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Salt tolerance of two wheat genotypes in response to the form of nitrogen

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Abstract – Two wheat genotypes (*Triticum aestivum* L. cv. Giza 157 and cv. Sakha 8) were grown hydroponically under greenhouse conditions. Plants were subjected to different levels of salinity: 0, 75 and 150 mM NaCl in nutrient solutions containing either NH_4^+ , or NO_3^- as the sole nitrogen source at a concentration of 12 mM. Growth of the two cultivars, particularly Sakha 8, was better under nitrate than under ammonium nutrition. Ammonium-fed plants were poorly developed with a distinctly lower root: shoot ratio and thick, short and highly branched roots compared with nitrate-fed plants. The two cultivars exhibited greater salt (NaCl) tolerance under nitrate than under ammonium nutrition. Both ammonium nutrition and salinity reduced the uptake of K^+ and Ca^{2+} , but increased the uptake of Na^+ by both cultivars; this led to lower K^+/Na^+ ratios relative to either nitrate-fed, or non-saline plants. In addition, ammonium nutrition reduced the proportions of plant K^+ , Na^+ and Ca^{2+} retained by the root. The toxic effect of ammonium nutrition on wheat can thus be related to retarded uptake of K^+ and Ca^{2+} and to enhanced uptake of Na^+ . The results suggest that nitrate, rather than ammonium, is favored as a nitrogen source for cultivars Giza 157 and Sakha 8 of wheat, particularly under salt stress.

ammonium / nitrate / salinity / wheat

Résumé – Tolérance au sel de deux génotypes de blé en fonction de la forme sous laquelle l'azote est apporté. Deux génotypes de blé (*Triticum aestivum* L. cv. Giza 157 et cv. Sakha 8) ont été cultivés hydroponiquement sous serre. Les plantes ont été soumises à différents niveaux de salinité : 0, 75 et 150 mM NaCl dans une solution nutritive contenant par ailleurs NH_4^+ ou NO_3^- comme unique source d'azote à la concentration de 10mM. La croissance des deux cultivars, et plus particulièrement de Sakha 8, a été meilleure pour la nutrition avec l'ion nitrate qu'avec l'ion ammonium. Les plantes alimentées avec l'ion ammonium se sont faiblement développées avec un rapport racine/partie aérienne particulièrement bas et des racines courtes et fortement divisées comparativement aux plantes alimentées avec l'ion nitrate. Les deux cultivars ont montré une plus grande tolérance au sel (NaCl) avec la nutrition par les ions nitrate que par les ions ammonium. La nutrition par les ions ammonium ainsi que la salinité ont réduit l'absorption de K^+ et Ca^{++} , mais ont accru l'absorption de Na^+ par les deux cultivars ; cela conduit à des rapports K^+/Na^+ plus faibles pour ce qui concerne aussi bien les plantes alimentées en nitrate que celles qui sont conduites sans apport de sel. De plus, la nutrition avec l'ion ammonium a réduit les proportions de K^+ , Na^+ et Ca^{++} retenues par les racines. L'effet toxique de la nutrition par l'ion ammonium sur le blé peut être ainsi relié au retardement de l'absorption de K^+ et Ca^{++} et à un accroissement de l'absorption de Na^+ . Les résultats suggèrent que l'ion nitrate plutôt que l'ion ammonium constitue une meilleure source d'azote pour les cultivars de blé Giza 157 et Sakha 8 sous stress salin.

ammonium / nitrate / salinité / blé

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1. INTRODUCTION

Plants can take up nitrogen from the soil as either the nitrate anion, or the ammonium cation. Most plant species, however, exhibit a preference for nitrate over ammonium [9]. In fact, nitrate assimilation requires more energy than ammonium, since the plant has to reduce it to ammonium for utilization in amino acid biosynthesis. Nevertheless, Zerihun et al. [30] demonstrated that, in the long term, the energy costs of nitrate are not substantially more than ammonium, since nitrate can be utilized as a potential osmoticum, whereas ammonium utilization leads to excretion of H^+ into the medium which necessitates pH regulation. Furthermore, ammonium has been found to be toxic to many plant species which can lead to retardation of growth and yield, with the appearance of specific toxicity symptoms [24]. However, wheat dry matter production was found to be better with ammonium than with nitrate [28]. Furthermore, Botella et al. [2] found that ammonium-fed wheat produced more tillers and spikes (but lower grains per spike) compared with nitrate-fed plants. The total grain yield was thus not affected by the form of nitrogen and Lips et al. [15] found that ammonium-fed wheat plants diverted assimilates to developing tillers, whereas nitrate-fed plants diverted assimilates to the ear.

