11 dS m^{-1} , it is also possible that growth in quinoa is slightly stimulated by increased internal levels of Na^+ , though this is not certain from our data. Based on our analysis of tissue ion level using the Gapon convention, it also seems that quinoa's ability to sustain leaf K^+ levels by maintaining $\text{K}^+:\text{Na}^+$ selectivity, possibly by sustaining $\text{Ca}^{2+}:\text{Na}^+$ selectivity, is important. Quinoa may then have a place in irrigated agriculture on soils that once supported wheat, but are now used to reduce agricultural drainage waters.

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