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Leaf morphology and water status changes in *Triticum durum* under water stress

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Water relations, leaf morphology and the chemical composition of cell walls in irrigated and unirrigated plants of three durum wheat cultivars were measured at two growth stages (booting and flowering). Plant response to water stress differed at the two stages: cell wall elasticity increased at booting and osmotic potential values decreased at flowering; this may be due to the changes in stress history, leaf development and plant growth stage between the two harvests. Leaf tissue characteristics were modified by water stress only at flowering: accumulation of fibrous constituents and hemicellulose in the cell walls, reduction of acid detergent fiber (ADF) per unit of leaf area, increase in specific leaf weight (SLW), decrease in turgid weight/dry weight ratio (TW/DW) and alteration in mesophyll cell morphology (cell area / cell perimeter ratio) were observed.

Generally, cv. Valforte (the less drought-resistant cultivar) had the greatest mesophyll cell area and perimeter and it had greater values of neutral detergent fiber (NDF) at the booting stage than cv. Appulo. Reactivity to water stress differed in the cultivars: Valforte showed the greatest increase in hemicellulose content and decrease in cell dimensions under drought at flowering.

No significant relationships between osmotic potential and mesophyll cell characters were observed; there were no correlations among cell wall elasticity, cell morphology and the chemical components of leaf tissue. The total fiber content and the hemicellulose per unit of leaf area were correlated with the TW/DW ratio at flowering. This parameter decreased more in plants subjected to water stress owing to accumulation of hemicellulose. Correlations between leaf structural constituents and Ψ_{π}^{100} suggest that the absorptive capacity of the cell wall may significally affect the osmotic volume of the cell.

Key words – Cell morphology, cell wall chemistry, cell wall elasticity, hemicellulose, osmotic potential, *Triticum durum*, water stress.

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Introduction

Leaf tissue characters are variously affected by water stress: a decrease in cell size and/or cell number was observed in cotton epidermis (Ivanitskaya 1962, Cutler et al. 1977, Levitt 1980, Kriedemann 1986) and in palisade and mesophyll cells (Wignarajah et al. 1975, Wilson et al. 1980), while an increase in epidermal cell dimensions was reported by Meiri and Poljakoff-Mayber (1967). Results for the amount of leaf structural tissue were also contrasting in water-stressed plants. Levitt (1980) and Pitman et al. (1983) observed a greater total cell wall content and an increase in vascular tissues and/or in thickness of cell walls relative to unstressed plants, but an opposite response was reported by Wilson and Ng (1975).

An increase in leaf thickness can generally be induced by water stress (Poljakoff-Mayber 1975, Wignarajah et

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al. 1975, Pitman et al. 1983). The results of a field study on drought-stressed durum wheat (Rascio et al. 1988) showed that leaf structure (leaf turgid weight/dry weight ratio) is correlated with its osmotic potential. These findings agree with observations of several authors (Wilson et al. 1980, Joly and Zaerr 1987) who hypothesized an influence of leaf tissue characteristics on components of the water relations. In fact, an increase in cell wall thickness and reduction of cell sizes induced by water stress lowers the cellular osmotic potential, contributing to turgor maintenance when the leaf water potential decreases (Cutler et al. 1977). Tyree and Jarvis (1982) considered these results unconvincing and asserted that the bulk modulus of elasticity (ε) depends on structural properties of the tissue and individual cell walls.

The objective of the present investigation was to evaluate if there are associations between leaf structural components and water relation parameters under drought stress. Mesophyll cells were analyzed in particular because these cells are important in osmotic adjustment (Daie 1988).

Abbreviations – ADF, acid detergent fiber; ε, bulk modulus of elasticity; NDF, neutral detergent fiber; Ψ_π^{100}, osmotic potential at full turgor; Ψ, water potential; SR, stomatal resistance; SLW, specific leaf weight; TW/DW, turgid weight/dry weight ratio.

Materials and methods

Plant material and experimental design

A field trial was conducted on 3 durum wheat cultivars (*Triticum durum* Desf.): Valforte, Appulo and Capeiti 8. On the basis of field performance, Valforte is a more drought-sensitive cultivar, but it has a higher yield in irrigated environments than Appulo and Capeiti 8. Sowing date was 6th December 1987, seed density was 400 seeds m^{-2} and plots were 7.50 × 1.70 m. Fertilization was applied at stem elongation with 300 kg ha^{-1} of ammonium nitrate. The soil was of medium texture. A split-plot design was used for sowing with 2 treatments: a) irrigated (230 mm from April to May); b) unirrigated.

