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Changes in response to drought stress of triticale and maize genotypes differing in drought tolerance

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Abstract

Direct effects and after-effects of soil drought for 7 and 14 d were examined on seedling dry matter, leaf water potential (ψ), leaf injury index (LI), and chlorophyll (Chl) content of drought (D) resistant and sensitive triticale and maize genotypes. D caused higher decrease in number of developed leaves and dry matter of shoots and roots in the sensitive genotypes than in the resistant ones. Soil D caused lower decrease of ψ in the triticale than maize leaves. Influence of D on the Chl *b* content was considerably lower than on the Chl *a* content. In triticale the most harmful D impact was observed for physiologically younger leaves, in maize for the older ones. A period of 7-d-long recovery was too short for a complete removal of an adverse influence of D.

Additional key words: dry matter partioning; shoot to root ratio; species differences; water potential; *Zea*.

Introduction

Visible syndromes of plant exposure to drought (D) in the vegetative phase are leaf wilting, decrease of plant height, number and area of leaves, and delay in occurrence of buds and flowers (Boyer 1982, Passioura *et al.* 1993). Invisible effects are injuries of cytoplasmatic membranes, disturbances in water status of different organs, and decrease in the chlorophyll (Chl) content (Blum and Ebercon 1981, Trapani and Gentinetta 1984, Martiniello and Lorenzoni 1985, Palta 1990, Grzesiak 2001) and many other ones. Changes in tissue water status occur after few hours from beginning of D, however, loss of membrane permeability and Chl content occur later, but they are often irreversible, especially under severe and prolonged exposure to D (Conroy *et al.* 1988, Day and Vogelmann 1995, Chaves *et al.* 2002, Grzesiak 2004, Grzesiak *et al.* 2006). These changes depend on plant species, level and duration of D, growth phase, and plant age.

Numerous papers show an existence of differences between species in responses to D, however, relatively less data concern differences among the genotypes or cultivars. Also the variability of tolerance to D within the plants belonging to the same species is not sufficiently explained. Among crop species some genotypes exist that differ in susceptibility to D stress, *e.g.* in maize (Trapani and Gentinetta 1984, Martiniello and Lorenzoni 1985, Grzesiak 2001), wheat (Lorens *et al.* 1987, Winter *et al*. 1988), and triticale (Grzesiak *et al*. 2003). Many studies were performed with transgenic plants to evaluate the molecular cause of D resistance (Riera *et al*. 2005, Zhang *et al*. 2005). In the previous paper (Grzesiak *et al.* 2006) we have shown differences in dynamics of changes in water status and gas exchange between D-resistant and D-sensitive triticale and maize genotypes. Obtained results of measurements of the water potential and leaf gas exchange parameters indicate that one of the physiological reasons of different susceptibility to D between sensitive and resistant genotypes is more efficient

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Abbreviations: Chl – chlorophyll; D – drought; DM – dry matter; DR – recovery from drought; LI – leaf injury index; R – root; RGR – relative growth rate; S – shoot; ψ – leaf water potential.
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protection of tissue water status in resistant genotypes by higher decrease in stomatal conductance and limiting of transpiration rate as compared to the sensitive ones. Other reason might be, observed in resistant genotypes during the recovery, more efficient removal of detrimental effects of D.

The aim of this work was estimation of differences in dry matter (DM) of shoot and root, leaf water potential (ψ), membrane injury, and Chl content between water stressed and non-water stressed genotypes of D-resistant and D-sensitive triticale and maize after the direct influence of short-term (7 d) and prolonged (14 d) D and after 7 d of recovery.

Materials and methods

Plants and growing conditions: The experiment was carried out on 2 spring triticale (×*Triticosecale* Wittmack) breeding strains and 2 maize (*Zea mays* L.) single cross hybrids. Chosen genotypes differed in the D-susceptibility index (DSI) values, which were calculated using formulas of Fischer and Maurer (1978), Blum and Ebercon (1981), and Grzesiak *et al*. (2003). According to Grzesiak (2004), the triticale strain CHD-247 and maize hybrid Tina were included into the group of D-resistant genotypes (DSI = 0.368 and 0.381, respectively), and the triticale strain CHD-12 and maize hybrid Ankora to the group of D-sensitive genotypes (DSI = 0.544 and 0.650, respectively).

