

Investigation of the salt tolerance of new Polish bread and durum wheat cultivars

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Abstract In some regions of the world, low annual precipitation necessitates irrigation of crop plants which usually leads to soil salinity. Due to climatic changes this effect is also expected in the countries of Central Europe, and so in Poland. The aim of the study was (1) to compare tolerance to salt stress of Polish *Triticum aestivum* cvs. ‘Bogatka’ and ‘Banderola’ with *T. durum* cv. ‘Komnata’ and breeding line 121, and (2) to indicate the physiological parameter/parameters most suitable for such comparison. The investigation was performed in two experiments. In the first one, the germination ability of caryopses and coleoptiles’ growth were estimated at 0–250 mM of NaCl. The second experiment was conducted on plants grown in a glasshouse in saline soil at 0–150 mM of NaCl for 6 weeks. Salt tolerance was evaluated on the basis of following parameters: chlorophyll fluorescence, net

photosynthesis rate (P_N), transpiration rate (E), stomatal conductance (g_s), cell membrane permeability (EL), proline content, fresh weight (FW), dry weight (DW), and relative water content (RWC). Highest germination of caryopses of durum cultivars was recorded at all the salinity levels; however, their coleoptiles were shorter than coleoptiles of bread wheat cultivars. Analysis of chlorophyll fluorescence showed that applied salt doses did not disturb the light phase of photosynthesis in all cultivars under study. Plants of durum wheat showed the higher dissipation of energy excess at the level of the antenna chlorophyll (Df_o/CSm) under salinity as compared to plants of bread wheat. Both ‘Komnata’ and line 121 showed stronger P_N reduction as an effect of salinity. A decline of P_N was closely connected with a decrease in g_s . The P_N correlated with a decrease in DW in all studied cultivars except ‘Bogatka’. Control plants of ‘Komnata’ and line 121 were characterized by higher EL and proline level than bread wheat cultivars. An increasing cell membrane permeability correlated with a decrease of RWC in ‘Banderola’ and ‘Komnata’. The content of proline under the increasing salinity correlated with changes of RWC in ‘Banderola’, ‘Komnata’ and line 121, which indicate protective role of proline against dehydration of tissue. Dry weight and RWC seem to be the parameters most useful in the salt-tolerance estimation of wheat plants. Taking into account the studied parameters ‘Banderola’ could be recognized as more salt tolerant, the degree of salinity tolerance of ‘Bogatka’ is the same as line 121, while ‘Komnata’ seems to be the most salt sensitive. The salt tolerance of *T. aestivum* and *T. durum* depends on the cultivar rather than the wheat species.

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Abbreviations

ABS/CSm	Light energy absorbed by leaf cross-section (CS)
DIo/CSm	Dissipation of energy flux at the level of the antenna chlorophylls
DW	Dry weight
E	Transpiration rate
EL	Electrolyte leakage
ETo/CSm	Quantum yield of photosynthetic electron transport chain after Q_A per cross-section (CS)
F_v/F_m	Potential photochemical PSII efficiency
FW	Fresh weight
g_s	Stomatal conductivity
OEC	The fraction of O_2 evolving centres PSII in comparison with the control sample
$PI_{(CSm)}$	The performance index defined on a cross-section (CS) basis and calculated as: $PI_{(ABS)} \times ABS/CSm$ where: $PI_{(ABS)} = (RC/ABS) \times (\varphi_{Po}/(1 - \varphi_{Po})) \times (\psi_o/(1 - \psi_o))$ RC is for reaction centre ABS is for absorption flux, φ_{Po} is for maximum quantum yield for primary photochemistry, and ψ_o is for the quantum yield for electron transport
P_N	Net photosynthesis rate
PSII	Photosystem II
SSI	Salt susceptibility index
Q_A	The first stable electron quinone acceptor in PSII
TRo/CSm	Trapped energy flux per cross-section (CS), quantum yield of primary photochemistry (from RC to Q_A) per CS
RWC	Relative water content

Introduction

The area affected by salinity in the world amounts to more than 800 million hectares of land, so salinity is becoming a serious problem for crop productivity (Munns and Tester 2008). Apart from natural soil salinity it is also evoked by such agronomic practices, such as improper irrigation and fertilization. In some regions of the world, low annual precipitation necessitates irrigation of crop plants with water which sometimes could not be completely desalted. However, in most cases soil salinity is an effect of salt accumulation over long cultivation periods and deforestation (Brini et al. 2009). In Poland, located in Central Europe, the progressive reduction of the groundwater level and more frequent periods of drought cause 30 % losses of grain yield, which results in the need for plant watering

(Schar et al. 2004; Martyniak et al. 2007; Walter et al. 2011). It can, therefore, be expected that soil salinity will also affect regions that have not yet experienced such important problem with this environmental stress.

Salinity may cause osmotic stress and ion toxicity stress due to Na^+ and Cl^- . Osmotic stress has an immediate effect on plant growth and stronger influence growth rates than ionic stress (Munns and Tester 2008). A high concentration of sodium ions disturbs the osmotic balance and results in physiological drought-inhibiting water uptake by the plant. The toxic influence of Na^+ may be manifested by the premature death of leaves, degradation of the cell membranes, inhibition of many enzymes, as well as damages of photosynthetic apparatus (Mitsuya et al. 2003). The biochemical strategies of plants within defence response to salinity are, among others: selective build-up or exclusion of salt ions, control uptake of ions by roots and transport into leaves, ion compartmentation, synthesis of osmolytes, changes in membrane structure, as well as activation of antioxidant defence system (Munns and Tester 2008). The threshold level of salt stress for most plants is approximately 40 mM NaCl, which is equivalent to 4 dS m^{-1} , while 50–100 mM NaCl is recognized as moderate salinity (Munns and James 2003). The latter authors maintain that only salinity over 200 mM of NaCl identifies more salt tolerant genotypes of such plant species as wheat. However, Rawat et al. (2011) stated that 1.5 dS m^{-1} injures most plants. Most of the crops respond to salinity as typical glycophytes and demonstrate differentiated tolerance levels to this stress. According to Munns and Tester (2008), barley can be recognized as the most salt-tolerant cereal, while rice as the most sensitive one.

