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Vigor and salt tolerance in 3 lines of tall wheatgrass

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The F_1 progeny of the cross of two salt-tolerant lines of *Thinopyrum elongatum* [Host] D. R. Dewey grew better than either parent under non-saline and saline growth conditions. Under non-saline conditions, the hybrid produced 1.8 times as much vegetative tissue as one parent and 3.2 times more than the other parent in the same length of time. The relative growth rates of the 2 parental lines decreased equally as media osmotic potentials decreased. The relative growth rate of the hybrid did not decrease as rapidly as that of the parents; therefore, it was concluded that the greater growth of the hybrid was due to increased salt tolerance. Carbohydrate reserves and water-soluble solutes believed to be involved in osmotic adjustment were assayed to determine if there were any differences between the hybrid and its parents in their abilities to accumulate these compounds. The concentrations of these constituents were measured at dawn and at dusk of the same day in plants grown in media at osmotic potentials ranging from −0.1 to −1.2 MPa. There were no differences in pool sizes of the organic compounds in the 3 lines. Starch increased 10–40 fold in leaves from dawn to dusk and sucrose increased 100-fold. However, this pattern was unaffected by salinity. Conversely, betaine concentrations increased with increasing salinity but were the same at dawn and dusk. Na^+ and K^+ were affected by both light and salinity. Cl^- was one-half ($Na^+ + K^+$) on a molar basis under all conditions. Proline accumulated when ($Na^+ + K^+$) exceeded 200 μmol (g fresh weight)$^{-1}$. Since this amount of ($Na^+ + K^+$) existed only in tissues harvested at dusk from severely saline-stressed plants, only leaves from such plants harvested at dusk contained proline.

Key words – Carbohydrate reserves, F_1 progeny, light-salinity interaction, osmotic adjustment, salt tolerance, tall wheatgrass, *Thinopyrum elongatum*, vigor.

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Introduction

Drought and salinity have enormous effects on agricultural productivity by causing decreases in plant yield (e.g. vegetative growth, fruit production, etc.). Despite a great deal of research on stress damage to plants, the metabolic sites at which these environmental agents harm plants, or conversely, the mechanisms utilized by plants to survive in harmful environments, are largely unknown. The main problem is that there are no indicators in plants' responses to drought or salinity to suggest which plant properties to investigate. For example, almost the only observable symptom of moderate (less than severe) damage by these two stresses is stunted growth. Many approaches have been used to study stress damage. This paper will describe the results of a genetic and biochemical approach to this problem. A knowledge of the metabolism and nutrition of plants is essential for an understanding of the genetics of salt tolerance (Epstein 1985, Shannon 1985, Tal 1985). Metabolic and molecular biological aspects of the genetics of salt tolerance have been reviewed recently (Epstein 1985, Tal 1985, Epstein and Rains 1987).

Tall wheatgrass *(Thinopyrum elongatum)* [Host] D. R. Dewey (formerly *Agropyron elongatum* [Host] Beauv.; see Dewey 1984) is a commercially important forage grass. Shannon (1978) studied the salt tolerances of 32 accessions of tall wheatgrass and classfied 7 of them as extremely salt tolerant. The criteria used by Shannon for salt tolerance was (a) withstanding high

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salinity without the leaves becoming chlorotic, and (b) survival as shown by the ability of plants to rapidly resume growth when the saline stress was removed. With this classification of phenotypes, it seemed appropriate to begin a study of the inheritance patterns of salt tolerance by crossing accessions and studying salt tolerance patterns in the progeny.

In tall wheatgrass, vegetative growth is the product (yield) of importance, because the crop is regularly submitted to multiple harvestings (cutting back) or to grazing by animals. Therefore, the selection criterion in screening progeny of crosses of accessions for further study was vigorous growth under saline conditions. Then, in order to study salinity affects on laboratory plants in a manner resembling how field plants are grown and utilized, selected lines were grown under saline stress and vegetative material harvested by cutting back the tops of the plants several times in the course of a year. The yields were measured after each cutting. The effect of salinity on parents and F_5 progeny of Rhodes grass has been studied in a similar manner (Malki and Waisel 1986). These authors concluded that mass selection can be used to isolate lines with improved capabilities of surviving high salt stress.