Experimental plants were grown in air-conditioned growth cabinets: day/night temperature 23/18 °C (±2.5 °C), relative humidity (RH) 70/60 % (±5 %), and 16-h photoperiod with artificial irradiation from high pressure sodium lamps (*Philips SON-T AGRO,* 400 W) yielding photosynthetically active radiation (PAR) of about 500 μmol m^{-2} s^{-1}. Plants were grown in plastic pots (11.0 cm diameter and 21.0 cm high) filled with mixture of soil, peat, and sand (1 : 1 : 3, v/v/v) and till the 28th d after sowing they were maintained well-watered (65 % of soil field water capacity – FWC). Subsequently, drought treatment (30 % FWC) was started and applied for 7 or 14 d. After this period, for the next 7 d well watering was re-established. The pots were weighed every day, and the amount of the water loss by transpiration was refilled to keep the constant mass of pots in each treatment.

Measurements: DM values of shoots and roots were determined 28, 35, 42, and 49 d after plant sowing. Relative Growth Rate (RGR) index was calculated according to the formula published by Květ *et al*. (1971).

ψ was measured by a psychrometer *HR 33T* (*Wescor*, Logan, USA) in "dew point" mode, equipped with a sample chamber *C-52 SF* (*Wescor*) and a digital multimeter *Metex M-3640 D*. Measurements were made on leaf discs (diameter 0.3 cm for triticale and 0.5 cm for maize) cut from the middle part of the 3rd, 5th, and 7th leaves, immediately placed inside the psychrometer chamber, and left to balance temperature and water vapour equilibrium for 30 min before measurements.

On the same leaves, index of leaf injury (LI) was evaluated according to Sullivan and Eastin (1974). Measurements were done on leaf discs (5 discs for 1 replication; diameter 0.3 cm for triticale and 0.5 cm for maize).

Leaf Chl content was determined using the method of Arnon (1949). One gram of fresh mass was triturated in 80 % acetone and absorbances were measured at the wavelengths of 645, 652, and 663 nm using a spectrophotometer *Ultrospec II* (*LKB*, Cambridge, England). Determinations of DM, ψ, LI, and Chl were done in 10 replications for each treatment and day of harvest.

Data were statistically analysed using Duncan's multiple range tests and standard error of mean was calculated. Angular transformations (arc sin$\sqrt{x}$) were performed when the variable involved was expressed in percent.

Results

Dry matter partitioning: Under control conditions (C), DM of D-resistant genotypes (CHD-247, Tina) was lower than in the D-sensitive ones (CHD-12, Ankora). One-week (D7) or two-weeks (D14) long D-exposure caused decrease in number of developed leaves and DM of above-ground parts and roots, and at D14 the observed changes were high in sensitive genotypes. During the recovery (D7R7, D14R7) a partial, but not complete removal of harmful effects of D was observed. Our results indicate an almost insignificant impact of D on shoot/root ratio (S/R). Statistically significant increase in S/R was observed only for treatment D7R7 (Table 1).

Daily values of RGR for both triticale genotypes were lower than for maize genotypes (Table 2). In comparison to C plants, D caused decrease of RGR values for shoots and roots and the decrease was always higher for the sensitive genotypes. After 7 d of recovery following the 7- or 14-d-long D (D7R7, D14R7) only partial removal of the adverse effects of the D-exposure was observed.

ψ: Mean values of ψ for C triticale leaves were lower than those for maize leaves. Moreover, ψ in successive leaves of triticale was decreasing and in leaves of maize increasing. D7 and D14 caused about 2.0 and 2.5 times decrease of ψ in triticale leaves and about 2.5 and 3.4 times in maize leaves, respectively. For resistant and sensitive triticale genotype a decrease in ψ was similar for 3rd, 5th, and 7th leaf. Similar dependences were observed

Table 1. Effect of drought on the number of developed leaves, dry matter (DM) of above-ground part and root, and ratio of DM of above-ground/root of triticale (CHD12, CHD247) and maize (Ankora, Tina) genotypes. Means within columns followed by the same letter do not differ significantly according to Duncan`s multiple range test (α = 0.05).