The most considerable criterion of salt tolerance is a production of biomass, which is significantly declined due to soil salinity. In cereals, the major effect of salinity is a reduction of the number of tillers (Munns and James 2003). According to Ashraf and Ali (2008), the selection of species sensitive to environmental stresses have been based on such parameters as relative growth and relative growth reduction. Reduced leaf development results in a build-up of unused photosynthate and may generate feedback signals to downregulate photosynthesis (Munns et al. 2000; Paul and Foyer 2001). Salt stress causes stomatal closure, which limits CO_2 fixation. Lower rate of photosynthesis stimulates the generation of reactive oxygen species (ROS), which disturb the photochemical processes in thylakoids and can evoke strong photoinhibition (Sairam and Tyagi 2004).

The degree of salt and drought tolerance is often estimated on the basis of ion leakage (EL) from leaves as a parameter of cell membrane permeability (Munns and James 2003; Hura et al. 2007; Filek et al. 2012). These authors have stated that membrane permeability is affected

by both osmotic and ion toxic stresses. Damage of membrane structure as a result of salinity can be due to toxic influence of Na^+ ions which cause strong membrane depolarization and the consequent effect of lipid peroxidation (Yasar et al. 2006).

Plant response to salinity is an accumulation of osmo-protectant proline. It provides membrane stability and alleviates cell membrane destruction caused by a high salt concentration. Moreover, proline may contribute to the osmotic regulation that maintains water content in leaves (Mansour 1998).

Bread wheat (*Triticum aestivum* L.) is the main cereal cultivated in Poland and in most countries around the world. Although cultivation of *T. durum* Desf. has not been yet popular in Poland, in recent years several new Polish spring and winter cultivars of this cereal have been bred. *Triticum durum* is the second most important wheat in Southern Europe and the Middle East. In addition, it is often cultivated on soils affected by salinity although, according to some reports, durum wheat is less salt tolerant compared to bread wheat (Noori and McNeilly 2000; Munns and James 2003). Greenway and Munns (1980) have stated that the growth and photosynthetic efficiency in wheat may be reduced by salinity even at a low salt concentration. Munns and James (2003) maintain additionally that the plant resistance degree to salinity depends on stress duration, so screening of plant resistance to salt should last at least 2–3 weeks.

The aim of the presented work was to evaluate if new Polish cultivars of *T. durum* are less tolerant to salinity than cultivars of *T. aestivum*. The response of plants of both wheat species to salinity was estimated on the basis of the parameters most often described in the literature. The study was performed on germinating caryopses at 0–250 mM NaCl level and plants grown at 0–150 mM NaCl. The caryopses germination ability in different salt concentrations, chlorophyll fluorescence, photosynthesis and transpiration rate, stomatal conductance, ion leakage from leaves, proline content, as well as fresh and dry weight of plants grown under salt stress were evaluated. On the basis of results obtained in two independent experiments performed in the controlled conditions, the parameters most useful in the screening of plant salt tolerance were chosen.

Materials and methods

Plant material

The study was performed on *T. aestivum* winter cultivars ‘Bogatka’ and ‘Banderola’, and *T. durum* winter cultivar ‘Komnata’ and line 121. Caryopses of *T. aestivum* were obtained from the Department of Cereal Plants of the Plant

Breeding and Acclimatization Institute in Kraków (Poland), while *T. durum* from Plant Breeding Smolice, Plant Breeding and Acclimatization Institute Group (Poland).

Germination of caryopses and coleoptiles length

Caryopses were sterilized in 0.5 % NaOCl for 15 min, then washed three times with sterile distilled water and placed on Petri dishes ($\varnothing = 10$ cm) with filter paper wetted with NaCl solutions of the following concentrations: 0 (control), 20, 40, 70, 100, 150, 200, and 250 mM. Fifteen caryopses were put on each dish. The evaluation was conducted in five replicates (five dishes for each salt concentration). Caryopses were germinated in the dark at 25 °C for 6 days. After this time, a percentage of germinated caryopses was calculated for each dish, while the length of coleoptiles was measured individually for 20 seedlings grown at each salt treatment. The influence of salinity was expressed as salt susceptibility index (SSI) calculated as below:

$\text{SSI} = (1 - G_1/G_2) \times 100$, where: G_1 grain germination in salt solution, G_2 grain germination in pure water (control). Analogically, SSI for coleoptiles length was calculated. The presented results are the means of two independent experiments.

Plant cultivation and salt treatments

Pots (4 dm³) were filled with commercial substrate (pH 6) and watered with solutions of the following NaCl concentrations: 0 (control), 20, 40, 70, 100, 125, and 150 mM. The applied salt concentrations were chosen on the basis of results relating to germination ability of seeds, obtained in the first stage of the investigation. To state the real salt content in the soil, the conductivity of soil solution was estimated for each NaCl treatment. Soil was air-dried at 70 °C for 2 days, mixed with the water in a ratio of 1:5 and conductivity of the soil solution was analyzed using a conductometer (CI 317, Elmetron, Poland). The results of the conductivity test for studied NaCl concentration are presented in Table 1.