In addition, the foliar concentrations of carbohydrate reserves (sucrose and starch) and of several solutes believed to be involved in osmotic adjustment of stressed plants were assayed. The purposes of the biochemical studies were to determine (a) if there might be some biochemical marker for salt tolerance, and (b) if the osmotic adjustment patterns in progeny of crosses or their ability to store carbohydrate reserves might be modified in some manner. Carbohydrate reserves undergo diurnal fluctuations in many non-stressed plants (Baysdorfer and Robinson 1985, Fondy and Geiger 1985, Sicher 1986). Therefore, the concentrations of starch and water-soluble solutes were measured at dawn and dusk.

The present paper will focus on the results obtained with 2 tall wheatgrass accessions and their F_1 hybrid. These particular lines were selected for a detailed study, because the hybrid grew more vigorously under non-saline and saline conditions than either parent. The study was undertaken to establish whether or not the increased growth rate and yield of the hybrid were due to enhanced salt tolerance, and if a specific physiological criterion could be associated with any difference in salt tolerance.

Abbreviations – EC, electrical conductivity; OP(s), osmotic potential(s); $(Na^+ + K^+)$, the sum of sodium and potassium ions in leaf tissue; PL1, parental line P.I. 276399; PL2, parental line P.I. 297874.

Materials and methods

The two parental lines used in these experiments were accessions P.I. 276399 and P.I. 297874 of *Thinopyrum elongatum*. They will be referred to in the text as PL1 and PL2, respectively. The line that is a result of their cross will be identified as 'hybrid'.

Plants were grown from seed for 8 weeks in non-salinized media (Shannon 1978). In May, three 8-week-old seedlings of each line were transplanted into each of 36 outdoor sand-culture plots. The design of the experiment was to subject the plants to 12 salinity conditions with each condition being replicated 3 times. The plots were 1.5×1 m in size and filled to a depth of 2 m with medium-textured sand. Each plot had a 4 000-l reservoir of nutrient solution composed of 6 m*M* KNO_3, 6 m*M* $Ca(NO_3)_2$, 3 m*M* $MgSO_4$, 0.18 m*M* KH_2PO_4, 0.1 m*M* Fe as the diethylene-triamine pentaacetate salt, 46 μ*M* H_3BO_3, 9 μ*M* $MnCl_2$, 0.8 μ*M* $ZnSO_4$, 0.3 μ*M* $CuSO_4$ and 0.1 μ*M* H_2MoO_2. The plots were irrigated 3 times each 24 h period by flooding the surface with 4 000 l of medium from the reservoir. The medium, which drained through the sand, was recycled back into the reservoir. Any water loss was replenished daily. Salinity and pH were measured and adjusted every other day. Media in reservoirs were replaced at bi-monthly intervals.

The plants were allowed to grow 18 more weeks without being subjected to saline stress. During this time, plant material was harvested twice (on 24 July and 28 August) by cutting back the tops of the shoots, leaving a plant that was 7–8 cm high. The fresh and dry weights of the harvested tissue were measured.

Salinization of media began on 30 September by adding a solution of a mixture of NaCl and $CaCl_2$ in a 5:1 molar ratio to the reservoirs in sufficient quantity to increase the salt concentration in media by 25 m*M* (20.83 m*M* NaCl and 4.17 m*M* $CaCl_2$). This was repeated daily until a pre-selected concentration was reached (see Results and discussion). The salinity levels were measured in dS m^{-1} by electrical conductivity (EC) and converted to osmotic potentials (OPs) in MPa by the equation $OP = -EC \times 0.051$. The OPs reported in the text are the sum of the basic OP of non-salinized media, which was slightly lower than −0.1 MPa, and that due to the added salt.

