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Changes of leaf water potential and gas exchange during and after drought in triticale and maize genotypes differing in drought tolerance

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Abstract

Influence of drought (D) on changes of leaf water potential (Ψ) and parameters of gas exchange in D-resistant and D-sensitive genotypes of triticale and maize was compared. Soil D (from –0.01 to –2.45 MPa) was simulated by mannitol solutions. At –0.013 MPa significant differences in Ψ, net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and internal CO_2 concentration (C_i) of D-resistant and D-sensitive triticale and maize genotypes were not found. Together with the increase in concentration of the mannitol solution the impact of D on E and g_s for D-sensitive genotypes (CHD-12, Ankora) became lower than for the D-resistant ones (CHD-247, Tina). Inversely, impact of D on Ψ was higher in D-sensitive than D-resistant genotypes. From 1 to 3 d of D, a higher decrease in P_N was observed in D-resistant genotypes than in the D-sensitive ones. Under prolonged D (5–14 d) and simultaneous more severe D the decrease in P_N was lower in D-resistant than in D-sensitive genotypes. Changes in Ψ, P_N, E, and g_s caused by D in genotypes differing in the drought susceptibility were similar for triticale and maize. Compared to control plants, increase of C_i was different for triticale and maize genotypes. Hence one of the physiological reasons of different susceptibility to D between sensitive and resistant genotypes is more efficient protection of tissue water status in resistant genotypes reflected in higher decrease in g_s and limiting E compared to the sensitive ones. Other reason, observed in D-resistant genotypes during the recovery from D-stress, was more efficient removal of detrimental effects of D.

Additional key words: internal CO_2 concentration; net photosynthetic rate; osmotic drought; stomatal conductance; transpiration; *Zea*.

Introduction

Leaf water content and gas exchange are very sensitive to drought (D) stress. Reductions in leaf water potential (Ψ) result in photosynthetic competence in many plant species (Boyer 1982, Bradford and Hsiao 1982). Under mild D, decreases in photosynthesis are generally considered to be the result of reduced availability of CO_2 due to stomatal closure (Mansfield and Davis 1981). However when D is prolonged, a decrease of photosynthesis is controlled by "non-stomatal" mechanisms of gas exchange connected with damages of mesophyll cells, membranes, and chloroplasts, decrease in chlorophyll content, and disturbances in assimilate synthesis and transport (Cornic and Massacci 1996, Giardi *et al*. 1996, Mullet and Whitsitt 1996, Keutgen *et al.* 1997). Limitations of photosynthesis by stomatal as well as non-stomatal mechanisms depend not only on duration and intensity of D-stress but also on plant species, stage of plant development, and leaf age (Kicheva *et al.* 1994). Some of the observed changes in leaf water status and gas exchange are reversible and subside after finishing exposure to D. They may be irreversible and remain even at sufficient water supply (Tripathy *et al*. 1972, Berkowitz *et al*. 1983, Bunce 1988, Passioura *et al*. 1993, Mullet and Whitsitt 1996, Janáček 1997, Šesták and Šiffel 1997). Decrease in net photosynthetic rate (P_N) under water stress is related to disturbances of biochemical processes of non-stomatal nature, caused by oxidation of chloroplast lipids and changes in structure of pigments and proteins (Graan and Boyer 1990, Lauer and Boyer 1992, Moran *et al.* 1994, Menconi *et al.* 1995, Sgherri and Navari-Izzo 1995).

D-stress causes increase in content of the reactive oxygen species (ROS). In response to D-induced oxidative stress plants increase activity of anti-oxidative

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enzymes such as superoxide dismutase (SOD), catalase, peroxidase, or glutathion reductase (Neill *et al*. 2002). The superoxide anion radical occurs in photosystem 1 (PS1) under limited supply of NADP. In photosystem 2 (PS2), the occurrence of ROS is caused by damage of thylakoid membranes, when electrons from water are transferred to oxygen. Very sensitive to oxidative stress are chloroplasts mainly due to high concentration inside these organelles of oxygen, which as a result of irradiation is transformed into singlet oxygen (Sgherri *et al*. 1993, 1996).