Table 1 Conductivity of commercial soil watered with NaCl solutions of 0, 20, 40, 70, 100, 125, and 150 mM

NaCl (mM)	dS m ⁻¹ s ⁻¹
0	1.695
20	2.675
40	5.005
70	8.365
100	11.250
125	13.750
150	17.200

Seeds, sterilized as described above, were sown in pots and nine plants per pot were maintained. The plants were grown for 6 weeks under glasshouse conditions at 22 °C, in daylight (April–May) supplemented with the light of 400 $\mu\text{mol m}^{-2} \text{s}^{-2}$ PPFD (AGRO Philips sodium lamps) up to a 16-h photoperiod. The plants were watered with NaCl solutions of the same volume, and once a week with Hoagland's medium (Hoagland and Arnon 1938) was added to the salt solutions to obtain NaCl concentration as above. The described plant growth conditions were the same in two independent experiments. All analyses were performed after a 6-week cultivation of plants under salt stress. Similarly as in the case of evaluation of seed germination capacity, the presented results are the means of both experiments.

Chlorophyll fluorescence

Chlorophyll fluorescence was measured in the third upper well-developed leaf using the Plant Efficiency Analyser (PEA) (Hansatech Ltd., Kings Lynn, UK). Before measurements, the LED—light source of the fluorometer was calibrated using an SQS light meter (Hansatech Ltd., Kings Lynn, UK). The excitation irradiance had an intensity of 3,000 $\mu\text{mol m}^{-2} \text{s}^{-2}$ (peak at 650 nm). Measurements were taken after 30 min of leaf adaptation to darkness (clips with a 4-mm diameter hole). Fluorescence intensity was measured with a PIN-photodiode after being passed through a long-pass filter. Changes in fluorescence were registered during irradiation between 10 μs and 1 s. During the initial 2 ms, the data were collected every 10 μs with 12-bit resolution. After this period, the frequency of measurements was reduced automatically. On the basis of these measurements, the following parameters (per excited leaf cross-section, CS) were calculated based on the theory of energy flow in PSII and using the JIP test as has been described elsewhere (Lazár 1999; Strasser et al. 2000): ABS/CSm, TRo/CSm, ETo/CSm, DIo/CSm, PI_(CSm), OEC, F_v/F_m . The measurements were performed in 15 replicates.

Gas exchange

Net photosynthetic (P_N), transpiration (E) rates and stomatal conductance (g_s) of plants in the stage of the fifth leaf were measured by means of an infrared gas analyzer (Ciras-1, Hansatech Ltd., Kings Lynn, UK) with a Parkinson leaf chamber (PLC6) automatically controlling the measurement conditions. The irradiation system consisted of halogen lamps. The leaf chamber was fastened on the middle part of the fourth leaf. The flow rate of air with constant CO_2 concentration [400 $\mu\text{mol}(\text{CO}_2) \text{mol}^{-1}(\text{air})$] through the assimilation chamber was 300 $\text{cm}^{-3} \text{min}^{-1}$. The temperature of the leaves was 25 °C, the air humidity

40 %, and the irradiance 800 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$. The measurements were performed in 15 replicates.

Electrolyte leakage

Ion leakage determining the plasma membrane's integrity was measured in the fourth upper, well-expanded leaves. Leaf discs ($\varnothing = 1 \text{ cm}$) were washed in distilled water, put into plastic vials containing 10 cm^3 deionised water and shaken for 24 h (50 rpm) at 20 °C. Next, ion conductivity was measured (EL_1) using a conductometer (CI 317, Elmetron, Poland). Then the samples were frozen at $-40 \text{ }^\circ\text{C}$ for 24 h after thawing they were shaken again for 24 h and, next, total ion leakage (EL_2) was measured. Membrane permeability was expressed as a percentage of total electrolyte leakage ($\text{EL}_1 \times 100/\text{EL}_2$). The measurements were done in ten replicates for each NaCl treatment.

Proline content

The content of free proline in wheat leaves was determined as described by Bates et al. (1973). Samples were homogenized in 3 % (w/v) sulfosalicylic acid to precipitate protein, and centrifuged at 14,000 $\times g$ for 10 min. The reaction mixture contained 2 cm^3 glacial acetic acid, 2 cm^3 ninhydrin reagent (2.50 % w/v ninhydrin in 60 % v/v 6 M phosphoric acid) and 2 cm^3 of supernatant. The incubation lasted for 1 h at 90 °C then, after stopping the reaction with ice, 4 cm^3 of toluene was added and mixed by vortex. The upper toluene phase was decanted into a glass cuvette and absorbance was measured at $\lambda = 520 \text{ nm}$. The concentration was assayed using proline as the calibration standard. Each assay was performed in seven replicates representing seven leaves from different plants for each treatment. The content of proline was expressed as mg g^{-1} of DW.

Fresh and dry weight and relative water content

Fresh weight (FW) of the above ground part of the plants was weighed, next their dry weight (DW) was estimated after 48-h drying at 70 °C. RWC in leaves was calculated according to the formula: $(\text{FW} - \text{DW})/\text{DW}$. The RWC parameter means number of grams of water needed to hydrate 1 g of plant dry weight. Analyses were done in 15 replicates.

Statistical analyses

All data were analyzed with Statistica 9.0 software (Statsoft, Tulsa, OK, USA) using a one-way ANOVA. The differences between means were analyzed according to multiple range Duncan's test at $p < 0.05$.