The plants were allowed to grow until they were over 1 year old. During this period, leaf tissue was harvested and weighed on 2 and 30 October, 29 November, 21 January, 24 March, 22 April and 21 May. Harvested tissue on all dates except 22 April were handled as described above for tissue harvested from young non-salinized plants.

Shoots harvested on 22 April were handled differently so that the fresh tissue could be extracted for the determination of the concentrations in leaves of starch and low-molecular weight, water-soluble solutes. April 22nd was a sunny day. Approximately one-half of the leaf tissue of a plant was harvested at dawn (5:30 a.m.) and the other half was harvested at dusk (12 h later). A 2–4 g sample, accurately weighed, of fresh leaf material from each line was extracted with toluene as described previously (Weimberg 1986). The solutes Na^+, K^+, Cl^-, proline, betaine, sucrose, glucose and fructose were

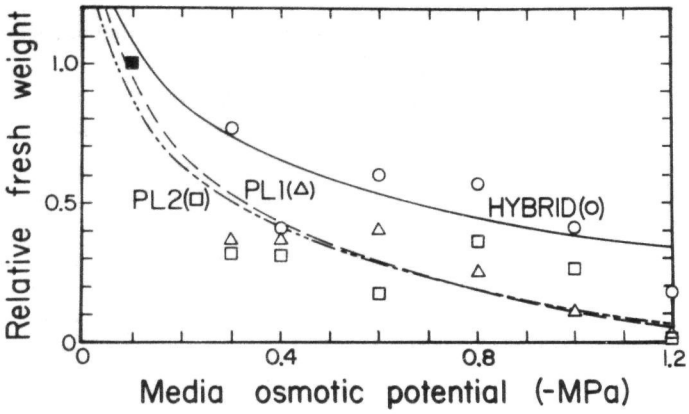

Fig. 1. Relative yields of 3 lines of *T. elongatum* as a response to increasing salinity. Yields are the sums of shoot material harvested on 24 March, 22 April and 21 May. The yields from plants at −0.1 MPa (control conditions) for lines PL1, PL2 and hybrid were 200, 114 and 360 g, respectively. Relative yields are the yields from plants grown at each medium OP divided by yields of control plants. The general equation for the 3 curves is $Y = A + B \log X$. The regression estimates for parameter A of the curves for PL1, PL2 and hybrid are 0.105, 0.142 and 0.353, respectively. The respective regression estimates for parameter B are −0.36, −0.30 and −0.30. Correlation coefficients for the same sequence of curves are −0.95, −0.87 and −0.89. The solid square symbol is the control (100% relative yield) point for all 3 curves.

assayed as before (Weimberg 1986). In addition, Ca^{2+} and Mg^{2+} were determined by atomic absorption spectrophotometry. The residue of the toluene extraction was used for starch determination by a small modification of the procedure described by Aslam et al. (1986). The tissue, after toluene extraction, was dried in a dessicator at −20°C. The dried material was chopped into pieces not more than 1 cm in length and extracted 3 times with 10 ml of boiling 80% ethanol. The ethanol supernatants were discarded. The residue was suspended in 10 ml of 0.2 *M* KOH and heated in a boiling water bath for 30 min. After cooling, 2 ml of 1 *M* acetic acid and 2 ml of 0.2 *M* K-acetate buffer, pH 5.5, were added followed by 1 ml of a 1:50 dilution (approximately 28 units ml^{-1}) of amyloglucosidase (Sigma Chemical Co.). This reaction mixture was incubated at 55°C with occasional swirling. After 1 h, the reaction mixture was placed in a boiling water bath for 3 min, cooled, filtered through miracloth and the filtrate assayed for glucose. The starch content of the tissue is reported in terms of glucose units.