Leaves under optimal growth conditions possess a mechanism by which they can down-regulate photosynthesis to avoid over-excitation of PS2 reaction centres (RCs) when they are exposed to irradiances above those at which maximal quantum efficiencies of photosynthesis can be realized. Decrease in Ψ, which results in stomatal closure and reduction in P_N, increases flux of electrons to O_2 to dissipate a large proportion of the excitation energy that had previously been utilized to drive carbon dioxide assimilation (Cornic and Briantais 1991, Baker 1993).

However, increases in rate of reduction of O_2 will not be sufficient to dissipate the excess excitation energy in PS2 antennae and increased down-regulation of photosynthesis will occur and minimize photo-damage to PS2 RCs. Under prolonged mild or severe water deficit the electron transport to O_2 and down-regulation may be unable to dissipate excitation energy in PS2 antennae and, consequently, photo-damage and net loss the D1 protein (32 kDa) of PS2 RCs can result (Baker 1993, Day and Vogelman 1995).

Variability of the tolerance to D within plants belonging to the same species is not completely explained. Among crop species genotypes exist that differ in susceptibility to drought 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). The aim of this work was to estimate changes in water potential and leaf gas exchange for genotypes of triticale and maize resistant and sensitive to D during the direct influence of short-term and prolonged mild and severe osmotic D and during re-hydration.

Materials and methods

Plants: The experiment was carried out on two spring triticale (×*Triticosecale* Wittmack) breeding strains and two maize (*Zea mays* L.) single cross hybrids. The triticale grain was obtained from the Polish Breeding Station, Choryn, Poland and maize grain was from *Sempol Holding*, Trnava, Slovakia. The chosen genotypes differ in drought-susceptibility index (DSI), which was calculated using formulae published by Fischer and Maurer (1978) and Blum and Ebercon (1981). On the basis of field and laboratory tests of D-susceptibility, 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 triticale strain CHD-12 and maize hybrid Ankora to the group of D-sensitive genotypes (DSI = 0.544 and 0.650, respectively) (Grzesiak 2004).

Seedling growth: Experimental plants were grown in air-conditioned growth cabinets under the following day/night conditions: temperature 23/18 °C (±2.5 °C), relative humidity (RH) 70/60 % (±5 %), and 16-h day (artificial irradiance from high pressure sodium lamps, *Philips SON-T AGRO*, 400 W). Photosynthetically active radiation (PAR) was about 500 μmol m^{-2} s^{-1}.

Germinated grains of triticale and maize genotypes were placed on the polystyrene foam plates in hydroponic containers (volume 18 000 cm^3, surface 5 800 cm^2). Hydroponic solutions were aired with compressed air (700 cm^3 h^{-1}). Conditions of simulated D in hydroponic cultures were obtained by using mannitol (*Lobe Chemia*) water solutions. Concentration of mannitol in the hydroponic solution (from –0.25 to –2.45 MPa) at the required chemical water potential (Ψ_S) was calculated according to Michel *et al.* (1983). The seedlings were fed on diluted Hoagland nutrient solution. After 21 d of seedling growth in control conditions (Ψ_S = –0.013 MPa) the 14-d-long D exposure was established. From 1st to 7th d of D, Ψ_S of hydroponic solution was gradually decreased from –0.013 to –1.750 MPa, changing Ψ_S in the following days by –0.250 MPa per day. From 8th till 14th day, Ψ_S was decreased by 0.100 MPa daily, from –1.750 to –2.450 MPa. After 7 or 14 d in groups of seedlings (treatments D-7 and D-14) control conditions were re-established for 7 d (R = recovery) (Fig. 1).

Measurements: The leaf water potential (Ψ) and gas exchange parameters were measured in leaves of full physiological activity, which means maximal leaf area. Between 21st and 28th d of growth, measurements were taken on the fourth leaf, from 29th and 35th d on the fifth leaf, and between 36th and 42nd d on the sixth leaf.