Genotype	Treatment	Number of leaves	DM [g plant^{-1}] Stem+leaves (S)	Root (R)	S+R	S/R
CHD12	C	7.8 a	2.10 a	0.87 a	2.97 a	2.41 a
	D7	7.1 b	1.88 c	0.79 b	2.67 c	2.38 a
CHD247	C	7.7 a	1.99 b	0.86 a	2.85 b	2.31 b
	D7	7.0 b	1.88 c	0.82 b	2.70 c	2.29 b
Ankora	C	7.8 a	3.21 a	1.56 a	4.77 a	2.06 a
	D7	7.4 b	2.83 b	1.35 b	4.18 b	2.10 a
Tina	C	7.7 a	2.61 c	1.35 b	3.96 a	1.93 b
	D7	7.3 b	2.41 d	1.30 b	3.71 b	1.85 b
CHD12	C	8.3 a	2.78 a	1.16 a	3.94 a	2.40 b
	D7R7	7.9 b	2.31 b	0.89 c	3.20 c	2.60 a
	D14	7.4 c	2.11 c	0.85 c	2.96 d	2.48 b
CHD247	C	8.3 a	2.49 b	1.08 b	3.57 b	2.31 c
	D7R7	7.7 b	2.24 b	0.86 c	3.10 c	2.60 a
	D14	7.5 bc	2.08 c	0.85 c	2.93 d	2.45 b
Ankora	C	9.2 a	4.39 a	2.19 a	6.58 a	2.00 b
	D7R7	8.1 b	3.67 b	1.71 bc	5.38 b	2.15 a
	D14	7.7 c	3.18 c	1.59 d	4.77 c	2.00 b
Tina	C	9.2 a	3.53 b	1.80 b	5.33 b	1.96 b
	D7R7	8.3 b	3.14 c	1.65 cd	4.79 c	1.90 c
	D14	7.6 c	2.89 d	1.51 d	4.40 d	1.91 bc
CHD12	C	9.4 a	3.62 a	1.54 a	5.16 a	2.35 ab
	D14R7	8.0 b	2.54 c	1.06 c	3.60 c	2.40 a
CHD247	C	9.3 a	3.13 b	1.36 b	4.49 b	2.30 b
	D14R7	8.1 b	2.48 c	1.03 c	3.51 c	2.41 a
Ankora	C	10.1 a	6.07 a	2.98 a	9.05 a	2.04 a
	D14R7	8.6 b	4.08 c	1.96 c	6.04 c	2.08 a
Tina	C	9.9 a	4.71 b	2.38 b	7.09 b	1.98 ab
	D14R7	8.5 b	3.69 d	1.89 c	5.58 d	1.95 b

Table 2. Effect of drought on Relative Growth Ratio, RGR [(kg kg^{-1} d^{-1})×100] of triticale (CHD12, CHD247) and maize (Ankora, Tina) genotypes.

	CHD12		CHD247		Ankora		Tina	
	Stem + leaves	Root	Stem + leaves	Root	Stem + leaves	Root	Stem + leaves	Root
C	3.62	3.52	3.12	3.15	4.58	4.86	3.73	3.73
D7	2.04	2.14	2.30	2.47	2.78	2.80	2.59	3.19
%C	56.4	60.8	73.7	78.4	60.7	57.6	69.4	85.5
C	4.01	4.11	3.20	3.25	4.47	4.85	4.31	4.11
D7R7	2.94	3.84	2.50	3.15	3.71	3.38	3.78	3.41
%C	73.3	93.4	78.1	96.9	83.0	69.7	87.7	83.0
C	3.81	3.81	3.16	3.20	4.52	4.85	4.02	3.92
D14	1.84	1.59	1.87	1.49	2.66	2.57	2.59	2.66
%C	48.3	41.7	59.2	46.6	58.9	53.0	64.4	67.9
C	3.77	4.05	3.27	3.29	4.63	4.40	4.12	3.99
D14R7	2.65	3.15	2.51	2.74	3.56	2.99	3.49	3.21
%C	70.3	77.8	76.8	83.3	76.9	68.0	84.7	80.6

Table 3. Effect of drought on leaf water potential in leaves of triticale (CHD12, CHD247) and maize (Ankora, Tina) genotypes. Means within columns followed by the same letter do not differ significantly according to Duncan`s multiple range test (α=0.05).