Results and discussion

The growth characteristics of 3 lines of tall wheatgrass as affected by salinity were studied. Shoot growth was determined at 9 intervals, twice before the plants were subjected to salinity and 7 times after initiating the stress. Because of seasonal variations in growth rates, the sum of only the last 3 harvestings of each line were used for statistical analysis. The yield of non-salinized plants of the hybrid was 3.2 times greater than PL2 and 1.8 times greater than PL1. Relative yields were analyzed using regression statistics and for all 3 lines the regression curves were found to have the best goodness of fit to a linear-log model with the equation $Y = A + B \log X$, where Y is yield and −X is the OP of the irrigation solutions. Although the average yields of the two parental lines at each OP level differed from one another, the regression curves were not significantly different. Therefore the yield data for the parental lines were pooled to obtain a regression curve of $Y = 0.134 - 0.298 \log X$ with a correlation coefficient of −0.87. Standard errors for the A and B parameters were 0.046 and 0.050, respectively (Fig. 1). The yields of the hybrid at all OP levels were consistently higher than those of either parent. Indeed, at −1.2 MPa, the hybrid was still capable of some growth, while the growth of the parents was essentially nil. The regression curve of the hybrid was calculated as $Y = 0.353 - 0.293 \log X$. The correlation coefficient was −0.89 and SE for the A and B parameters were 0.072 and 0.068, respectively. The data suggest that the hybrid is more salt tolerant than either parent. Therefore, the larger yields of the hybrid are due both to enhanced vigor and greater salt tolerance.

Dry weight/fresh weight ratios increased almost equally in all lines as the levels of stress were increased (Tab. 1). There are no data for the parental lines at −1.2 MPa, because these lines did not grow sufficiently for harvesting at this stress level.

One distinctive characteristic of most salt-stressed plants is that the concentrations of certain water-soluble solutes in leaves increase in amounts that are roughly proportional to the degree of stress. Any effect of vigor on solute concentrations in tissues is, at present, unknown. In order to determine if there was any interaction between either vigor or salt tolerance and storage of carbohydrates combined with osmotic adjustment patterns in saline-stressed plants, the amounts of starch and the concentrations of several water-soluble solutes were determined. Since both starch and sucrose increase in leaves in daylight and decrease at night, the concentrations of these two components and the other metabolites were measured at dawn and at dusk. The

Tab. 1. Dry weight/fresh weight ratios. Values are the means of 3 replicated ratio measurements at each experimental condition ±SD.

Osmotic potential (−MPa)	Line PL1	Line PL2	Hybrid
0.1	0.17±0.04	0.17±0.01	0.19±0.02
0.4	0.18±0.04	0.22±0.03	0.21±0.02
0.8	0.23±0.05	0.26±0.04	0.23±0.02
1.0	0.26±0.07	0.26±0.08	0.26±0.02
1.2	no growth	no growth	0.29±0.06

Tab. 2. Concentrations of solutes at dawn and dusk in leaf tissue of *T. elongatum* hybrid. Values of Na^+, K^+, $(Na^+ + K^+)$ and Cl^- are in mmol (g fresh weight)$^{-1}$; values for proline, betaine and sucrose are in μmol (g fresh weight)$^{-1}$; and starch values are in μmol (g fresh weight)$^{-1}$ of glucose moieties. All values are the mean of 3 replicates ±SD.