Ψ was measured with psychrometer *HR 33T* (*Wescor*, USA) in the mode "dew point" equipped with sample chamber *C-52 SF* by *Wescor* and digital multimeter *Metex M-3640 D*. Measurements were done on leaf disks of diameter 0.3 cm for triticale and 0.5 cm for maize, cut from the middle part of the leaf. Results were calculated using a graph program *Metex*.

Gas exchange parameters (P_N, E, g_s, C_i) were measured using CO_2 IRGA analyzer *CI-301PS* (*CID*, Vancouver, USA) with Parkinson's assimilation chamber, type narrow regulator, and light attachment *CI-301 LA*. During

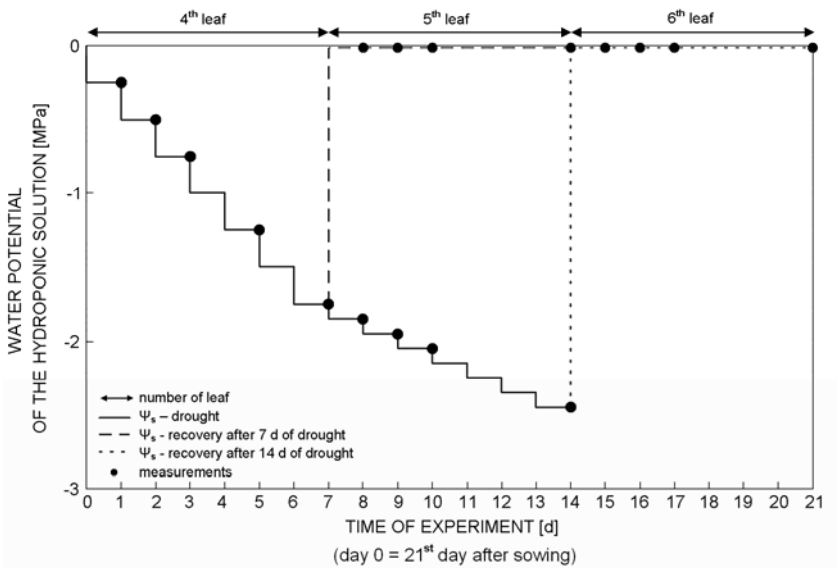

Fig. 1. Schedule of daily changes of water potential of the hydroponic solutions (Ψ_S), days of measurement of leaf water potential, (Ψ) and gas exchange parameters, and number of leaf on which the measurements were taken.

measurements an open system was used. A flow rate of ambient air with constant CO_2 concentration [360 µmol(CO_2) mol^{-1}(air)] through the assimilation chamber was 500 cm^3 min^{-1} and chamber temperature was kept under 25 °C until P_N was steady. Photosynthetic capacity at saturation irradiance was reached by exposing leaves to PAR of 800 µmol(quantum) m^{-2} s^{-1}.

For each of 14 d, measurements of Ψ or gas exchange parameters of examined genotypes (2) and treatments (2 or 3) were done between 11:00 and 13:00 h in 5 replications.

Statistical analysis used Duncan's multiple range tests.

Results

Ψ: In control conditions (–0.013 MPa), no statistically significant differences were observed in Ψ of D-resistant or D-sensitive triticale strains and maize hybrids. Increase in mannitol concentration of hydroponic solution caused in sensitive genotypes (CHD-12, Ankora) a higher decrease in Ψ than in resistant genotypes (CHD-247, Tina).

Table 1. The changes of leaf water potential (Ψ) [MPa] of drought sensitive (CHD 12, Ankora) and drought resistant (CHD 247, Tina) genotypes of triticale and maize. C – control, D – drought, R – recovery. Means within columns followed by the same letter do not differ significantly according to Duncan's multiple range test (α = 0.5).