Treatment	Genotype	Leaf number			Genotype	Leaf number		
		3	5	7		3	5	7
C	CHD12	–0.57 a	–0.60 a	–0.62 a	Ankora	–0.52 a	–0.52 a	–0.50 a
D7		–1.15 b	–1.18 c	–1.18 c		–1.30 c	–1.26 c	–1.27 c
C	CHD247	–0.55 a	–0.57 a	–0.57 a	Tina	–0.51 a	–0.50 a	–0.50 a
D7		–1.11 b	–1.11 b	–1.08 b		–1.25 b	–1.20 b	–1.22 b
C	CHD12	–0.59 a	–0.60 a	–0.65 a	Ankora	–0.55 a	–0.53 a	–0.51 a
D7R7		–0.88 c	–0.88 b	–0.90 b		–0.74 c	–0.70 c	–0.65 b
D14		–1.51 d	–1.53 c	–1.54 c		–1.70 e	–1.74 e	–1.80 d
C	CHD247	–0.62 b	–0.64 a	–0.68 a	Tina	–0.53 a	–0.51 a	–0.50 a
D7R7		–0.88 c	–0.89 b	–0.89 b		–0.67 b	–0.65 b	–0.61 b
D14		–1.49 d	–1.56 c	–1.57 c		–1.58 d	–1.59 d	–1.71 c
C	CHD12	–0.69 a	–0.70 a	–0.71 a	Ankora	–0.60 a	–0.58 a	–0.55 a
D14R7		–1.01 c	–0.99 b	–1.07 c		–0.88 c	–0.92 c	–0.93 b
C	CHD247	–0.68 a	–0.69 a	–0.69 a	Tina	–0.59 a	–0.57 a	–0.57 a
D14R7		–0.96 b	–0.97 b	–1.03 b		–0.81 b	–0.85 b	–0.90 b

Table 4. Effect of drought on leaf injury index of leaves differing in age of triticale (CHD12, CHD247) and maize (Ankora, Tina) genotypes (mean ± standard error).

Treatment	Genotype	Leaf number		
		3	5	7
D7	CHD12	18.1 ± 0.73	14.8 ± 0.58	10.8 ± 0.53
	CHD247	13.2 ± 0.61	10.3 ± 0.65	8.3 ± 0.67
	Ankora	25.2 ± 0.49	21.3 ± 0.84	13.5 ± 0.39
	Tina	20.9 ± 0.41	15.6 ± 0.45	12.2 ± 0.42
D7R7	CHD12	19.2 ± 0.52	11.2 ± 0.39	8.8 ± 0.53
	CHD247	12.9 ± 0.37	8.4 ± 0.41	7.6 ± 0.41
	Ankora	23.3 ± 0.39	18.4 ± 0.58	9.3 ± 0.31
	Tina	19.3 ± 0.48	11.5 ± 0.54	8.5 ± 0.81
D14	CHD12	29.0 ± 0.55	27.2 ± 0.39	18.0 ± 0.61
	CHD247	25.2 ± 0.33	21.5 ± 0.51	14.2 ± 0.71
	Ankora	33.2 ± 0.43	31.2 ± 0.67	18.9 ± 0.71
	Tina	30.2 ± 1.11	22.3 ± 0.33	13.3 ± 0.52
D14R7	CHD12	28.9 ± 0.53	22.3 ± 0.42	14.9 ± 0.58
	CHD247	25.6 ± 0.58	17.5 ± 0.77	13.2 ± 0.78
	Ankora	31.3 ± 0.77	30.2 ± 0.54	13.6 ± 0.31
	Tina	27.8 ± 0.78	23.5 ± 0.78	11.2 ± 0.25

for maize genotypes but only for plants subjected to D7. In the treatment D14, D caused larger decrease in ψ of younger leaves, especially in the D-sensitive genotype Ankora. After the 7-d-long recovery (D7R7, D14R7), ψ values for plants earlier subjected to D significantly differed to those in C plants. In triticale genotypes, the differences in ψ for the D-resistant genotype (CHD247) and the D-sensitive one (CHD12) were statistically insignificant, in contrast to maize genotypes (Table 3, Fig. 1*A*).