Solute	Time of day	Media osmotic potentials (−MPa)				
		0.1	0.4	0.8	1.0	1.2
Na^+	dawn	0 ±0	0.05±0	0.05±0	0.05±0.01	0.06±0.01
	dusk	0.01±0	0.06±0	0.07±0.01	0.08±0.01	0.07±0.01
K^+	dawn	0.10±0.01	0.11±0.02	0.10±0.01	0.12±0.02	0.15±0.01
	dusk	0.14±0.01	0.11±0.01	0.11±0.01	0.14±0.01	0.17±0.02
$(Na^+ + K^+)$	dawn	0.10	0.16	0.15	0.17	0.21
	dusk	0.15	0.17	0.18	0.22	0.24
Cl^-	dawn	0.06±0.02	0.08±0.01	0.06±0.01	0.08±0.01	0.09±0.01
	dusk	0.06±0.01	0.09±0	0.08±0.01	0.09±0.01	0.12±0
$Cl^-/(Na^+ + K^+)$	dawn	0.6	0.5	0.4	0.5	0.4
	dusk	0.4	0.5	0.4	0.4	0.5
Sucrose	dawn	0.2±0	0.2± 0	0.2±0	0.2±0	0.2±0
	dusk	27.7±1.7	30.1±1.6	27.9±1.9	31.2±1.9	36.7±5.1
Starch	dawn	0.7±0.1	0.4±0.1	0.8±0.2	0.3±0	0.8±0.2
	dusk	12.6±0.8	12.7±0.7	13.2±1.0	11.0±0.8	11.3±1.8
Proline	dawn	0.09±0.05	0.11±0.05	0.08±0.05	0.39±0.1	2.1±0.09
	dusk	0.09±0.04	0.15±0.05	0.10±0.08	1.2±0.2	3.2±0.2
Betaine	dawn	4.4±2.2	29.1±3.9	36.8±5.3	44.0±6.2	71.1±10.8
	dusk	4.7±1.2	29.4±5.6	32.7±6.0	42.5±2.7	70.0±15.6

amounts by which these compounds changed due to salinity and light were markedly similar in all 3 lines. Therefore, the results obtained with the hybrid at 5 salinity levels are listed in Tab. 2, while only the results obtained at the −0.1 and −1.0 MPa levels with the parental lines are included in Tab. 3.

Sodium was at its lowest level in non-stressed plants. Its concentratioan increased 5 to 8-fold when media OPs were lowered to −0.4 MPa. It remained constant in plants grown at even lower media potentials. At all stress levels, Na^+ was higher at dusk than at dawn, but the proportion of increase was never large. Potassium

Tab. 3. Concentrations of solutes at dawn and dusk in leaf tissue of lines PL1 and PL2 of *T. elongatum*. Details as for Tab. 2.

Solute	Time of day	Line PL1		Line PL2	
		−0.1 MPa	−1.0 MPa	−0.1 MPa	−1.0 MPa
Na^+	dawn	0 ±0	0.04±0	0.01±0	0.04±0
	dusk	0.01±0	0.08±0.01	0.01±0	0.04±0
K^+	dawn	0.09±0	0.06±0	0.12±0.01	0.07±0.03
	dusk	0.15±0.01	0.13±0.02	0.15±0.01	0.17±0.02
$(Na^+ + K^+)$	dawn	0.09	0.10	0.13	0.11
	dusk	0.16	0.21	0.16	0.21
Cl^-	dawn	0.04±0	0.05±0	0.04±0	0.06±0
	dusk	0.07±0.01	0.13±0	0.07±0.01	0.09±0.01
$Cl^-/(Na^+ + K^+)$	dawn	0.4	0.5	0.3	0.5
	dusk	0.4	0.6	0.4	0.4
Sucrose	dawn	0.4±0.3	0.3±0.1	0.3±0.2	0.3±0.2
	dusk	22.5±2.5	25.1±2.5	22.6±0.8	27.6±2.9
Starch	dawn	1.0±0.3	0.8±0.2	0.4±0.1	0.5±0.1
	dusk	11.9±1.5	12.8±1.3	10.9±1.8	11.5±2.1
Proline	dawn	0.03±0	0.05±0.1	0.04±0	0.04±0
	dusk	0.03±0	1.1 ±0.4	0.03±0	1.1 ±0.4
Betaine	dawn	1.7±0.9	45.5±4.8	2.7±0.6	42.9±6.0
	dusk	5.4±1.8	37.9±1.0	3.7±1.7	36.5±8.2