Eight samples were taken during the stem elongation to milk stage period to determine plant water status: the youngest, fully expanded leaves were selected at random from one plant of each plot. Leaf water potential was measured with a pressure chamber (Scholander et al. 1965) (PMS Instrument Co., Corvallis, OR, USA) and stomatal resistance with a steady-state porometer (Licor LI-1600). Pressure-volume curves and leaf structural parameters were determined at booting and at flowering on leaves of cvs Valforte and Appulo and at flowering on Capeiti 8.

At the first sampling the leaf immediately below the flag leaf was collected. It had suffered drought when the lamina was completely expanded. At the second sampling the flag leaf was collected; it had been subjected to drought during lamina expansion.

Pressure-volume curves

At each sampling one of the youngest fully expanded leaves was taken at random from one plant for each plot. Pressure-volume curves and parameters were obtained as described earlier (Rascio et al. 1988). Reciprocals of Ψ were plotted against water saturation deficit. The following parameters were determined from pressure-volume curves: Relative water content at zero turgor (RWC_o), osmotic potential at full turgor (Ψ_π^{100}) (Wilson et al. 1979) and bulk modulus of elasticity (ε) using Warren Wilson's (1967) formula:

$$\varepsilon = \mathrm{tg}\ \alpha \times RWC_o$$

where α is the slope of the regression line for a plot of turgor potential (obtained from P-V curves) vs RWC. Leaf turgid weight was measured by Ladiges' (1975) method. Leaf area was determined by an area meter model AAM-73, (Hayashi Denkoh Co., LTD, Tokyo Japan). Specific leaf weight was obtained as leaf dry weight/leaf area ratio.

Cell Measurements

For analysis of mesophyll cells, a 2.5 mm section was cut from the middle of 6 fully expanded leaves per replicate. Each portion was fixed in formalin: acetic acid: ethanol (2:1:17). The fixed tissue was immersed in 6 NaOH for 24–36 h to obtain isolated cells and then rinsed in water and macerated on a glass slide in one drop of 0.1% aqueous safranin. Isolated cells were examined by light microscopy and photographed using a microscope-mounted camera. Camera lucida drawings were obtained from the outline of the separated mesophyll cells (Parker and Ford 1982). Plane area and cell perimeter were measured by an image analyser (Morphomat-10, Zeiss, Germany).

Chemical analysis of cell wall

About 1 g of dry leaf tissue was ground to pass though a 20-mesh screen. Neutral detergent fiber (NDF), mainly insoluble hemicellulose, cellulose and lignin, and acid detergent fiber (ADF), the sum of raw lignin and cellulose, were determined as described by Goering and Van Soest (1970). Hemicellulose was calculated as the difference between NDF and ADF. Values of chemical parameters are expressed as mg/unit of leaf area.

Results and discussion

The time course of some environmental variables (rainfall and evaporation) during the period from September 1986 to June 1987 is shown in Fig. 1. Starting from

April, at stem elongation, leaf water potential for unirrigated plants (Fig. 2) decreased rapidly (stress rate ca 0.14 MPa day^{-1}) until heading, when it reached values of −4.5 MPa and then increased at the same rate, reaching about −2.5 MPa at flowering. The trend of stomatal resistance was well related to the changes in water potential. From stem elongation onward, both parameters differed significantly between unirrigated and irrigated plants. Plant reactivity to water stress was very different at flowering and booting; this may be due to the fact that stress history, leaf development and plant growth stages changed for the two harvests.

At the first harvest (booting stage) the duration of the water stress period was about 10 days and the leaf immediately below the flag leaf was fully expanded. Analysis of variance (Tab. 1) on parameters obtained from pressure-volume curves showed that only cell wall elasticity increased under drought stress. Mesophyll cell morphology (Tab. 2) and cell wall constituents (Tab. 3) were not affected by water stress. Genotypic differences were observed; Valforte (the less drought-resistant cultivar) had greater values of NDF, mesophyll cell area and perimeter than Appulo, and its cell plane area increased under drought.