LI*:* For both species, injuries of older leaves were always higher than those of the younger ones. Mean LI for treatments D7 and D14 were about 12 and 18 % of triticale leaves and about 22 and 25 % for maize, respectively. D-resistant genotypes of triticale and maize (CHD247, Tina) showed significantly lower LI compared to D-sensitive genotypes (CHD12, Ankora). After the 7-d-long recovery, LI changed slightly especially in plants subjected to a D14 (Table 4, Fig. 1*B*).

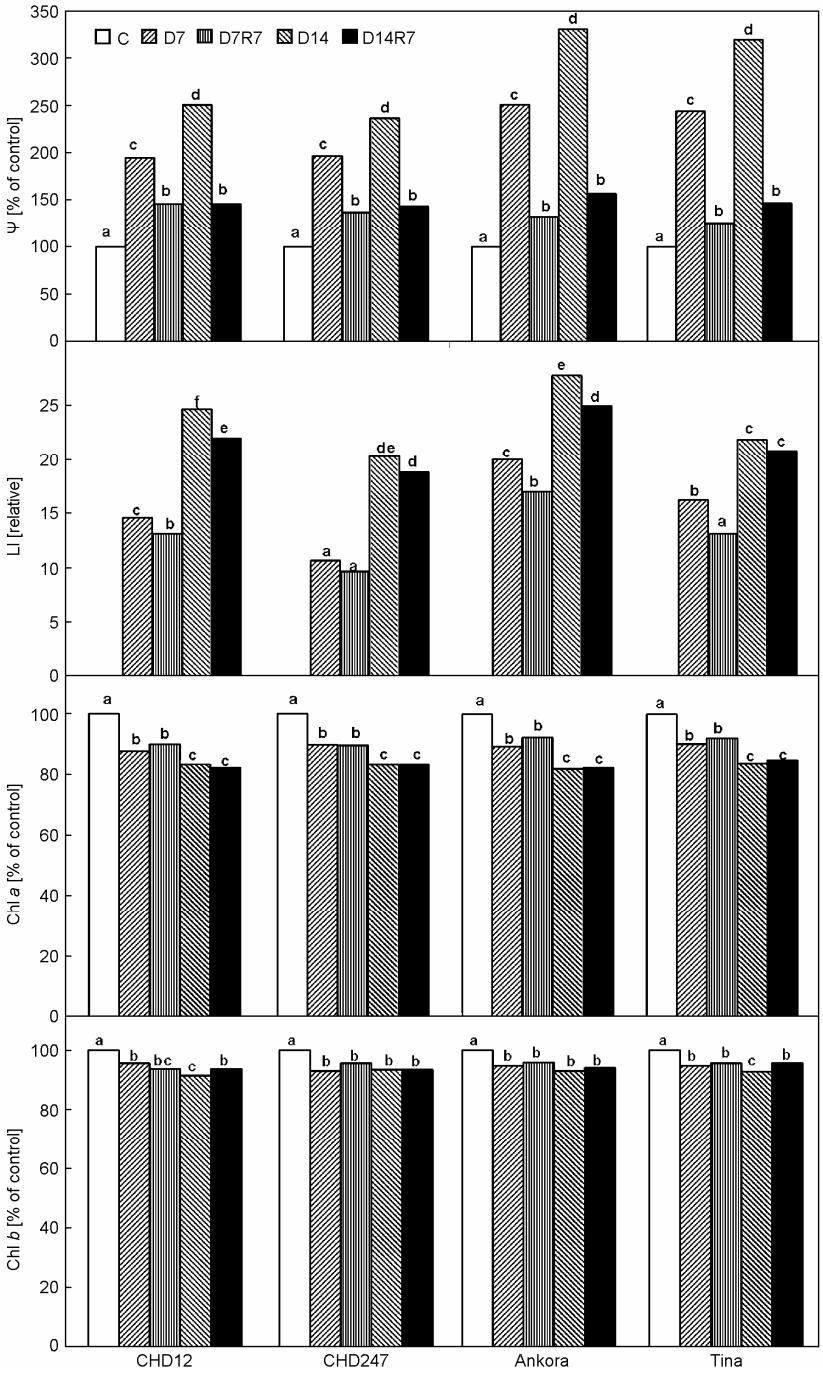

Fig. 1. Direct effect and after-effect of 7 and 14 d of soil drought on (*A*) leaf water potential (ψ), (*B*) leaf injury index (LI), and (*C, D*) chlorophyll (Chl) *a* and *b* contents. Means from measurements on 3rd, 5th, and 7th leaf; values within the same species bars followed by the same letter do not differ significantly according to the Duncan's multiple range test (α=0.05).