The toxicity of ammonium may be indirectly related to K^+ deficiency arising from competition between K^+ and NH_4^+ for uptake sites at the root plasma membrane [25]. Thus, it seems reasonable that K^+ requirements of ammonium-fed plants might be higher compared with nitrate-fed plants. In this respect, Lips et al. [15] reported an improvement in the growth of ammonium-fed tomato and wheat plants by increasing the K^+ level of the medium, but with no response in nitrate-fed plants. It is well documented [29] that Na^+ , a non-essential nutrient, can to some extent substitute for certain non-specific functions of K^+ , such as osmoregulation. Therefore, plant performance under ammonium nutrition might be improved with mild salinity. The competition between NH_4^+ and Na^+ uptake has been reported by Silberbush and Lips [26], where the increase in NH_4^+/NO_3^- ratio of the medium decreased the Na^+ concentration in wheat leaves.

Salinity represents a common stress of glycophytic crops in various habitats. The present work was carried out to investigate the response of two wheat cultivars (*Triticum aestivum* L. cv. Giza 157 and cv. Sakha 8) with contrasting stress tolerance to salinity, and either NH_4^+ or NO_3^- as the sole nitrogen source. The effects of salinity and the nitrogen form on the uptake of K^+ , Na^+ and Ca^{2+} were also investigated. It has been reported that cv. Sakha 8 is more salt tolerant than cv. Giza 157 [18].

Unfortunately, it is difficult to predict the extent of yield reduction from vegetative growth response to salinity since Leidi and Lips [14] found that moderate salinity (50 mM NaCl) led to a small yield decrease of wheat grain, although it affected vegetative growth to a larger extent. This might be related to enhanced translocation of assimilates from the flag leaf to developing grain under salt stress, an effect which was more pronounced in nitrate-fed plants than in those fed with ammonium.

2. MATERIALS AND METHODS

2.1. Experimental design

An experiment with ($2 \times 2 \times 3$) factorial design was conducted. It consisted of two wheat cultivars, two nitrogen sources (NH_4^+ and NO_3^-) and three salinity levels (0, 75 and 150 mM NaCl). These 12 treatments were replicated four times for a total of 48 pots; each pot contained four plants which were bulked together and treated as one replicate.

2.2. Plant material and growth conditions

Grains of *Triticum aestivum* L. cv. Giza 157 (salt sensitive) and cv. Sakha 8 (salt tolerant) were kindly provided by the Agricultural Research Centre, Giza, Egypt. The caryopses were selected for uniformity, then sown into plastic trays full of vermiculite saturated with tap water. After 5 days, the seedlings were transplanted into plastic pots (four plants per pot) containing 350 ml of aerated nutrition solution containing 0.5 mM calcium sulfate. At this stage the seedlings had roots and shoots of about 6 and 5 cm long, respectively. After two days from transplantation (7 days from sowing), plants of each cultivar were divided into two groups each receiving nutrient solution containing either ammonium or nitrate as the sole nitrogen source. The nutrient solution with only ammonium-N contained the following macronutrients [mM]: $(NH_4)_2SO_4$ [6], KH_2PO_4 [1], $CaSO_4$ [4], $MgSO_4$ [1.5], K_2SO_4 [2], Na_2SO_4 [2]. The nitrate-N solution contained [mM]: KNO_3 [4], $NaNO_3$ [4], KH_2PO_4 [1], $CaSO_4$ [2], $Ca(NO_3)_2$ [2], $MgSO_4$ [1.5]. In addition, both solutions contained the following micronutrients [μ M]: Fe-EDTA [100], $MnSO_4$ [10], $ZnSO_4$ [1], $CuSO_4$ [1], H_3BO_3 [50], $(NH_4)_2MoO_4$ [0.5], NaCl [100], $CoSO_4$ [0.2]. The pH of nutrient solutions was adjusted to 5.5 ± 0.2 by the addition of H_2SO_4 or NaOH. During the first two days of nutrient solution application, half-strength nutrient solution was used and the full-strength nutrient solution thereafter. Twelve days from sowing (5 days from application of nutrient solution), the