		[d]	1	2	3	5	7	8	9	10	14	15	16	17	21
		Leaf	L4					L5				L6			
		Ψ_S	–0.25	–0.50	–0.75	–1.25	–1.75	–1.85	–1.95	–2.05	–2.45				
Triticale	CHD-12	C	–0.62a	–0.63a	–0.65a	–0.59a	–0.67a	–0.65a	–0.67a	–0.70a	–0.65a	–0.65a	–0.65	–0.68	–0.74a
		D	–1.26b	–1.41c	–1.60c	–1.95b	–2.47c	–2.45e	–2.46d	–2.54c	–2.65c				
		D7R						–1.56c	–1.49c	–1.13b	–0.83a				
		D14R										–2.13b	–1.63b	–1.65c	–1.11b
	CHD-247	C	–0.58a	–0.65a	–0.67a	–0.63a	–0.65a	–0.68a	–0.64a	–0.72a	–0.61a	–0.60a	–0.62a	–0.67a	–0.71a
		D	–1.13b	–1.25b	–1.39b	–1.45c	–1.94b	–2.11d	–2.20d	–2.21c	–2.28b				
		D7R						–1.34b	–1.18b	–1.00b	–0.73a				
		D14R										–1.95b	–1.45b	–1.35b	–0.95ab
Maize	Ankora	C	–0.67a	–0.53a	–0.65a	–0.65a	–0.56a	–0.68a	–0.62a	–0.60a	–0.57a	–0.58a	–0.56a	–0.65a	–0.65a
		D	–1.42c	–1.61c	–1.85c	–2.11c	–2.31c	–2.53d	–2.55d	–2.50d	–2.67d				
		D7R						–1.91b	–1.56b	–1.13c	–1.11b				
		D14R										–1.99b	–1.73b	–1.53b	–1.33c
	Tina	C	–0.70a	–0.49a	–0.69a	–0.62a	–0.52a	–0.65a	–0.58a	–0.64a	–0.56a	–0.55a	–0.53a	–0.67a	–0.67a
		D	–1.11b	–1.26b	–1.39b	–1.65b	–1.88b	–2.07c	–2.18c	–2.11d	–2.13c				
		D7R						–1.76b	–1.35b	–0.94bc	–0.81ab				
		D14R										–1.88b	–1.59b	–1.39b	–1.13b

Differences between D-resistant and D-sensitive triticale and maize genotypes were statistically significant in most cases. After 7 or 14 d of R, Ψ differed from the control significantly, with the exception of D-resistant maize hybrid Tina after 7-d D (Table 1, Fig. 2).

Gas exchange parameters: Similar to Ψ, in control conditions no statistically significant differences between resistant and sensitive triticale and maize genotypes were found for most gas exchange parameters (Tables 2 to 5). During the 3-d exposure to osmotic D, D-resistant genotypes (CHD-247, Tina) showed a larger decrease in P_N than the D-sensitive genotypes (CHD-12, Ancora). From the 4th d of D-period the decrease in P_N was progressing slower and stabilized at higher level in D-resistant genotypes than in the D-sensitive ones (Table 2, Fig. 3*A*). During 14 d of D, the D-resistant genotypes showed greater decrease in E and g_s than the D-sensitive ones (Tables 3 and 4, Fig. 3*B*,*C*). Distinct differences in response to the D-stress between triticale and maize seedlings were observed in C_i. The increase in C_i in comparison to control plants was most distinct for the D-sensitive genotypes (Table 5, Fig. 3*D*).

During recovery (R) of plants subjected to 7 or 14 d of D, a return of gas exchange parameters to the control values was noticed. In the D-sensitive genotypes after 7 d of R the differences in results were larger then those found for the D-resistant ones. It may indicate that especially in D-sensitive genotypes the 7-d-long period of R is insufficient to alleviate the detrimental effects of D.