At the second harvest (flowering stage), the duration of water stress was ca 1 month and it occurred when flag leaves were not fully expanded. Osmotic potential values were more negative in unirrigated plants than in irrigated ones, TW/DW ratio and leaf area decreased, SLW increased, while the bulk modulus of elasticity (ε) remained constant (Tabs 4 and 5). As observed in previous work (Kikuta and Richter 1988, Rascio et al. 1988), osmotic adjustment occurs independently of stress rate, but the growth stage may greatly affects the plant response.

Osmotic potential seems to be a leaf parameter connected to drought resistance, in fact it had the highest values in Valforte. The effectiveness of this parameter as a drought tolerance mechanism was pointed out by Morgan (1983), who supposed that a single gene controlled this character. The grain yield under drought conditions in wheat selected from highly osmoregulating lines was greater than from poorly osmoregulating ones (Morgan 1983).

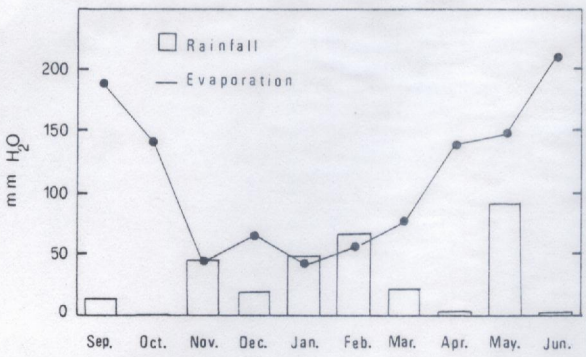

Fig. 1. Monthly evaporation and rainfall values from September 1986 to June 1987.

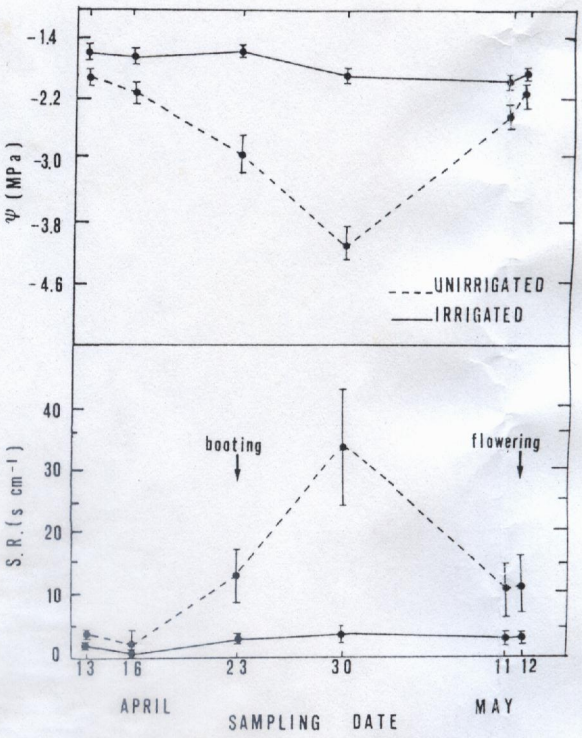

Fig. 2. Seasonal variations in leaf water potential (Ψ) and stomatal resistance measured at midday for unirrigated and irrigated plants. Means ± SE (n = 16).

At flowering the fiber content of the cell wall per unit of leaf area (NDF) increased for water-stressed leaves that had greater content of hemicellulose and lower ADF content per unit of leaf area than well watered plants (Tab. 6). Generally, mesophyll cell morphology was the only parameter to change under drought as showen by the reduction in cell area/cell perimeter ratio (Tab. 5). Differences among cultivars were observed in mesophyll cell morphology and dimensions: Valforte had the greatest cell area and perimeter, but it also reacted differentially to water stress, in fact it only showed reduction in cell plane area and cell perimeter under drought. The hemicellulose content of cv. Valforte increased greatly for unirrigated plants. The reactivity of this cultivar to water stress may partially compensate for the lack of xerophytic characters visible in its SLW, Ψ_π^{100}, TW/DW, cell area and cell perimeter values under irrigated conditions.

Linear correlation coefficients between parameters obtained by pressure-volume curves and structural characters for irrigated and unirrigated plants confirmed our previous results, but only at the flowering stage, when the decrease in TW/DW ratio was correlated with changes in Ψ_π^{100} (Tab. 7). Reduction in leaf area under drought was not correlated with mesophyll cell area. This indicates that expansive processes in the cell are

Tab. 1. Pressure-volume curve parameters from irrigated and unirrigated leaves of two durum wheat cultivars. Booting stage. Values are means of 4 determinations. Significance of F (Fisher's test) values are shown (*,** = significant at 0.05 and 0.01 probability levels, respectively; n.s. = not significant).