salinity treatments started. Salinity stress was imposed with gradual increments of NaCl to avoid salt shock. Plants from each nitrogen source were divided into two groups, one to serve as a control (0 mM NaCl) and the other was subjected to 75 mM NaCl incorporated with the nutrient solution. Two days later, the second group (75 mM NaCl) was further subdivided into two groups: one continued to receive 75 mM NaCl and the other received 150 mM. Aerated nutrient solutions were renewed on alternate days. Plants were grown under greenhouse conditions with a 13 h photoperiod of natural daylight, maximum and minimum temperatures were 26 °C and 18 °C, respectively and relative humidity was 40% on average.

2.3. Measurements

Plants growing on each nitrogen source were harvested 12 days from sowing (i.e. “start” plants), just before application of salinity, and 18 days from sowing (i.e. “end” plants), 6 days from application of salinity. Plants were washed with distilled water, separated into shoots and roots, blotted gently and fresh weights were recorded. Dry weights were recorded after drying at 80 °C for 48 h. Dried plant material was digested according to the H_2O_2/H_2SO_4 method of Allen et al. [1]. The concentrations of K^+ , Na^+ and Ca^{2+} were determined in the extract by using a Jenway PFP7 flame photometer.

2.4. Statistical analysis

Two way analysis of variance (ANOVA) with a randomized block structure was used to demonstrate the significance of factors (N source and salinity) and their interactions in affecting plant growth and tissue ion concentrations of each cultivar separately. L.S.D. at $p < .05$ was used to compare the difference between means. For the data at the “start” plant stage (Tab. I), a one way ANOVA was used since there was only one factor (N source) at this stage.

3. RESULTS

Plant growth and tissue ion concentrations of the two cultivars at the start of the treatments (just before application of salinity) are presented in Table I. The growth of the two wheat cultivars, particularly Sakha 8, was better under nitrate than under ammonium nutrition. With ammonium-N there was a greater reduction in the growth of roots relative to shoot growth; the dry weights of roots of ammonium-fed plants were almost half those of nitrate-fed plants and there was a significantly lower root/shoot (R/Sh) ratio in ammonium-fed plants. Furthermore, the appearance of the root systems was different: under nitrate nutrition, roots of the two cultivars appeared healthy, smooth and long, while under

Table I. Dry weights and concentrations of K^+ , Na^+ and Ca^{2+} of shoots and roots of cv. Giza 157 and cv. Sakha 8 of wheat grown with either ammonium or nitrate as the sole nitrogen source at the “start” stage, just before application of salinity (12 d from sowing). Total nitrogen concentration was 12 mM. Each value is the mean of 4 replicates \pm SE. Values of each cultivar with different letters are statistically different at the 5% level of significance.

Nitrogen source	DW (mg/plant)	R/Sh ratio	K^+	$\mu\text{mol}\cdot\text{g}^{-1}$ dry weight Na^+	Ca^{2+}	K/Na ratio
(A) cultivar Giza 157						
<i>Shoot</i>						
NH_4^+	22.0 \pm 2 ^b	0.569 \pm 0.03 ^b	496 \pm 27 ^b	108 \pm 12 ^a	376 \pm 2 ^b	4.74 \pm 0.77 ^b
NO_3^-	26.7 \pm 1 ^a	1.158 \pm 0.03 ^a	939 \pm 111 ^a	101 \pm 2 ^a	678 \pm 77 ^a	9.32 \pm 1.28 ^a
<i>Root</i>						
NH_4^+	11.0 \pm 1 ^b		326 \pm 10 ^b	208 \pm 48 ^a	329 \pm 39 ^b	1.82 \pm 0.55 ^b
NO_3^-	17.7 \pm 1 ^a		952 \pm 138 ^a	144 \pm 2 ^b	501 \pm 24 ^a	6.58 \pm 0.98 ^a
(B) cultivar Sakha 8						
<i>Shoot</i>						
NH_4^+	25.3 \pm 2 ^b	0.587 \pm 0.03 ^b	432 \pm 20 ^b	82 \pm 15 ^a	383 \pm 15 ^b	5.83 \pm 1.55 ^b
NO_3^-	30.6 \pm 1 ^a	1.158 \pm 0.04 ^a	1135 \pm 25 ^a	79 \pm 2 ^a	599 \pm 7 ^a	14.5 \pm 0.12 ^a
<i>Root</i>						
NH_4^+	11.8 \pm 1 ^b		263 \pm 14 ^b	204 \pm 9 ^a	273 \pm 33 ^b	1.29 \pm 0.10 ^b
NO_3^-	20.8 \pm 1 ^a		894 \pm 42 ^a	115 \pm 5 ^b	486 \pm 21 ^a	7.76 \pm 0.32 ^a