and ($Na^+ + K^+$) were the only solutes whose changes in concentrations due to salinity were different in the hybrid from those in the two parental lines. Potassium fluctuated in balance with sodium changes to maintain a certain pattern of change in ($Na^+ + K^+$). In the hybrid line, ($Na^+ + K^+$) increased with decreasing OPs until, at −1.2 MPa, dawn levels of ($Na^+ + K^+$) were twice those in non-stressed plants. At the same time, in parental lines growing in media at OPs from −0.1 to −1.0 MPa, ($Na^+ + K^+$) at dawn did not change because of stress. At dusk, the pattern was different in that ($Na^+ + K^+$) levels were higher than at dawn at each salinity level and, also, were equal in all 3 lines at each salinity level. As a result, the percentage increases from dawn to dusk at −1.0 MPa, for example, in parental lines were greater than that for the hybrid. The data do not permit any conclusions to be drawn as to whether or not these observed differences between the F_1 hybrid and the two parents are related to salt tolerance or vigor. Also, the 100% increase in ($Na^+ + K^+$) from dawn to dusk in stressed plants of PL1 and PL2 cannot be explained. It does not seem likely that the increase in concentration was due to a decrease in water status of the tissues, because the concentrations of another solute, betaine (to be discussed below), actually, slightly decreased over the same diurnal period.

Ca^{2+} and Mg^{2+} concentrations were always below 0.1 μmol (g fresh weight)$^{-1}$ and were unaffected by salinity or light (data not presented). Cl^- levels were ca one-half those of ($Na^+ + K^+$) on a molar basis under all growth conditions in all lines.

Storage levels of the carbohydrates sucrose and starch at dawn and dusk were unaffected by salinity. Starch levels increased 10- to 40-fold and sucrose increased about 100-fold at dusk over their concentrations at dawn. The concentration of sucrose at dawn was too low to play a role in osmotic adjustment. Glucose and fructose were barely detectable in the extracts under all experimental conditions (data not presented). Aslam et al. (1986) have reported similar effects of light and salinity on carbohydrate reserves in leaves of 3- to 4-week-old seedlings of the halophyte, *Atriplex amnicola*. On the other hand, sucrose levels increased and starch deceased as a function of salt stress in leaves of soybean plants (Rathert 1986). Unfortunately, the effect of light was not studied. A possible explanation for the difference between the results with the glycophyte from those with the two halophytes is that *A. amnicola* and *T. elongatum* are considered to be non-carbohydrate accumulators when subjected to stress (Jefferies and Rudmik 1983), whereas *Glycine max* does accumulate carbohydrate.

Proline was measurable above trace amounts only in extracts from plants with more than 200 μmol (g fresh weight)$^{-1}$ of ($Na^+ + K^+$). Thus, proline was essentially absent from tissues of all lines at dawn with the exception of the hybrid at −1.2 MPa. Proline was detected in extracts of plants at dusk only under severe conditions of saline stress. This threshold of 200 μmol (g fresh weight)$^{-1}$ of ($Na^+ + K^+$) for proline accumulation to begin has been reported previously in *T. elongatum* (Weimberg 1986), *Sorghum bicolor* (Weimberg et al. 1984) and barley (Voetberg and Stewart 1983). There are not enough data points to calculate accurately the proline/($Na^+ + K^+$) ratio, but it appears to be 1:20, which is the value reported in previous studies.

Betaine was the only solute of those measured whose concentrations increased with increasing stress but were independent of light. In other words, at any one stress level, the concentration of betaine was almost the same at dawn and dusk. Betaine concentrations increased 10- to 20-fold as the stresses to which the plants were subjected increased from the least to the most severe levels and were equal in all 3 lines at each stress level.