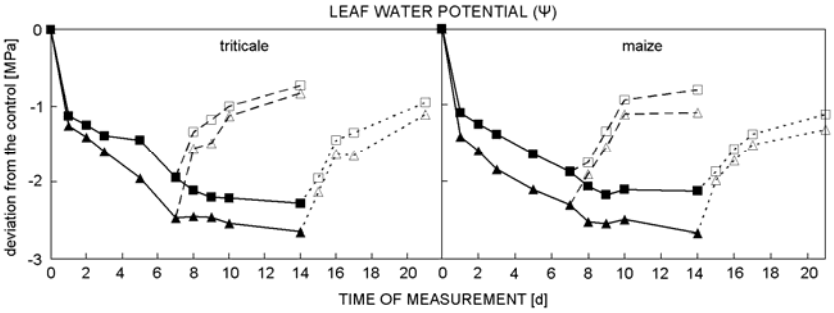

Fig. 2. Changes of leaf water potential for drought sensitive (CHD-12, Ankora) and drought resistant (CHD-247, Tina) triticale and maize genotypes. Drought (*full line*): ▲ (CHD-12, Ankora), ■ (CHD-247, Tina). Recovery after 7-d-long (*dashed line*) or 14-d-long (*dotted line*) drought: Δ (CHD-12, Ankora), □ (CHD-247, Tina). Results presented as a deviation from the control.

Table 2. Changes of net photosynthetic rate (P_N) [μmol(CO_2) m^{-2} s^{-1}] of drought-sensitive (CHD 12, Ankora) and drought-resistant (CHD 247, Tina) genotypes of triticale and maize. C – control, D – drought, R – recovery. Means within columns followed by the same letter do not differ significantly according to Duncan's multiple range test (α = 0.05).

		[d]	1	2	3	5	7	8	9	10	14	15	16	17	21
		Leaf	L4					L5				L6			
		Ψ_S	–0.25	–0.50	–0.75	–1.25	–1.75	–1.85	–1.95	–2.05	–2.45				
Triticale	CHD-12	C	15.8a	16.2a	16.7a	17.2a	15.6a	15.3a	15.8a	15.9a	16.7a	16.8a	16.9a	15.8a	15.7a
		D	14.4b	14.4b	14.2c	10.5c	8.1b	8.1d	7.7c	7.3d	7.8c				
		D7R						8.7cd	10.9b	12.7c	15.1b				
		D14R										8.8c	10.3c	12.1b	12.7c
	CHD-247	C	15.6a	16.0a	15.3b	15.8b	15.1a	15.3a	15.5a	16.7a	14.7b	14.6b	15.4b	14.7a	14.0b
		D	13.3c	13.0c	12.2d	10.1c	9.0b	9.0c	8.4c	8.3d	7.0c				
		D7R						9.9b	11.5b	14.4b	13.6b				
		D14R										7.8c	9.5c	11.5b	12.0c
Maize	Ankora	C	27.1a	28.0a	29.3a	24.1b	25.1b	27.6a	24.3a	27.1a	26.9a	25.8a	28.1a	28.0a	26.5a
		D	16.3b	26.2b	26.2b	18.3c	17.9d	19.2d	14.7e	14.8d	14.3c				
		D7R						20.7c	20.2c	24.1b	24.8b				
		D14R										15.7b	18.4c	19.5c	20.6c
	Tina	C	27.4a	27.3a	29.1a	26.2a	26.5a	26.0b	25.2a	24.3b	27.2a	25.1a	26.9b	27.2a	26.5a
		D	26.0b	24.5c	23.8c	20.9b	20.6c	20.1cd	16.5d	14.7d	15.0c				
		D7R						20.5c	22.3b	22.6c	26.4a				
		D14R										15.7b	19.0c	21.7b	22.6b

Table 3. Changes in transpiration rate (E) [mmol(H_2O) m^{-2} s^{-1}] of drought-sensitive (CHD 12, Ankora) and drought resistant (CHD 247, Tina) genotypes of triticale and maize. C – control, D – drought, R – recovery. Means within columns followed by the same letter do not differ significantly according to Duncan's multiple range test ($\alpha = 0.05$).