ammonium nutrition the roots were thick, short and extensively branched.

Table II shows the interactions of N form and salinity stress on the growth of both cultivars. The data show that there was significantly higher growth of both cultivars under nitrate than under ammonium nutrition, but the effect of salinity on both cultivars was similar and more pronounced on shoot than on root growth. For example, 150 mM NaCl reduced shoot dry weight of ammonium-fed Giza 157 and Sakha 8 by 20% and 23%, respectively from the non-saline controls, whilst the respective reduction values under nitrate nutrition were 28% and 31%. Moreover, root dry weight of Giza 157 and Sakha 8 was reduced by 9% and 21% under ammonium nutrition and

by 21% and 13% under nitrate nutrition, respectively. Consequently, this led to slightly higher R/Sh dry weight ratio of saline, relative to non-saline plants and the effect was consistent both with ammonium and nitrate (data not shown).

The form of nitrogen source had a considerable effect on K^+ concentration of both cultivars. At the start, K^+ concentrations of the shoots and roots of ammonium-fed Giza 157 plants were respectively about 53% and 34% of those of nitrate -fed plants; the respective values of K^+ concentration in Sakha 8 were 38% and 29% (Tab. I).

With the "end" plants (Tabs. III and IV), K^+ concentrations of the shoots and roots of the two cultivars, particularly Giza 157, were significantly lower under

Table II. Dry weights of shoots (ShDW) and roots (RDW) of cv. Giza 157 and cv. Sakha 8 of wheat grown under different levels of salinity for 6 d with either ammonium or nitrate as the sole nitrogen (12 mM) source. Each value is the mean of 4 replicates \pm SE. Values of each cultivar with different letters are statistically different at the 5% level of significance.

Nitrogen source	mM NaCl	Cultivar Giza 157		Cultivar Sakha 8	
		ShDW (mg/plant)	RDW (mg/plant)	ShDW (mg/plant)	RDW (mg/plant)
NH_4^+	0	56.5 \pm 3 ^b	14.0 \pm 1 ^d	57.0 \pm 4 ^b	15.6 \pm 1 ^c
	75	44.8 \pm 4 ^d	12.6 \pm 1 ^d	44.0 \pm 4 ^c	12.0 \pm 1 ^d
	150	45.4 \pm 3 ^d	12.8 \pm 1 ^d	44.0 \pm 3 ^c	12.4 \pm 1 ^d
NO_3^-	0	70.0 \pm 4 ^a	36.4 \pm 2 ^a	76.2 \pm 3 ^a	35.7 \pm 2 ^a
	75	58.6 \pm 3 ^b	32.9 \pm 2 ^b	52.2 \pm 4 ^b	29.0 \pm 2 ^b
	150	50.7 \pm 2 ^c	28.9 \pm 2 ^c	52.9 \pm 3 ^b	30.9 \pm 2 ^b

Table III. Concentrations of K^+ , Na^+ and Ca^{2+} and K/Na ratio of shoots and roots of wheat cv. Giza 157 grown under different levels of salinity for 6 d with either ammonium or nitrate as the sole nitrogen source. Total nitrogen concentration was 12 mM. Each value is the mean of 4 replicates \pm SE. Values with different letters are statistically different at the 5% level of significance.