Results

Germination of caryopses

The percentage of germinated grains of ‘Bogatka’ was similar in NaCl concentrations of 0–150 mM, only higher salt levels (200 and 250 mM of NaCl) significantly decreased its caryopses germination ability (Table 2). In ‘Banderola’, a significant reduction of germination was noted already at 20 mM of NaCl. This cultivar was also characterized by the highest salt susceptibility amongst all the studied cultivars (SSI at 250 mM of NaCl amounted to 33.6, 16.2, 2.2, and 0.7 % for ‘Banderola’, ‘Bogatka’, line 121 and ‘Komnata’, respectively). Both cultivars of durum wheat demonstrated non-significant salinity influence on the number of germinated grains.

Salt stress affected stronger coleoptiles’ growth than seed germination (Table 3). In control combination coleoptiles of durum wheat were shorter as compared to coleoptiles of bread wheat. ‘Bogatka’ showed considerable reduction of its coleoptiles’ length already at 20-mM concentration, while ‘Banderola’ at 70 mM and higher. The pattern of salt influence on coleoptiles’ length noted for ‘Banderola’ was similar as in both durum cultivars. The values of SSI showed that the coleoptiles of both bread wheat cultivars were less sensitive to salinity than the durum wheat ones: SSI for ‘Bogatka’ and ‘Banderola’ at 250 mM amounted to 84.3 and 83.7 %, respectively, while for line 121 and ‘Komnata’ it amounted to 87.9 and 89.3 %, respectively.

Chlorophyll fluorescence

Analysis of chlorophyll fluorescence clearly divided the plant response to salt stress into two groups: bread wheat

Table 2 Germination of caryopses of *T. aestivum* and *T. durum* cultivars treated with salt solutions of concentrations in the range of 0–250 mM

NaCl (mM)	<i>T. aestivum</i>				<i>T. durum</i>			
	Bogatka		Banderola		Komnata		Line 121	
	%	SSI	%	SSI	%	SSI	%	SSI
0	94.5a	0	100a	0	97.2a	0	97.6a	0
20	91.8a	2.9	94.0b	6.0	97.2a	0	96.6a	2.0
40	94.5a	0	94.0b	6.0	97.2a	0	97.7a	0
70	94.5a	0	94.0b	6.0	97.2a	0	93.3a	4.4
100	91.8a	2.9	91.9b	8.1	90.6a	6.8	96.1a	1.5
150	84.6ab	10.5	79.1bc	20.9	97.1a	0.1	96.7a	1.0
200	81.1b	14.2	72.6 c	27.4	95.8a	0.9	97.6a	0
250	79.2b	16.2	66.4c	33.6	96.5a	0.7	95.5a	2.2

Left column: percentage of germinating grains, right column: values of SSI coefficient (%). Means ($n = 5$) within each column marked with the same letters do not differ statistically according to multiple range Duncan’s test ($p < 0.05$)

Table 3 Length of the coleoptiles of *T. aestivum* and *T. durum* cultivars germinating in salt solutions of concentrations in the range of 0–250 mM

NaCl (mM)	<i>T. aestivum</i>				<i>T. durum</i>			
	Bogatka		Banderola		Komnata		Line 121	
	mm	SSI	mm	SSI	mm	SSI	mm	SSI
0	61.0a	0	64.3a	0	55.1a	0	48.6a	0
20	47.7b	21.8	63.4a	1.4	49.2a	10.7	46.6a	4.1
40	34.5c	43.4	60.5a	5.9	48.2a	12.5	42.4a	12.8
70	27.2cd	55.4	40.3b	37.3	26.9b	51.2	28.7b	40.9
100	23.5d	61.5	27.7c	56.9	23.6b	57.2	26.6b	45.3
150	23.0d	62.3	25.9c	59.7	18.0bc	67.3	15.1c	68.9
200	18.0de	70.5	23.5c	63.5	9.6c	82.6	10.4c	78.4
250	9.6e	84.3	10.5d	83.7	5.9c	89.3	5.9d	87.9

Left column: length of the coleoptiles (mm) 6 days after germination, right column: values of SSI coefficient (%). Means ($n = 20$) marked within each column with the same letters do not differ statistically according to multiple range Duncan’s test ($p < 0.05$)

and durum wheat cultivars. In the case of ‘Bogatka’, most studied parameters reached the highest values in NaCl concentration of 40 and 70 mM (Table 4). Salt concentration of 100–150 mM decreased the values of such parameters as ABS/CSm, TRo/CSm, ETo/CSm and DIO/CSm, while F_v/F_m and PI_{CSm} reached the highest level in plants grown at 150 mM. Efficiency of OEC did not change under rising salinity. ‘Banderola’ also showed the highest efficiency of photosynthetic apparatus at 70 mM of NaCl. Only F_v/F_m reached the highest level at 150 mM, while the OEC parameter—similarly as in ‘Bogatka’—was generally not sensitive to salt stress. Likewise as in ‘Bogatka’, DIO/CSm (energy dissipation) reached the maximal values at 70 mM, while a higher salt concentration caused its decrease.

Both cultivars of *T. durum* demonstrated the highest efficiency of photosynthetic apparatus in plants grown at 125 and 150 mM of NaCl. In the case of ‘Komnata’, OEC reached the highest values in plants grown at 40 and 100 mM, while in line 121 it increased at 40 mM and at higher salt levels. Potential photochemical efficiency (F_v/F_m) did not change in ‘Komnata’, while it increased gradually in higher salt concentrations. In both durum cultivars DIO/CSm was maximal at the highest salt concentration.