Chl content*:* C maize genotypes were characterized by higher Chl *a* and *b* contents per fresh mass unit compared to the triticale. D-resistant genotypes (CHD247, Tina) showed significantly lower content of Chl *a* than the D-sensitive ones. Impact of D on Chl *b* content was significantly less than that on Chl *a* content. D caused higher decrease in Chl *a* content in D-sensitive genotypes. Similarly as ψ, the most harmful impact of D concerned younger leaves in triticale and the older ones in maize. After the 7-d-long recovery, the decrease in Chl content remained constant showing that this period was insufficient to remove or alleviate adverse impact of D on Chl content. Similarly as in the case of after-effects of D on plant DM, ψ, and cell membranes, also in measurements of Chl content of D-resistant genotypes a more efficient removal of D impact was found than in the D-sensitive ones (Table 5, Fig. 1*C,D*).

Discussion

D-stress during the vegetative phase of plant growth causes an inhibition of growth in above-ground part as well as in roots. Our results confirm other results on the differences between the genotypes in D-impact on the production and distribution of DM, grain yield, leaf injury, Chl content, and Chl fluorescence (Kriedemann and Downton 1981, Poljakoff-Mayber 1981, Lorens *et al.* 1987, Schweiger *et al.* 1996, Šesták and Šiffel 1997, Grzesiak *et al*. 2001, 2003). Observed slight direct impact of D on S/R ratio seems to show that during the vegetative growth this parameter is under a genetic control and photosynthates are equally delivered to both developed leaves and roots (Grzesiak *et al.* 1992).

Table 5. Effect of drought on chlorophyll (Chl) *a* and *b* contents in leaves differing in age of triticale (CHD12, CHD247) and maize (Ankora, Tina) genotypes. Means within columns followed by the same letter do not differ significantly according to Duncan's multiple range test (α=0.05).

Genotype	Treatment	Chl *a*			Chl *b*		
		Leaf number					
		3	5	7	3	5	7
CHD12	C	1.11 a	1.18 a	1.13 a	0.44 a	0.47 a	0.45 a
	D7	0.99 c	1.06 c	0.95 c	0.42 ab	0.44 ab	0.43 ab
CHD247	C	1.07 b	1.11 b	1.08 b	0.42 ab	0.43 ab	0.43 ab
	D7	0.98 c	1.03 c	0.92 c	0.39 b	0.41 b	0.40 b
Ankora	C	1.78 a	1.95 a	1.89 a	0.68 a	0.74 a	0.72 a
	D7	1.53 b	1.75 c	1.72 c	0.64 b	0.70 b	0.68 b
Tina	C	1.75 a	1.90 b	1.85 b	0.67 a	0.73 a	0.72 a
	D7	1.52 b	1.72 c	1.72 c	0.63 b	0.69 b	0.68 b
CHD12	C	1.10 a	1.31 a	1.18 a	0.42 a	0.52 a	0.46 a
	D7R7	1.01 b	1.18 bc	1.04 b	0.40 ab	0.49 b	0.43 b
	D14	0.94 c	1.13 cd	0.94 c	0.39 b	0.48 b	0.42 b
CHD247	C	1.03 b	1.22 b	1.16 a	0.41 ab	0.48 b	0.46 a
	D7R7	0.95 c	1.09 d	1.03 b	0.38 b	0.46 c	0.44 ab
	D14	0.88 c	1.05 d	0.93 c	0.39 b	0.45 c	0.43 b
Ankora	C	1.65 a	1.94 a	1.90 a	0.63 a	0.75 a	0.72 a
	D7R7	1.48 c	1.80 cd	1.78 b	0.59 bc	0.72 b	0.69 bc
	D14	1.33 d	1.57 e	1.61 c	0.57 c	0.70 b	0.67 cd
Tina	C	1.60 b	1.88 b	1.88 a	0.61 ab	0.72 bc	0.71 ab
	D7R7	1.44 c	1.76 d	1.75 b	0.59 bc	0.69 c	0.68 c
	D14	1.31 d	1.57 e	1.63 c	0.57 c	0.67 c	0.65 d
CHD12	C	1.05 a	1.28 a	1.17 a	0.42 a	0.50 a	0.47 a
	D14R7	0.89 b	1.07 c	0.93 b	0.39 ab	0.48 b	0.43 b
CHD247	C	1.03 a	1.20 b	1.16 a	0.40 ab	0.48 b	0.46 a
	D14R7	0.89 b	1.01 c	0.93 b	0.38 b	0.45 c	0.43 b
Ankora	C	1.59a	1.92 a	1.99 a	0.51 c	0.73 a	0.76 a
	D14R7	1.29 b	1.56 c	1.68 c	0.48 d	0.69 b	0.73 b
Tina	C	1.58 a	1.83 b	1.91 b	0.59 a	0.70 ab	0.73 b
	D14R7	1.28 b	1.57 c	1.65 d	0.56 b	0.67 c	0.69 c