Nitrogen source	mM NaCl	K^+	Concentration ($\mu\text{mol}\cdot\text{g}^{-1}$ DW)		K/Na ratio
			Na^+	Ca^{2+}	
NH_4^+	0	653 \pm 28 ^d	Shoot 47 \pm 2 ^a	287 \pm 8 ^{bc}	13.83 \pm 0.770 ^b
	75	622 \pm 40 ^d	1265 \pm 89 ^c	348 \pm 10 ^b	0.502 \pm 0.072 ^c
	150	599 \pm 20 ^{de}	1362 \pm 190 ^d	328 \pm 8 ^b	0.440 \pm 0.137 ^c
NO_3^-	0	930 \pm 34 ^a	36 \pm 1 ^a	480 \pm 12 ^a	25.76 \pm 1.168 ^a
	75	787 \pm 97 ^b	774 \pm 83 ^b	445 \pm 15 ^a	1.041 \pm 0.175 ^c
	150	739 \pm 18 ^c	843 \pm 381 ^b	444 \pm 42 ^a	0.877 \pm 0.110 ^c
NH_4^+	0	302 \pm 18 ^c	Root 178 \pm 3 ^b	204 \pm 9 ^c	1.701 \pm 0.121 ^b
	75	223 \pm 17 ^d	696 \pm 4 ^d	180 \pm 19 ^d	0.320 \pm 0.024 ^d
	150	210 \pm 17 ^e	843 \pm 50 ^f	183 \pm 20 ^d	0.252 \pm 0.033 ^d
NO_3^-	0	764 \pm 16 ^a	120 \pm 3 ^a	380 \pm 7 ^a	6.300 \pm 0.290 ^a
	75	481 \pm 19 ^b	624 \pm 54 ^c	279 \pm 11 ^b	0.777 \pm 0.040 ^c
	150	310 \pm 32 ^c	790 \pm 105 ^e	220 \pm 18 ^c	0.402 \pm 0.046 ^d

Table IV. Concentrations of K^+ , Na^+ and Ca^{2+} and K/Na ratio of shoots and roots of wheat cv. Sakha 8 grown under different levels of salinity for 6 d with either ammonium or nitrate as the sole nitrogen source. Total nitrogen concentration was 12 mM. Each value is the mean of 4 replicates \pm SE. Values with different letters are statistically different at the 5% level of significance.

Nitrogen source	mM NaCl	Concentration ($\mu\text{mol}\cdot\text{g}^{-1}$ DW)				K/Na ratio
		K^+	Na^+	Ca^{2+}		
NH_4^+	0	705 \pm 280 ^{bc}	49 \pm 1 ^a	350 \pm 39 ^b	15.02 \pm 5.300 ^b	
	75	642 \pm 64 ^c	1091 \pm 250 ^c	343 \pm 14 ^b	0.593 \pm 0.142 ^c	
	150	571 \pm 29 ^c	1262 \pm 230 ^c	256 \pm 8 ^c	0.542 \pm 0.200 ^c	
NO_3^-	0	909 \pm 58 ^a	35 \pm 2 ^a	392 \pm 15 ^a	26.53 \pm 3.040 ^a	
	75	790 \pm 74 ^b	474 \pm 127 ^b	368 \pm 15 ^a	1.840 \pm 0.770 ^c	
	150	740 \pm 98 ^b	619 \pm 277 ^b	356 \pm 17 ^{ab}	1.190 \pm 0.700 ^c	
NH_4^+	0	320 \pm 30 ^c	118 \pm 12 ^a	220 \pm 36 ^a	2.800 \pm 0.510 ^b	
	75	201 \pm 14 ^d	529 \pm 68 ^b	220 \pm 6 ^a	0.392 \pm 0.050 ^c	
	150	159 \pm 19 ^e	772 \pm 53 ^d	116 \pm 7 ^b	0.222 \pm 0.026 ^c	
NO_3^-	0	500 \pm 52 ^a	88 \pm 11 ^a	225 \pm 20 ^a	5.840 \pm 1.050 ^a	
	75	381 \pm 11 ^b	550 \pm 40 ^b	207 \pm 6 ^a	0.690 \pm 0.038 ^c	
	150	318 \pm 43 ^c	680 \pm 50 ^c	184 \pm 20 ^{ab}	0.467 \pm 0.039 ^c	

ammonium than under nitrate nutrition. The effect was more pronounced in the roots relative to shoots. K^+ concentrations of the tissues of both cultivars, particularly those of roots, were reduced by salinity; the effect was most pronounced in cv. Giza 157 under nitrate-nutrition and in cv. Sakha 8 under ammonium-nutrition. In cv. Giza 157, 150 mM NaCl reduced the K^+ concentration of the shoots by 8% and 21% and that of the roots by 30% and 59% below the levels of non-saline plants under ammonium and nitrate nutrition, respectively. The reductions in the case of cv. Sakha 8 were 20% and 19% for the shoots and 50% and 36% for the roots, respectively. The data show that the magnitude of the salinity effect was more or less comparable in the two cultivars.