Gas exchange

All the studied cultivars, with the exception of ‘Bogatka’, showed a decrease in P_N under rising soil salinity (Table 5). ‘Bogatka’ reached the highest P_N rate at 125 mM of NaCl, while at 150 mM it declined up to the

Table 4 Chlorophyll fluorescence parameters of *T. aestivum* and *T. durum* cultivars grown in soil treated with salt solutions of concentrations in the range of 0–150 mM

	NaCl (mM)						
	0	20	40	70	100	125	150
<i>T. aestivum</i>							
Bogatka							
ABS/CSm	35,003b	37,845b	40,643a	41,375a	36,950b	35,048b	36,653b
TRo/CSm	27,616c	30,051ab	32,298a	32,253a	29,233b	27,768c	29,428b
ETo/CSm	15,047c	16,483b	17,667a	17,840a	16,306b	15,524c	16,698b
DIo/CSm	7,387c	7,793c	8,345b	9,122a	7,716c	7,280c	7,224c
PI _(CSm)	61,5178c	676,708b	728,863a	692,419ab	676,997b	637,052c	770,766a
OEC	0.4325a	0.4466a	0.4548a	0.4455a	0.4384a	0.4764a	0.4890a
F_v/F_m	0.833b	0.839b	0.840ab	0.823c	0.835b	0.838b	0.846a
Banderola							
ABS/CSm	24,078d	27,921c	29,345b	33,932a	25,409cd	26,239c	29,917b
TRo/CSm	19,089d	223,59bc	23,473bc	27,030a	20,328c	20,920c	24074b
ETo/CSm	10,517d	12,638b	12,881b	15,661a	11,428c	11,881c	13,625b
DIo/CSm	4,988c	5,562bc	5,871b	6,901a	5,080c	5,318bc	5,843b
PI _(CSm)	431,991d	576,892c	557,714c	709,867a	510,813c	545,928c	63,7240b
OEC	0.4766ab	0.4979ab	0.4615b	0.5151ab	0.4816ab	0.5374a	0.5253ab
F_v/F_m	0.838b	0.843ab	0.845a	0.836b	0.843ab	0.839b	0.847a
<i>T. durum</i>							
Komnata							
ABS/CSm	40,258d	42,312b	42,304b	41,562c	41,556c	41,304c	44,143a
TRo/CSm	31,449d	33,423b	33,504b	32,758c	33,029b	32,534c	35,106a
ETo/CSm	1,6479d	1,8570c	19,007b	18,425c	18,499c	18,068c	19,924a
DIo/CSm	8,809b	8,889b	8,800b	8,803b	8,526c	8,770b	9,037a
PI _(CSm)	599,760d	72,9270c	827,867b	769,277c	841,910b	753,967c	911,118a
OEC	0.4185c	0.4506b	0.4846a	0.4479b	0.4982a	0.4367b	0.4367b
F_v/F_m	0.827b	0.836a	0.835a	0.831a	0.836a	0.823a	0.836a
Line 121							
ABS/CSm	24,971e	24,542e	25,798d	26,832c	26,175c	27,403b	28,566a
TRo/CSm	19,895bc	19,207c	20,458b	21,252ab	20,861b	22,001a	22,136a
ETo/CSm	10,641c	10,983c	12,079b	12,462b	12,249b	12,742a	12,850a
DIo/CSm	5,075c	5,334b	5,339b	5,579b	5,313b	5,402b	6,430a
PI _(CSm)	413,166c	420,727c	50,9048b	501763b	537,695ab	579,274a	59,400a
OEC	0.4024c	0.4843b	0.5411a	0.5123ab	0.4985ab	0.4982ab	0.4984ab
F_v/F_m	0.828c	0.828c	0.837b	0.840b	0.841ab	0.847a	0.851a

Means ($n = 15$) for each parameter marked with the same letters do not differ statistically according to multiple range Duncan's test ($p < 0.05$)

control level. 'Banderola' showed a significant decrease in P_N at 40 mM, while in both durum cultivars at 20 mM. However, at NaCl concentration above 40 mM no changes in P_N in line 121 were shown, while in 'Komnata' the considerable decrease of this parameter was observed. Finally at 150-mM NaCl concentration, the decline of P_N amounted to 26 % in 'Komnata' and line 121, and to 4 and 24 % in 'Bogatka' and 'Banderola', respectively. The transpiration rate (E) in 'Bogatka' declined by 27 % only at 150 mM, while in both 'Banderola' and line 121 it decreased already at 40 mM, and finally at 150 mM was

reduced by 43 %. Transpiration efficiency and stomatal conductivity in 'Komnata' plants was limited already at 20 mM and proceeded in higher salt concentrations, reaching at 150 mM of NaCl a 50 % lower level compared to the control. In 'Bogatka', g_s decreased under increasing salinity; however, the significant limitation of this parameter was observed only at 150 mM. Taking into account the reduction of gas exchange parameters, 'Bogatka' demonstrated the lowest sensitivity to salinity among the studied cultivars of both wheat species. However, it is necessary to underline that, even at highest salt concentration, the P_N

Table 5 Net photosynthesis rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), transpiration efficiency ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), and stomatal conductance ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of seedlings of *T. aestivum* and *T. durum* cultivars grown in soil treated with salt solutions of concentrations in the range of 0–150 mM