		[d]	1	2	3	5	7	8	9	10	14	15	16	17	21
		Leaf	L4					L5				L6			
		Ψ_S	–0.25	–0.50	–0.75	–1.25	–1.75	–1.85	–1.95	–2.05	–2.45				
Triticale	CHD-12	C	3.11a	3.54a	3.44a	3.31a	3.41a	3.22a	3.45a	3.39a	3.71a	3.54a	3.47a	3.56a	3.65a
		D	2.81b	3.02b	2.73b	2.30b	2.06b	1.76c	1.54c	1.53d	1.49c				
		D7R						2.04b	2.42b	2.55c	3.32b				
		D14R										1.98b	2.10b	2.47b	2.56b
	CHD-247	C	2.88b	2.95b	3.11a	3.13a	3.18a	3.39a	3.49a	3.41a	3.11b	3.18a	3.39a	3.65a	3.45a
		D	2.34c	2.31c	2.22c	1.94b	1.72c	1.68c	1.36c	1.40d	1.11c				
		D7R						2.11b	2.43b	2.73b	2.93b				
		D14R										1.57c	2.13b	2.75b	2.84b
Maize	Ankora	C	2.11a	2.07b	2.08a	2.13a	2.39a	2.41a	2.49a	2.22a	2.55a	2.76a	2.54a	2.36a	2.61a
		D	1.90b	1.77c	1.69b	1.61b	1.32b	1.41bc	1.48c	1.00c	1.03d				
		D7R						1.57b	1.60b	1.60b	2.05b				
		D14R										1.76b	1.54c	1.54c	2.02b
	Tina	C	2.13a	2.39a	2.11a	2.06a	2.45a	2.28a	2.47a	2.05a	1.98bc	1.87b	1.90b	1.95b	2.08b
		D	1.89b	1.93bc	1.59c	1.32c	1.23b	1.16d	1.32d	0.94c	0.76d				
		D7R						1.35bc	1.53bc	1.55b	1.78c				
		D14R										1.20c	1.21c	1.31c	1.69c

Table 4. Changes in stomatal conductance (g_s) [mmol(CO_2) m^{-2} s^{-1}] of drought sensitive (CHD 12, Ankora) and drought resistant (CHD 247, Tina) genotypes of triticale and maize. C – control, D – drought, R – recovery. Means within columns followed by the same letter do not differ significantly according to Duncan's multiple range test ($\alpha = 0.05$).

		[d]	1	2	3	5	7	8	9	10	14	15	16	17	21
		Leaf	L4					L5				L6			
		Ψ_S	–0.25	–0.50	–0.75	–1.25	–1.75	–1.85	–1.95	–2.05	–2.45				
Triticale	CHD-12	C	95.4a	88.4a	93.2a	97.2a	95.3a	87.6a	90.2a	93.2a	94.4a	88.4b	88.1a	86.5a	95.4a
		D	91.2ab	85.1b	79.2bc	74.5c	59.8b	56.5d	51.2d	52.3d	48.2d				
		D7R						60.4c	62.3c	70.3c	90.8b				
		D14R										75.3d	71.9b	76.9c	91.2bc
	CHD-247	C	89.5b	84.5	84.2b	80.2b	94.2a	86.7a	88.9a	94.8a	90.0b	95.2a	91.1a	89.6a	94.2a
		D	81.8c	71.3c	59.3d	56.0d	58.3b	56.7d	52.6d	49.0d	50.3d				
		D7R						64.2b	67.5b	77.6b	83.0c				
		D14R										82.9c	74.9b	82.3b	87.4c
Maize	Ankora	C	121.0a	122.3a	107.0b	113.1b	118.3a	108.3b	113.5b	120.9a	119.6a	113.8a	121.5a	123.2a	113.0b
		D	111.0b	84.5b	88.8c	70.8c	72.3b	65.4de	59.5d	52.0d	45.2b				
		D7R						70.2d	75.0c	88.8c	124.3a				
		D14R										67.1b	72.4b	85.2b	101.1c
	Tina	C	123.5a	120.5a	119.1a	124.2a	123.5a	121.4a	123.9a	120.4a	128.3a	120.5a	118.7a	126.4a	126.2a
		D	98.7c	75.2c	70.2d	59.2d	51.4c	55.8e	41.5c	41.6e	39.0b				
		D7R						91.2c	71.2c	99.3b	125.4a				
		D14R										71.5b	70.6b	90.5b	107.9c