By contrast, Na^+ concentration of the tissues of both cultivars was significantly higher in the ammonium-fed plants than in those fed with nitrate. The difference was most pronounced in the shoots of cv. Sakha 8 under salinity stress (Tabs. III and IV). Under 150 mM NaCl, Na^+ concentration of the shoots of ammonium-fed Giza 157 and Sakha 8 were about 1.6 and 2.0 times those of nitrate-fed plants, respectively. The increase in Na^+ concentration of shoot tissues, in response to the increasing salinity level, was also greater under ammonium nutrition whilst in the roots, the effect was more pronounced under nitrate nutrition. The introduction of saline into the nutrient solution from 0 to 150 mM NaCl, increased shoot Na^+ concentrations of cv. Giza 157 and cv. Sakha 8 by 28 and 25 times, respectively under ammonium nutrition and by 22 and 16.7 times, respectively under

nitrate nutrition. The increases in root Na^+ concentration of cv. Giza 157 and cv. Sakha 8 were 3.7 and 5.5 times, respectively under ammonium nutrition and 5.6 and 6.7 times, respectively under nitrate nutrition (Tabs. III and IV).

As a consequence of retarded uptake of K^+ , along with enhanced uptake of Na^+ under ammonium nutrition, the K^+/Na^+ ratio of plant tissue in the "start" plants (Tab. I) was greater (about two times on average) under nitrate than under ammonium nutrition. The data in Tables III and IV show that the K^+/Na^+ ratios of both cultivars, averaged over all salinity levels, were significantly higher with nitrate than with ammonium. In addition, the reduction in K^+/Na^+ ratio by salinity was more pronounced in the shoots, which were characterized with relatively higher K^+/Na^+ ratios, than in the roots of both cultivars.

Ammonium nutrition reduced Ca^{2+} concentration of the shoots and roots of both cultivars below those of nitrate-fed plants. The difference was most pronounced in the early stages ("start" plants) of growth (Tab. I) where the Ca^{2+} concentration of the nitrate-fed shoots was almost twice the concentration of those fed with ammonium. The effect of salinity in reducing Ca^{2+} concentration in the "end" plant tissues was, however, very small (non-significant) compared with the reduction induced by ammonium (Tabs. III and IV).

The form of nitrogen had a considerable influence on the distribution of K^+ , Na^+ and Ca^{2+} in the shoots and

roots of the two cultivars. Table V shows the interaction of the N form and salinity in altering the proportions of the total K^+ , Na^+ and Ca^{2+} allocated to the root. Under ammonium nutrition, lower proportions of Ca^{2+} and particularly K^+ taken up by the two cultivars was allocated to the roots compared with nitrate nutrition. The effect of salinity in reducing root %K and root %Ca was small compared with the effect of ammonium. Nevertheless, salinity significantly reduced root %K and root %Ca in cv. Giza 157, but only under nitrate nutrition. Ammonium, compared with nitrate, led to smaller proportions of the sodium taken up by the two cultivars to be allocated to the roots; the effect was most evident under salinity stress. Similarly, salinity significantly lowered the root %Na, particularly under ammonium nutrition, but the reductions under nitrate nutrition were non-significant. Table V shows that in the absence of salinity, cv. Giza 157 allocated 46% of plant Na content to the roots under ammonium nutrition and 50% under nitrate nutrition. The respective values at 150 mM NaCl were 20% and 40%.