NaCl (mM)	<i>T. aestivum</i>						<i>T. durum</i>					
	Bogatka			Banderola			Komnata			Line 121		
	P_N	E	g_s	P_N	E	g_s	P_N	E	g_s	P_N	E	g_s
0	11.3cd	2.2ab	77ab	11.4a	2.1a	77a	13.5a	2.8a	107a	14.3.0a	2.8a	120a
20	11.7bc	2.1ab	77ab	11.6a	2.0a	75a	12.9b	2.3b	89b	13.0b	2.6a	105a
40	11.8bc	2.0ab	75ab	9.8b	1.6b	60b	13.0ab	2.2c	84b	10.9c	2.0b	88b
70	11.4c	1.9b	68b	8.6d	1.3cd	46cd	11.8c	1.6d	60c	10.5c	1.6cd	61c
100	12.2b	2.2a	82a	8.2d	1.2d	42d	8.3f	1.2f	42e	11.1c	1.8bc	70c
125	13.3a	2.0ab	76ab	9.4bc	1.4c	49c	10.8d	1.4e	52d	10.7c	1.5d	58c
150	10.9d	1.4c	52c	8.7cd	1.2d	44cd	10.01e	1.4e	51d	10.5c	1.6d	56c

Means ($n = 15$) within each column marked with the same letters do not differ statistically according to multiple range Duncan's test ($p < 0.05$)
 P_N net photosynthesis rate, E transpiration efficiency, g_s stomatal conductance

Table 6 Percentage of electrolyte leakage from leaf cells of *T. aestivum* and *T. durum* cultivars grown in soil treated with salt solutions of concentrations in the range of 0–150 mM

NaCl (mM)	<i>T. aestivum</i>		<i>T. durum</i>	
	Bogatka	Banderola	Komnata	Line 121
0	6.24 b	6.73 bc	12.62 d	18.87 b
20	4.72 b	4.14 c	18.31 c	17.33 b
40	6.66 b	5.50 bc	22.65 ab	18.07 b
70	7.05 b	4.31 c	20.51 b	24.09 a
100	6.61 b	12.46 a	19.35 bc	21.34 ab
125	14.24 a	11.90 a	24.40 ab	18.23 b
150	8.28 b	7.94 b	25.22 a	17.75 b

Means ($n = 10$) within each column marked with the same letters do not differ statistically according to multiple range Duncan's test ($p < 0.05$)

rate in leaves of both durum cultivars was the same as in leaves of 'Bogatka' and higher than in 'Banderola'. Probably the reason for this is the fact that in both *T. durum* cultivars photosynthetic apparatus was less injured by salt stress (which was documented by some chlorophyll fluorescence parameters), and natural P_N level in the control plants was higher than in *T. aestivum* cultivars.

Electrolyte leakage

The control plants of both species differed significantly in their natural cell membrane permeability (Table 6). Durum cultivars demonstrated a 2–3times higher electrolyte leakage from leaves than both bread wheat cultivars. Salinity increased EL in all plants under study. In 'Banderola', the highest ion leakage was observed at 100 and 125 mM of NaCl (an increase by 45 % in relation to the control), while in 'Bogatka' it was observed at 125 mM (57 %). In the

case of 'Komnata', an increasing ion leakage under a rising salt concentration was observed, and finally at 150 mM of NaCl it was twofold higher than in the control. Line 121 demonstrated the highest cell membrane permeability at 70 and 100 mM of NaCl (an increase in relation to the control amounted to 22 and 12 %, respectively). In all cultivars, with the exception of 'Komnata', the highest ion leakage was observed not only in the highest applied salt doses but in concentrations in the range of 70–125 mM. In 'Banderola' and 'Komnata', a negative correlation between EL and RWC was found ($r = -0.77$ and $r = -0.76$; $p < 0.05$, respectively), what means that an increase in cell membrane permeability caused a decrease in water content calculated per g of DW. A negative influence of an increase in EL on FW was proved only for 'Komnata' plants ($r = -0.76$; $p < 0.05$).

Proline content

Control plants of both durum cultivars contained about a 2–2.5 times greater proline amount than the studied cultivars of bread wheat (Table 7). In the case of 'Bogatka', the highest amount of this amino acid was observed in a salinity of 125 mM, while in 'Banderola' it was only at 20 mM of NaCl. 'Komnata' plants contained the highest level of proline at 70 mM, while plants of line 121 at 125, and 150 mM of NaCl. In summary, the pattern of proline amount change under salinity was similar for both 'Bogatka' and line 121, and for both 'Banderola' and 'Komnata'. This result suggests that proline accumulation as a defence response to salt stress is specific for the cultivar, not for wheat species. Only in the 'Bogatka' plants, a positive correlation between proline content and P_N was found ($r = 0.88$; $p < 0.05$). The proline content in tissue correlated with RWC in 'Banderola', 'Komnata' and line

121 (r coefficient amounted to 0.79, 0.76 and 0.87 at $p < 0.05$, respectively). These results evident confirm protection role of this osmolyte against tissue dehydration in most wheat plant grown in saline soil.

Fresh and dry mass and relative water content

Salinity stress decreased FW in all the studied cultivars (Table 8). In ‘Bogatka’ and ‘Banderola’, the reduction of FW was observed at 70 mM and at higher concentrations of NaCl. Fresh mass decreased in ‘Komnata’ at 100 mM, while in line 121 gradually from 20 mM. A salt concentration of 150 mM caused a decline of FW amounting to 50, 36, 48, and 66 % in the ‘Bogatka’, ‘Banderola’, ‘Komnata’ and line 121, respectively. A considerable decrease in DW was closely associated with the decrease in FW in the case of all plants. Salt concentration of 150 mM caused the strongest DW reduction in line 121 (it amounted to 38 %), while the lowest DW lost was noted in the case

of ‘Banderola’ (13 %). Plants of ‘Bogatka’ and ‘Komnata’ showed a decline of this parameter amounting to about 30 %. In the case of all studied cultivars except ‘Bogatka’, a reduction of DW correlated significantly with P_N limitation ($r = 0.33, 0.38$ and 0.34 at $p < 0.05$ for ‘Banderola’, ‘Komnata’ and line 121, respectively). It is worth to add, that only for line 121 a correlation between energy dissipation in PSII (Df_o/CSm) and FW ($r = -0.52$; $p < 0.05$) and DW ($r = -0.47$; $p < 0.05$) was found.