Osmoregulation is performed by low molecular mass saccharides, amino acids, organic acids, and potassium ions, and its efficiency is the basic mechanism of plant resistance to D-stress (Morgan 1984, 1992). Previous results (Grzesiak 2004) show that water potential for triticale and maize is significantly correlated with D-susceptibility index (DSI) and LI index but not with Chl content. Hence the mechanism of D-influence on current water status and membranes injuries may be different from the mechanism that influences Chl content. We also found that D-resistant genotypes of triticale and maize possess more efficient mechanism for protection of the water status of cells and tissues, *i.e*. a decrease of stomatal conductance (Grzesiak *et al.* 2006) and an increase of content of hydrophilic compounds and stress proteins (Muller and Whitsitt 1996, Shangguan *et al*. 1999, Lawlor 2002, Lawlor and Cornic 2002).

The ability to maintain structure and function of cytoplasmatic membranes under water deficit belongs to the most important physiological traits (Kriedemann and Downton 1981, Poljakoff-Mayber 1981, Boyer 1982). Conductometric measurements of LI reveal a loss of

selective permeability of cytoplasmic membranes and often are applied as a screening test for estimation of tolerance to various stresses (Vietor *et al*. 1977, Richards 1978, Blum and Ebercon 1981, Trapani and Gentinetta 1984, Martiniello and Lorenzoni 1985).

Differences between sensitive and resistant forms might be caused by the fact that D-resistant genotypes possess more efficient mechanisms protecting membrane functions and structure. Our results indicate that leaf age is highly important. These differences were the smallest in the older leaves (3rd leaf) and the youngest ones (7th leaf), however, the most visible changes were observed in the 5th leaf.

D-stress causes loosening of lamellar membranes in chloroplasts, loss of a certain amount of grana, and increase in a level of coarse-grain matrix (Ali 1977, Conroy *et al*. 1988, Haupt-Harting and Fock 2002, Lawlor and Cornic 2002, Tang *et al.* 2002). Some authors suggest that D-resistant plant species show stronger binding of Chl molecules to the lipid-protein complex of chloroplast membranes (Poljakoff-Mayber 1981, Conroy *et al.* 1988, Smirnoff and Colombé 1988, Bukhov *et al.* 1990). Water deficit in leaf tissues causes in most cases a decrease of Chl content and during the recovery these changes may have only a partly reversible character. Influence of D on the content and stability of assimilation pigments was examined in cabbage (Richards 1978), maize (Ali 1997), triticale and maize (Grzesiak 2004), *etc*. In the D-sensitive triticale genotype CHD12 the decrease in Chl *a* content was high for the 7th leaf in which a stronger influence of D on ψ was observed. In the maize D-sensitive genotype Ankora, D caused higher decrease of ψ in old leaves which was paralleled by the highest decrease in Chl *a* content.

We found that differences between D-resistant and D-sensitive triticale and maize genotypes occurred in response to direct and post-D influence estimated by its impact on the above-ground and root DM, ψ, LI, and leaf Chl content. These differences were small, but when D acted for a longer period, it might have induced genotypical variability of D-tolerance.

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