Discussion

Research on impact of D on photosynthesis is very frequent (Kriedemann and Dowton 1981, Mansfield and Davies 1981, Westgate and Boyer 1985, He *et al*. 1995, Lawlor and Cornic 2002). Actual plant water status depends on osmotic conditions of cells and transport of water from shoot. During the inhibition of water transport from root, osmotic regulation may actively influence water potential in assimilating tissues and limit detrimental effects of water deficiency on photosynthesis. Limitation in inhibiting photosynthesis under low Ψ might be caused by keeping relatively great volumes of protoplasts. In sunflower under periodical mild water

Table 5. Changes in internal CO_2 concentration (C_i) [μmol(CO_2) mol^{-1}(air)] of drought sensitive (CHD 12, Ankora) and drought resistant (CHD 247, Tina) genotypes of triticale and maize. C – control, D – drought, R – recovery. Means within columns followed by the same letter do not differ significantly according to Duncan's multiple range test (α = 0.05).

		[d]	1	2	3	5	7	8	9	10	14	15	16	17	21
		Leaf	L4					L5				L6			
		Ψ_S	–0.25	–0.50	–0.75	–1.25	–1.75	–1.85	–1.95	–2.05	–2.45				
Triticale	CHD-12	C	294.2bc	300.5b	287.3c	297.1bc	278.6d	299.4b	313.2b	325.2b	286.5c	285.6a	308.2ab	311.6a	300.5b
		D	311.0a	318.1a	313.0a	339.4a	341.5a	333.5a	341.0a	349.8a	311.4a				
		D7R						325.5a	291.5c	287.5d	277.1d				
		D14R										277.5b	313.0a	307.8a	311.0a
	CHD-247	C	287.5bc	254.6d	294.5b	287.2c	290.2c	300.5b	313.7b	308.0c	299.0b	291.3b	290.0b	307.5a	287.4c
		D	296.5b	274.2c	307.8a	308.7b	318.1b	311.7b	339.9a	329.5b	318.4a				
		D7R						285.2c	300.8bc	291.5d	301.8b				
		D14R										285.4a	280.0b	279.5b	284.6c
Maize	Ankora	C	155.8a	167.8a	170.2a	175.6a	175.4a	184.3a	175.2a	150.2b	168.3a	165.3b	154.2bc	158.1b	167.2a
		D	145.2b	152.6b	154.2b	149.5b	151.5c	140.2d	148.2b	139.2c	140.3b				
		D7R						169.5b	176.5a	161.1a	169.5a				
		D14R										167.5a	160.9b	160.5b	154.2c
	Tina	C	158.4a	155.4b	164.2a	172.4a	165.3b	157.2c	170.1a	161.4a	162.5a	159.7c	168.5b	159.9b	160.6bc
		D	149.2b	141.2c	149.8b	150.1b	149.2c	137.5d	143.2b	140.2c	142.3b				
		D7R						155.2c	169.2a	170.5a	165.7a				
		D14R										161.1bc	180.4a	170.4a	165.2ab