Relative water content declined under increasing salinity in all the cultivars (Table 8). The reduction of this parameter at 150 mM in ‘Banderola’, ‘Komnata’ and line 121 amounted to 30 %, whereas in ‘Bogatka’ to 40 %. In the case of the latter, the first symptoms of water loss were already observed at 20 mM, while in ‘Banderola’ at 100 mM, in ‘Komnata’ at 70 mM, and in line 121 at 40 mM. Taking into account the changes in DW and RWC, ‘Banderola’ differs significantly from the other cultivars under study and seems to be more salt tolerant.

Table 7 Proline content (mg g⁻¹ DW) in the leaves of *T. aestivum* and *T. durum* cultivars grown in soil treated with salt solutions of concentrations in the range of 0–150 mM

NaCl (mM)	<i>T. aestivum</i>		<i>T. durum</i>	
	Bogatka	Banderola	Komnata	Strain 121
0	2.07 b	1.98 b	4.20 bc	5.55 a
20	2.62 ab	3.15 a	5.36 b	3.41 b
40	2.56 ab	1.59 bc	3.40 c	2.90 b
70	1.99 b	2.02 b	6.03 a	1.83 d
100	2.47 ab	1.82 b	2.71 c	2.34 bc
125	3.22 a	1.32 c	2.83 c	5.43 a
150	2.23 b	1.55 bc	2.86 c	5.17 a

Means ($n = 7$) within each column marked with the same letters do not differ statistically according to multiple range Duncan’s test ($p < 0.05$)

Table 8 Fresh (g) and dry (g) weight and relative water content (g H₂O g⁻¹ of DW) of seedlings of *T. aestivum* and *T. durum* cultivars grown in soil treated with salt solutions of concentrations in the range of 0–150 mM

NaCl (mM)	<i>T. aestivum</i>						<i>T. durum</i>					
	Bogatka			Banderola			Komnata			Line 121		
	FW	DW	RWC	FW	DW	RWC	FW	DW	RWC	FW	DW	RWC
0	10.40a	1.13a	8.20a	11.4a	1.23a	8.27a	9.71a	1.10a	7.83a	11.5a	1.18a	8.75a
20	10.20a	1.10a	7.35b	12.0a	1.36a	7.82a	8.69a	1.01a	7.60a	8.84b	0.96ab	8.21ab
40	9.44a	1.20a	6.87c	9.92ab	1.20a	7.27ab	7.74ab	0.98a	6.90ab	7.78bc	0.94ab	7.28b
70	5.98b	0.79b	6.57c	7.27b	0.88b	7.26ab	6.79ab	0.95a	6.15b	5.33c	0.65b	7.20b
100	5.96b	0.86b	5.93cd	8.39ab	1.19a	6.05b	5.02b	0.76b	5.61b	4.99c	0.68b	6.34c
125	5.56b	0.81b	5.62d	7.68b	1.09a	5.97b	5.01b	0.76b	5.58b	5.01c	0.71b	6.15c
150	5.27b	0.79b	4.98d	7.36b	1.07a	5.88b	5.04b	0.78b	5.46b	5.03c	0.73b	5.89c

Means ($n = 15$) within each column marked with the same letters do not differ statistically according to multiple range Duncan’s test ($p < 0.05$)

FW fresh weight, DW dry weight, RWC relative water content

Discussion

Caryopses of both durum cultivars were germinated in the NaCl solutions of 0–250 mM. The ‘Banderola’ cultivar of *T. aestivum* showed a little (however statistically significant) decrease in caryopses germination already at 20 mM, whereas ‘Bogatka’ only at 200 and 250 mM of NaCl. Thus, germination ability under salt stress depends on cultivar specificity and not plant species. This conclusion confirms the earlier results of Noori and McNeilly (2000) who found that reduction of root and shoot length of *T. durum* plants under 100 mM NaCl depended on genotype. Rawat et al. (2011) observed a decrease in the germination rate of *T. aestivum* caryopses in soil with a salt concentration of 0–60 mM, while Hu et al. (2012) noted this effect at

0–200 mM of NaCl. Brini et al. (2009) found a significant decrease of caryopses germination of durum wheat under 200 mM of NaCl treatment. It is very interesting that germination ability in salt solutions is negatively correlated with seedling growth. Coleoptile length of both durum cultivars was the most reduced compared to both studied cultivars of bread wheat. So, durum cultivars are more tolerant to salinity at the germinating stage, while bread wheat ones are more salt tolerant in the seedling stage. This effect could be explained by stronger selection seeds of bread wheat, resulted in development of seedlings with higher vigour compared to durum ones.