4. DISCUSSION

The present work demonstrated that nitrate represents a better nitrogen source for the two wheat cultivars (cv. Giza 157, salt sensitive and cv. Sakha 8, salt tolerant) than ammonium and that the growth of plants was retarded by ammonium nutrition. The effect of ammonium was more severe on root growth, and ammonium-fed plants were characterized with short, thick, fragile and poorly developed roots and consequently lower (about half) R/Sh ratio compared with nitrate-fed plants. Cruz et al. [5] reported that ammonium-fed carob seedlings produced less biomass in the lower part of the root, more lateral roots of first and second order, shorter roots and greater root diameter compared with nitrate-fed plants. These responses have been demonstrated in hydroponically-grown plants. It is likely that plant response (particularly the morphology of the root system) to the form of nitrogen might differ markedly when plants are grown under the heterogeneous and more complex soil system. Ammonium, when applied as a sole nitrogen source, has been reported to be toxic to some plant species such as soybean [13], *Dactylorhiza incarnata* [6], pine [10] and maize [24]. Ammonium toxicity can be related to acidification of the rhizosphere [22], competition with the uptake of the nutrient cations K^+ , Ca^{2+} and Mg^{2+} [12], retardation of photosynthesis [3] and increased consumption of photosynthates for N assimilation [23], thus diverting photosynthates from structural growth.

The restricted allocation of dry matter to the roots which we demonstrated under ammonium nutrition, has

Table V. Amounts of K^+ , Na^+ and Ca^{2+} in the roots as a percentage of the total plant contents (Root %K, Root %Na and Root %Ca respectively) of cv. Giza 157 and cv. Sakha 8 of wheat grown under different levels of salinity for 6 d with either ammonium or nitrate as the sole nitrogen source. Total nitrogen concentration was 12 mM. Each value is the mean of 4 replicates \pm SE. Values of each cultivar with different letters are statistically different at the 5% level of significance.

Nitrogen source	NaCl	Root %K	Root %Na	Root %Ca
cultivar Giza 157				
NH_4^+	0	10.9 \pm 3.00 ^d	46.2 \pm 0.60 ^a	15.4 \pm 0.80 ^d
	75	8.90 \pm 0.06 ^d	13.2 \pm 1.30 ^c	12.3 \pm 1.20 ^d
	150	9.00 \pm 1.00 ^d	19.8 \pm 3.30 ^c	15.9 \pm 1.30 ^d
NO_3^-	0	30.7 \pm 1.10 ^a	49.9 \pm 6.60 ^a	29.9 \pm 0.70 ^a
	75	25.2 \pm 0.50 ^b	40.6 \pm 1.90 ^b	25.5 \pm 1.50 ^b
	150	17.2 \pm 0.60 ^c	40.1 \pm 9.00 ^b	22.1 \pm 1.20 ^c
cultivar Sakha 8				
NH_4^+	0	10.0 \pm 2.50 ^b	39.1 \pm 4.40 ^{ab}	14.0 \pm 2.50 ^b
	75	9.20 \pm 1.40 ^b	10.5 \pm 3.80 ^c	14.9 \pm 2.60 ^b
	150	7.80 \pm 1.70 ^b	18.6 \pm 5.00 ^c	10.9 \pm 1.20 ^b
NO_3^-	0	20.6 \pm 1.10 ^a	54.4 \pm 0.30 ^a	22.2 \pm 1.30 ^a
	75	19.5 \pm 1.00 ^a	44.3 \pm 8.10 ^a	26.4 \pm 0.40 ^a
	150	18.8 \pm 1.90 ^a	45.6 \pm 10.7 ^a	22.7 \pm 0.60 ^a

also been reported by Ericsson [7] to occur under adequate and excessive supplies of nitrogen, phosphorus and sulfur. It seems likely that there is something common between high nitrogen availability (or high plant nitrogen concentration) and ammonium nutrition; both would lead to low R/Sh ratio of plants and to thicker and shorter roots as well. The lower R/Sh ratio of ammonium-fed plants may be due to the fact that ammonium, unlike nitrate, cannot be stored in root cells, neither can it be transported to the shoot system, but must be assimilated first in the root tissue. This will enhance root respiration to meet the increasing demand for carbon skeletons for ammonium assimilation [20]; thus diverting more photosynthates to the roots to assimilate ammonium (amino acids and amides) which would then be transported to the shoot. The competition between the need for ammonium assimilation and root growth for available carbohydrates was confirmed by split root experiments [23] where the ammonium-fed half of the root system exhibited lower dry matter production relative to the nitrate-fed half. The effect of salinity on partitioning of dry matter within wheat plants (increasing R/Sh ratio) was, however, very small compared to the effect of nitrogen form. In agreement with our results, Cramer et al. [4] reported an increase in R/Sh ratio of barley under salinity stress.