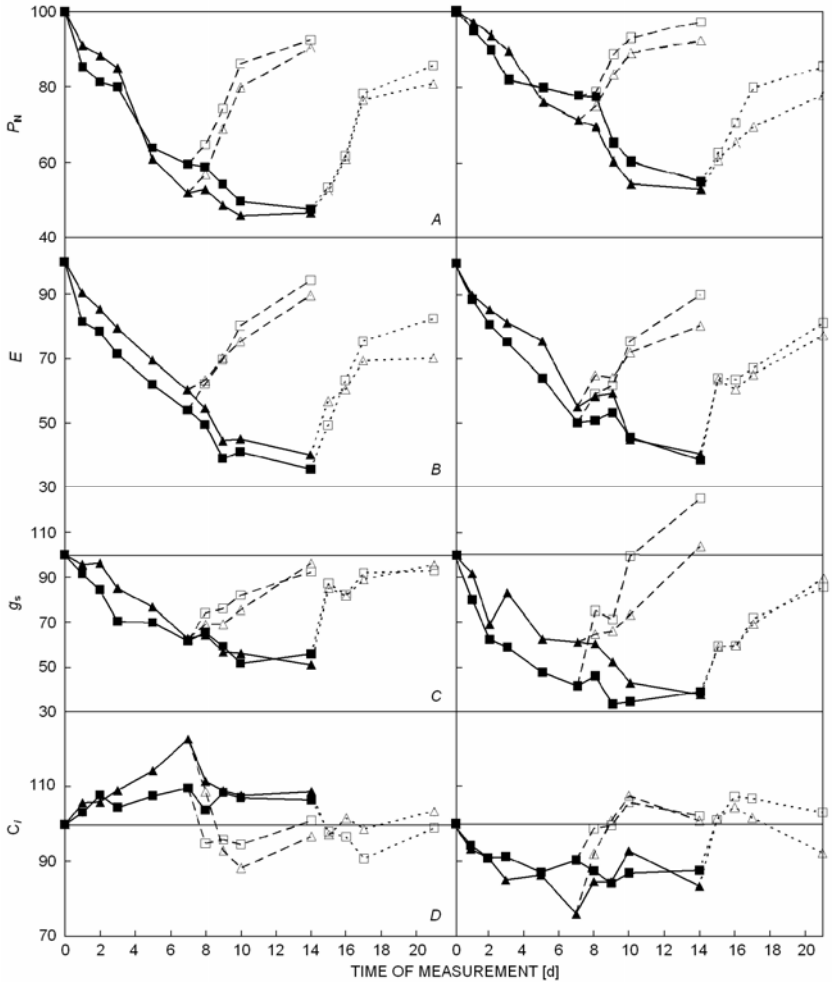

Fig. 3. Changes of leaf gaseous exchange parameters (net photosynthetic rate, P_N; transpiration rate, E; stomatal conductance, g_s; internal CO_2 concentration, C_i) for drought sensitive (CHD-12, Ankora) and drought resistant (CHD-247, Tina) triticale and maize genotypes. For symbols see the legend to Fig. 2. Results presented as a percent of control.

stress adaptations to low water potential were observed contrary to plants not acclimated to D, in which full inhibition of photosynthesis occurred (Matthews and Boyer 1984, Chaves *et al*. 2002, Cornic and Fresneau 2002, Medrano *et al.* 2002). Similarly, Shangguan *et al.* (1999) confirmed for winter wheat that at gradual increase of D, P_N is inhibited more slowly than at sudden exposure to D. According to the cited authors, for such impact of D on photosynthesis osmotic regulation in leaf tissue is responsible which directly influences stomatal regulation and adaptation of the photosynthetic apparatus. For the decrease in P_N during water deficit in tissues, stomatal (during the short-term or mild D) or non-stomatal mechanisms (during prolonged and severe D) are responsible. The "non-stomatal" mechanisms include changes in chlorophyll synthesis, functional and structural changes in chloroplasts, and disturbances in processes of accumulation, transport, and distribution of assimilates.

Our results for triticale and maize genotypes indicate that observed changes caused by D were similar for Ψ, P_N, E, and g_s but different for C_i. In comparison with control plants, increase of C_i for triticale genotypes and decrease of C_i for maize genotypes was observed. Changes in C_i and chloroplast dysfunctions reduce P_N in a leaf and might change the quantum efficiency of non-cyclic photosynthetic electron transport (Cornic and Briantais 1991, Baker 1993). Under severe D its impact on changes of P_N between D-resistant and D-sensitive genotypes was not always significant as that under mild D. Probably in these conditions the effect of non-stomatal mechanism regulation of photosynthesis occurred. Our recent work (Grzesiak 2004) showed in D-resistant genotypes a detrimental effect of D on membranes, chlorophyll content, and potential quantum efficiency of PS2. During D-stress the impact on Ψ was smaller in D-resistant genotypes. During this period in these genotypes a higher decrease in E was observed which undoubtedly limited the loss of water. It might indicate that D-resistant genotypes have more efficient protection mechanisms against water loss by cells. Measurements of water potential and gas exchange parameters during recovery indicate that the D-resistant genotypes tend to fast return to the condition observed for control plants which was especially distinct in measurements after 7-d-long D-exposure. It suggests that D-resistant genotypes have more efficient mechanisms to remove reversible injuries caused by D-stress.

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