The solute responses to salinity in the mature leaves of the lines used in this experiment were very similar to those reported earlier for another cultivar of *T. elongatum*, Arizona Gendale, harvested at a relatively young age (Weimberg 1986). The main conclusions to be drawn from the present growth study and biochemical assays are that the carbon flow from CO_2 to cell material occurs at different rates in each line. However, the pools of solutes did not differ, showing that the control mechanisms for pool size were unaffected by vigor and salt tolerance differences. Osmotic adjustment patterns were only slightly affected by vigor and salt tolerance. Therefore, it would be difficult to identify a particular character uniquely related to vigor and salt tolerance in the hybrid line. Finally, it is important to note the time that plants have been exposed to light, or dark if applicable, when tissues are harvested. Light radiation affected the amounts that accumulated in leaf tissue of all solutes studied here except betaine.

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References

Aslam, Z., Jeschke, W. D., Barrett-Leonard, E. G., Setter, T. L., Watkins, E. & Greenway, H. 1986. Effects of external NaCl on the growth of *Atriplex amnicola* and the ion relations and carbohydrate status of the leaves. – Plant Cell Environ. 9: 571–580.

Baysdorfer, C. & Robinson, J. M. 1985. Sucrose and starch synthesis in spinach plants grown under long and short photosynthetic periods. – Plant Physiol. 79: 838–842.

Dewey, D. R. 1984. The genomic system of classification as a guide to intergeneric hybridization with the perennial Triticeae. – *In* Gene Manipulation in Plant Improvement (J. P. Gustafson, ed.), pp. 209–280. Plenum Press, New York. ISBN 03-064-188-35.

Epstein, E. 1985. Salt tolerant crops: origins, development, and prospects of the concept. – Plant Soil 89: 187–198.

– *& Rains, D. W. 1987. Advances in salt tolerance.* – *In*- Genetic Aspects of Plant Mineral Nutrition (H. W. Gabelman and B. C. Loughman, eds), pp. 113–125. Martinus Nijhoff, Boston. ISBN 90-247-3494-0.
Fondy, B. R. & Geiger, D. R. 1985. Diurnal changes in allocation of newly fixed carbon in exporting sugar beet leaves. – Plant Physiol. 78: 753–757.
Jefferies, R. W. & Rudmik, T. 1983. The responses of halophytes to salinity: An ecological perspective. – *In* Salinity Tolerance in Plants. Strategies and Crop Improvement (R. C. Staples and G. H. Toennissen, eds), pp. 213–227. John Wiley and Sons, New York. ISBN 0-471-89674-8.
Malki, E. & Waisel, Y. 1986. Selection for salt resistance in Rhodes grass *(Chloris gayana)*. – Physiol. Plant. 66: 443–446.
Rathert, G. 1985. The influence of high salt stress on starch, sucrose, and degradative enzymes of two *Glycine max* varieties that differ in salt tolerance. – J. Plant Nutr. 8: 199–209.
Shannon, M. C. 1978. Testing salt tolerance variability among tall wheatgrass lines. – Agron. J. 70: 719–722.
– 1985. Principles and strategies in breeding for higher salt tolerance. – Plant Soil 89: 227–241.
Sicher, R. C. 1986. Sucrose biosynthesis in photosynthetic tissue: rate controlling factors and metabolic pathway. – Physiol. Plant. 67: 118–121.
Tal, M. 1985. Genetics of salt tolerance in higher plants: theoretical and practical considerations. – Plant Soil 89: 199–226.
Voetberg, G. & Stewart, C. R. 1983. Proline accumulation in stressed barley leaves. – Plant Physiol. 72 (Suppl.): 94.
Weimberg, R. 1986. Growth and solute accumulation in 3-week-old seedlings of *Agropyron elongatum* stressed with sodium and potassium salts. – Physiol. Plant. 67: 129–135.
– , Lerner, H. R. & Poljakoff-Mayber, A. 1984. Changes in growth and water-soluble solute concentrations in *Sorghum bicolor* stressed with sodium and potassium salts. – Physiol. Plant. 62: 472–480.

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