Parameter	Cultivar	Treatment			F values		
		Irrigated	Unirrigated	Average	Treatment	Cultivar	Interaction
Ψ_π^{100} (−MPa)	Appulo	1.4	1.3	1.4	n.s.	n.s.	n.s.
	Valforte	1.3	1.3	1.3			
TW/DW	Appulo	4.3	4.0	4.2	n.s.	n.s.	n.s.
	Valforte	4.3	3.9	4.1			
ε (MPa)	Appulo	11.7	5.2	8.1	**	n.s.	n.s.
	Valforte	10.3	6.2	7.2			

Tab. 2. Some morphological parameters for the last fully expanded leaves and mesophyll cell dimensions calculated from plane areas of 25 isolated cells. Booting stage. Significance symbols as for Tab. 1. Tukey's test as for Tab. 4.

Parameter	Cultivar	Treatment			F values		
		Irrigated	Unirrigated	Average	Treatment	Cultivar	Interaction
Specific leaf weight (mg cm^{-2})	Appulo	3.7	3.5	3.5	n.s.	n.s.	n.s.
	Valforte	4.3	4.3	4.3			
Leaf area (cm^2)	Appulo	23.7	25.1	24.4	n.s.	n.s.	n.s.
	Valforte	25.5	23.7	24.6			
Cell plane area (μm^2)	Appulo	4000 ab	3400 b	3700	n.s.	**	*
	Valforte	4600 ab	5800 a	5200			
Cell perimeter (μm)	Appulo	1400	1200	1300	n.s.	*	n.s.
	Valforte	2200	2200	2200			
Cell area/cell perimeter (μm)	Appulo	2.9	2.7	2.8	n.s.	n.s.	n.s.
	Valforte	2.7	2.7	2.7			

Tab. 3. Some cell wall components measured as mg cm^{-2} for leaves of cvs Appulo and Valforte at booting. Values are means of 4 determinations. Significance symbols as for Tab. 1. NDF, neutral detergent fiber; ADF, acid detergent fiber.

Parameter	Cultivar	Treatment			F values		
		Irrigated	Unirrigated	Average	Treatment	Cultivar	Interaction
NDF (mg cm^{-2})	Appulo	1.4	1.5	1.4	n.s.	*	n.s.
	Valforte	1.7	1.5	1.6			
Hemicellulose (mg cm^{-2})	Appulo	0.5	0.6	0.5	n.s.	n.s.	n.s.
	Valforte	0.7	0.6	0.6			
ADF (mg cm^{-2})	Appulo	0.9	0.9	0.9	n.s.	n.s.	n.s.
	Valforte	1.0	0.9	0.9			

Tab. 4. Parameters as in Tab. 1 for irrigated and unirrigated durum wheat cultivars. Flowering stage. Significance symbols as for Tab. 1. Averages followed by the same letters do not differ ($P > 0.005$) according to Tukey's test.

Parameter	Cultivar	Treatment			F values		
		Irrigated	Unirrigated	Average	Treatment	Cultivar	Interaction
Ψ_π^{100} (−MPa)	Appulo	1.5	1.8	1.7 ab	**	*	n.s.
	Valforte	1.3	1.7	1.5 b			
	Capeiti 8	1.5	1.9	1.7 a			
TW/DW	Appulo	3.3	2.9	3.1	**	n.s.	n.s.
	Valforte	3.7	3.1	3.4			
	Capeiti 8	3.3	3.0	3.2			
ε (MPa)	Appulo	9.6	9.0	9.3	n.s.	n.s.	n.s.
	Valforte	8.6	8.4	8.5			
	Capeiti 8	7.9	10.8	9.4			

Tab. 5. Parameters as in Tab. 2 for irrigated and unirrigated durum wheat cvs. Flowering stage. Significance symbols as for Tab. 1. Averages followed by the same letters do not differ ($P > 0.005$) according to Tukey's test.