In general, salinity levels applied in our work did not evoke a disturbance of PSII efficiency. The cultivars of *T. aestivum* showed the highest values of the most studied parameters of chlorophyll fluorescence at 70 mM of NaCl, while cultivars of *T. durum* at a much higher level i.e., 150 mM. Moradi and Ismail (2007) have stated that plant tolerance to salinity may be demonstrated by a higher dissipation of excess energy. The *T. durum* plants showed a greater ability for excess energy dissipation as a response to salinity than the *T. aestivum* ones; however, in line 121 a negative correlation between fresh weight, dry weight and DI_0/CS_m was found, which means that the changes in plant mass did not depend on high excess of energy. An increase in dissipation of excess energy could also indicate damage to the photosynthetic apparatus, and therefore the interpretation of changes in the values of this parameter is ambiguous (Kalaji et al. 2011). Analysis of chlorophyll fluorescence parameters, especially of $PI_{(CS_m)}$ and F_v/F_m in both studied wheat species suggests that the light phase of photosynthesis was not disturb under salinity. The results obtained in the presented study have found that this phase is more salt resistant than the subsequent stages of photosynthesis as well as transport and deposition of assimilates, which decide about plant mass production. This means, that under salt stress some processes of the light phase protect photosystems against excess of unused light.

A decrease of P_N in both bread and durum wheat under salt stress was closely connected with stomata closure. The decline in P_N under salinity proceeded in all the studied cultivars, but the reduction was the most visible in *T. durum* plants. Plants of ‘Bogatka’ demonstrated only 4 % reduction of P_N rate with simultaneously the lowest reduction of E and g_s compared to other cultivars under study. It is worth to mark that in ‘Bogatka’ no correlation between DW and P_N , E and g_s was found, while plants of other cultivars demonstrated significant association between DW and P_N rate. ‘Banderola’ showed the lowest DW reduction under salinity compared to the another. Sharma et al. (2005) observed a decrease of P_N , E and g_s in wheat genotypes under the influence of NaCl applied in the concentration adequate to 4–8 dS m^{-1} . These authors

stated that a reduction in the above-mentioned parameters was higher in salt sensitive genotype than in salt tolerant ones. Muranaka et al. (2002) observed that 100 mM NaCl inhibited the growth of *T. aestivum* plants, and this phenomenon was connected with a decrease in P_N and was evoked by a water deficit rather than the toxic influence of ions.

Stomata closure is a part of a plant’s defence mechanism against salinity stress. A decrease in transpiration rate can help to conserve water and limit salt loading in the plant (Romero-Aranda et al. 2001). In our study, durum cultivars demonstrated a stronger reduction in E and g_s compared to bread wheat plants, which may indicate that the durum cultivars cope better under drought conditions. On the other hand, these cultivars demonstrated a greater limitation in P_N than the bread wheat ones. The lowest limitation of P_N under 150 mM NaCl was observed in ‘Bogatka’, showing simultaneously the lowest decline in E and the highest water loss, which suggests inhibition of water uptake by the root system. Hence, DW and RWC seem to be the most important parameters indicating a degree of plant sensitivity to salinity. Taking this into account, ‘Banderola’ could be recognized as more salt resistant compared to the other cultivars under study.

To the physiological parameters measured during salt stress belongs electrolyte leakage from the leaf cells as an indicator of cell membrane permeability (Ashraf and Harris 2004; Sairam and Tyagi 2004). Khatkar and Kuhad (2000) observed a gradual increase in the EL from bread wheat leaves under influence of NaCl applied in the range of 0–200 mM. In the studied wheat plants any serious damage of membrane structures based on the ion leakage measurements was observed. The significant increase in membrane permeability was found at different salt levels for each cultivar. It is interesting that the NaCl concentration of 150 mM, caused a similar ion leakage from leaf cells as in the control plants. Percentage electrolyte leakage correlated with RWC in ‘Banderola’ and ‘Komnata’, what means that in these both cultivars an increase in membrane permeability decreased tissue hydration. In addition, in ‘Komnata’, a negative influence of rising ion leakage on fresh mass production was found.

To the compounds most commonly accumulated under osmotic stresses belongs proline (Flowers et al. 1977). Khatkar and Kuhad (2000) as well as Khan et al. (2009) observed a strong increase in proline content in wheat plants grown at moderate salinity. In the present investigation, control plants of durum cultivars were characterized by a twofold higher proline content compared to the bread wheat ones. The proline level in the leaves of both wheat species changed non-specifically. However, it is interesting that the pattern of proline changes under salinity was similar for the cultivars rather than for particular species.

The content of proline under the increasing salinity correlated with changes of RWC in ‘Banderola’, ‘Komnata’ and line 121. This result may imply protective role of proline against tissue dehydration in most wheat plants under salt stress.

Conclusion

Collating all the results obtained, we can state that the differences between genotypes can dominate over the differences between both analyzed species. In our opinion, the common statement that durum cultivars are more sensitive to salinity than bread wheat ones, is not quite right. A choice of one or two parameters, which clearly could be used for selection of salt tolerant plants is problematic. The ability to germinate in saline soil is a fundamental feature deciding salt tolerance. Percentage of germinated seeds and coleoptile growth are the indicators at the first stage of plant development. In the further stage, an increase in dry weight of plants seems to be the most important, so in our opinion these parameters should be used for plant selection. Taking into account the changes of DW and RWC under rising salinity, bread wheat cultivar ‘Banderola’ could be recognized as more salt tolerant. The degree of salinity tolerance of bread wheat ‘Bogatka’ is the same as durum line 121, while durum ‘Komnata’ is the most salt sensitive.

Author Contribution Agnieszka Płażek was the main contractor of the experiments, wrote the manuscript and interpreted data; Maria Tatrzańska, Maciej Maciejewski, Janusz Kościelniak, and Krzysztof Gondek performed analyses, Jarosław Bojarczuk is a breeder and author of used durum wheat cultivars; Franciszek Dubert designed and coordinated the study.

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