The present results (Tab. II) show that the “end” plants of the two wheat cultivars grew better with nitrate than with ammonium and that the two cultivars were both similarly affected by salinity. Also, the adverse effect of salinity on the growth of wheat was small compared with the effect of ammonium nutrition. A similar, slight effect of salinity relative to nitrogen form on peanut growth has been reported by Silberbush and Lips [26], although in that case plant growth was found to be better under ammonium than under nitrate nutrition. Although cv. Sakha 8 was described as salt tolerant and cv. Giza 157 as salt sensitive (see [18]), this was not demonstrated in the present work. It seems probable that the evaluation of salt tolerance of the two wheat cultivars used in the present work might be related to grain yield of mature plants, whilst in the present work, only young seedlings were used. The seedling stage has been found to be the most salt-sensitive in plant life [8]. Thus, cv. Sakha 8 (salt-tolerant) appears to be as sensitive as the other cultivar (Giza 157) in the early stages of growth and differential response to salinity may occur at later stages.

The depression of wheat growth, either under ammonium nutrition or under salinity stress, was accompanied with depression in the uptake of K^+ and Ca^{2+} , but with enhanced uptake of Na^+ . This might indicate competition between either NH_4^+ and Na^+ on the one hand, or K^+ and Ca^{2+} on the other hand. Competition between NH_4^+ and both K^+ and Ca^{2+} has been reported [12, 19, 21], and K^+ has been shown to act as a counter ion in the uptake of nitrate [11, 12]. Nevertheless, competition between NH_4^+ and Na^+ was not demonstrated in either of the present wheat cultivars, but Na^+ uptake was promoted by ammonium nutrition, particularly under salinity stress. In agreement with our results, Na^+ concentration of peanut leaves was found to increase with the increase in NH_4^+/NO_3^- ratio of a medium containing 50 mM NaCl [26]. In our study, ammonium-fed wheat plants were characterized by a distinctly lower K^+/Na^+ ratio relative to nitrate-fed plants; the effect was more pronounced in the case of shoots than with roots. The effect of salinity in reducing K^+/Na^+ ratio was greater than the effect of NH_4^+ . This is probably the result of an increase in Na^+ uptake along with retarded K^+ uptake under salt stress. Salinity has been reported to inhibit uptake of K^+ and Ca^{2+} by wheat [18] and Ca^{2+} uptake by barley [4] and corn [16].

In addition to affecting nutrient uptake, the treatments also affected the partitioning of K^+ , Na^+ and Ca^{2+} within the plant. The results show that ammonium nutrition, and to a lesser extent salinity, led to lower proportions of K^+ , Na^+ and Ca^{2+} to be retained by the roots relative to nitrate nutrition or in the absence of salinity, respectively.

This effect was more pronounced in cv. Giza 157 than in cv. Sakha 8. It is possible that ammonium impairs the selective mechanisms operating in the root to restrict uptake and transport of Na^+ , leading to greater amounts of Na^+ in the shoots of plants exposed to saline conditions. This is supported by the lower root %Na, and higher Na^+ concentrations in plant tissues, in ammonium-fed plants compared with those fed with nitrate. Sodium concentrations in the shoots and roots of the two cultivars under saline conditions, as mM on tissue water basis (data not shown), were two to three times higher under ammonium than under nitrate nutrition. The levels of Na^+ (tissue water basis) were, in general, higher in the shoots and roots of cv. Giza 157 than in those of cv. Sakha 8, which may explain a greater salt sensitivity expected in cv. Giza 157 at later stages of growth. The accumulation of Na^+ in plant tissues will result in severe growth reduction or death in glycophytic species. Therefore, the capacity of plants to restrict Na^+ in the cytoplasm and, hence, maintain a high cytosolic K^+/Na^+ ratio is likely to be one of the key elements of plant salt tolerance [17].

In conclusion, nitrate, rather than ammonium, would appear to be more suitable for both wheat cultivars (cv. Giza 157 and cv. Sakha 8), particularly under salt stress. The toxic effect of ammonium on wheat growth was associated with poor development of roots and with a reduction in the uptake of K^+ and Ca^{2+} , but enhanced uptake of Na^+ .

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