Parameter	Cultivar	Treatment			F values		
		Irrigated	Unirrigated	Average	Treatment	Cultivar	Interaction
Specific leaf weight ($mg\ cm^{-2}$)	Appulo	5.0 ab	5.2 a	5.1	*	n.s.	*
	Valforte	4.0 b	5.5 a	4.7			
	Capeiti 8	4.9 ab	5.0 ab	5.0			
Leaf area (cm^2)	Appulo	22.5	17.4	19.9	*	n.s.	n.s.
	Valforte	21.0	16.1	18.6			
	Capeiti 8	17.2	17.2	17.2			
Cell plane area (μm^2)	Appulo	3200 b	3800 ab	3500	n.s.	**	*
	Valforte	4800 a	4200 ab	4500			
	Capeiti 8	4000 ab	4400 ab	4200			
Cell perimeter (μm)	Appulo	1220 ab	1540 a	1380	n.s.	**	*
	Valforte	1860 a	1720 a	1790			
	Capeiti 8	1460 b	1660 ab	1560			
Cell area/ cell perimeter (μm)	Appulo	2.6	2.5	2.6 ab	*	**	n.s.
	Valforte	2.6	2.4	2.5 b			
	Capeiti 8	2.9	2.6	2.8 a			

Tab. 6. Major cell wall components measured as $mg\ cm^{-2}$ in irrigated and unirrigated leaves of 3 wheat cultivars (Appulo, Valforte and Capeiti 8) at flowering. Values are means of 4 determinations. Significance symbols as for Tab. 2. Abbreviations as for Tab. 3.

Parameter	Cultivar	Treatment			F values		
		Irrigated	Unirrigated	Average	Treatment	Cultivar	Interaction
NDF ($mg\ cm^{-2}$)	Appulo	2.0	2.1	2.1	**	n.s.	n.s.
	Valforte	1.7	2.4	2.1			
	Capeiti 8	2.1	2.2	2.1			
ADF ($mg\ cm^{-2}$)	Appulo	1.5	1.0	1.2	**	n.s.	n.s.
	Valforte	1.2	1.1	1.1			
	Capeiti 8	1.4	1.1	1.3			
Hemicellulose ($mg\ cm^{-2}$)	Appulo	0.6 ab	1.2 ab	0.9	**	n.s.	*
	Valforte	0.5 b	1.3 a	0.9			
	Capeiti 8	0.7 ab	1.1 ab	0.9			

not sensitive to drought stress; so a smaller number of cells could be in the leaves. No significant relationships between osmotic potential and mesophyll cell characters were observed for either sample; there were no correlations among cell wall elasticity (ε), morphology and chemical composition. High correlation coefficients among TW/DW ratio, NDF and hemicellulose content per unit of leaf area suggest that the reduction in TW/DW observed under drought stress was due to accumulation of fibrous constituents in the leaf, in particular hemicellulose. These cell wall components have important properties such as ion-binding capacity and water-holding capacity (Mongeau and Brassard 1979). The results indicate that the effect of the fibrous content of the cell wall on cellular osmotic volume is large in relation to the effect of mesophyll cell size. Several authors (Whitehead and Jarvis 1981, Joly and Zaerr 1987) have considered that the accumulation of cell wall material may affect the quantity of apoplasmic water that would act as a buffer against net water loss from the leaf. Such a shift in the distribution of leaf water could be responsible for some decrease in Ψ_π^{100} (Tyree and Jarvis 1982), but an active accumulation of solute may occur at the same time.

Since water stress not only induced quantitative but also qualitative changes in the chemical composition of

Tab. 7. Significance of correlation coefficients between morphological parameters and some leaf water status components. Significance symbols as for Tab. 1.

Parameter		Booting (n = 16)	Flowering (n = 24)
Ψ_π^{100}	– TW/DW	–0.27 n.s.	–0.72 **
Ψ_π^{100}	– Hemicellulose	–0.09 n.s.	0.84 **
Ψ_π^{100}	– Cell area	0.09 n.s.	–0.19 n.s.
TW/DW	– NDF	–0.37 n.s.	–0.92 **
TW/DW	– Hemicellulose	–0.19 n.s.	–0.96 **
NDF	– Hemicellulose	0.90 **	0.94 **
Leaf area	– Cell area	–0.19 n.s.	–0.19 n.s.
ε	– TW/DW	–0.02 n.s.	0.10 n.s.
ε	– Hemicellulose	0.06 n.s.	0.17 n.s.
ε	– Cell area	–0.11 n.s.	–0.10 n.s.

the cell wall, a more detailed analysis of matrix substances and their ability to store and release water reversibly is needed.

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